

## REVIEW

## Paraphyletic groups as natural units of biological classification

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**Abstract** Despite the broad acceptance of phylogenetic principles in biological classification, a fundamental question still exists on how to classify paraphyletic groups. Much of the controversy appears due to (1) historical shifts in terminology and definitions, (2) neglect of focusing on evolutionary processes for understanding origins of natural taxa, (3) a narrow perspective on dimensions involved with reconstructing phylogeny, and (4) acceptance of lower levels of information content and practicability as a trade-off for ease of arriving at formal classifications. Monophyly in evolutionary biology originally had a broader definition, that of describing a group with common ancestry. This definition thus includes both paraphyletic and monophyletic groups in the sense of Hennig. We advocate returning to a broader definition, supporting use of Ashlock's term holophyly as replacement for monophyly s.str. By reviewing processes involved in the production of phylogenetic patterns (budding, merging, and splitting), we demonstrate that paraphyly is a natural transitional stage in the evolution of taxa, and that it occurs regularly along with holophyly. When a new holophyletic group arises, it usually coexists for some time with its paraphyletic stem group. Paraphyly and holophyly, therefore, represent relational and temporal evolutionary stages. Paraphyletic groups exist at all levels of diversification in all kingdoms of eukaryotes, and they have traditionally been recognized because of their descent-based similarity. We review different methodological approaches for recognition of monophyletic groups s.l. (i.e., both holophyletic and paraphyletic), which are essential for discriminating from polyphyly that is unacceptable in classification. For arriving at taxonomic decisions, natural processes, information content, and practicability are essential criteria. We stress using shared descent as a primary grouping principle, but also emphasize the importance of degrees of divergence plus similarity (cohesiveness of evolutionary features) as additional criteria for classification.

**Keywords** cladistics; evolutionary classification; holophyly; monophyly; paraphyly

### ■ INTRODUCTION

The progress made in systematic biology over the past 50 years has been extraordinary. Fundamental aspects of classification involving the nature of categories have been evaluated and discussed, especially species, the basis of group formation, the inference of phylogenetic relationships, and the philosophical underpinnings of all activities. Several schools of classification have been championed, starting with the evolutionary school, which had its origin with Darwin, then phenetics, and finally cladistics. All aspects of operations have become more quantitative.

Despite these impressive achievements, numerous controversies still exist. We continue to struggle with definitions of species (e.g., Mayden, 1997; Wheeler & Meier, 2000; Hey, 2001; Coyne & Orr, 2004; Richardson, 2006), perhaps forgetting that different groups of organisms require different concepts (compare, for example, bacteria, lichens, and mammals). We also worry about the efficacy of data, realizing the immense phylogenetic power of molecular (especially DNA sequence) data but remembering that adaptations impact primarily the morphological phenotype. We struggle with ways to name organisms, especially the search for an homogenization of the three existing codes (bacteriological, zoological, botanical; the BioCode) and the possibility of providing names for clades in tree diagrams (the PhyloCode).

Fundamental to many of these considerations is the concept of paraphyly, that is, groups of organisms that have a common ancestor but that do not include all its descendants (Hennig, 1966). On one hand, it is useful to have a term that describes this condition of evolutionary groups that often occur in Nature, but on the other hand, many workers have reacted so negatively to any attempt to include paraphyletic groups in classification that conflicts have begun to arise. A good case in point is the recent cladistic classification of the angiosperms (Chase & Reveal, 2009), in which paraphyletic groups such as the basal angiosperms (Stuessy, 2010) are not included.

Much of the controversy is due to a misunderstanding of the role of paraphyly in evolutionary process, and to imprecise definitions of paraphyly and polyphyly. These misconceptions have led to an a priori negative view of paraphyly in cladistic classification. We believe that it is time, therefore, to examine specifically the issue of use of paraphyly in classification more directly. Specifically, this article presents (1) historical aspects and definitions of terms; (2) the fundamental role of paraphyly within the evolutionary process; (3) deficiencies in classification when using only a narrower, holophyletic (= monophyletic s.str.) perspective; (4) examples of utility of paraphyly at different levels of the taxonomic hierarchy; and (5) criteria for integration of perspectives and methods into modern evolutionary classification. We will focus here on the paraphyly issue. We have presented elsewhere comprehensive reviews on

cladistics in general (e.g., Stuessy, 2009a,b) and discussions of pros and cons of cladistic and evolutionary classifications (e.g., Hörandl, 2007).

## ■ WHAT PARAPHYLY IS AND IS NOT

The term paraphyly is a relatively new word, used first by Hennig (1962, 1966) to refer to groups that have a common ancestry but that do not include all descendents (see Hennig, 1966: fig. 45, p. 148). He did not directly and clearly define the word in his text, but he did state that groups are paraphyletic “if the similarity is based on symplesiomorphy” (p. 146). The term paraphyly did not originate from Darwin or from other evolutionary workers during the 19th and first half of the 20th centuries, although there was some interest in the concept of stem groups (e.g., Naef, 1919, cited in Willmann, 2003). The need for a term to describe the condition now called paraphyly originated from the cladistic school of classification and not from workers studying the evolutionary process.

To understand reasons for the origin of the term paraphyly requires reviewing briefly reasons for the origin of cladistics (reviewed in Stuessy, 2009a,b). Phenetics in the late 1950s and early 1960s focused on objectivity and repeatability in classification, but this came with a cost—evolutionary thinking was virtually eliminated from consideration, not because it was not important, but because it was viewed as too difficult to deal with in a precise fashion. Cladistics put considerations of evolution, i.e., phylogeny, back into classification. However, inferences of relationship were limited. Patterns of relationship but not degrees of divergence were considered. The branching pattern of relationship was a topological pattern based solely on shared derived character states (synapomorphies). To simplify use of this branching pattern in classification, two fundamental rules were established. First, sister groups must have the same rank. This is simply a logical perspective. Second, only groups are acceptable in classification if they contain all descendents from the common ancestor. This was done to allow group formation to be more objective, so that the cladogram could be easily reconstructed from the classification and vice versa. This was called monophyly, which was modified from the broader earlier meaning (coined by Haeckel, 1866), which was simply a group that had a common ancestor (for historical overview see Willmann, 2003: 458). Ashlock (1971, 1984) pointed out that the more specific concept of monophyly formulated by Hennig (1966) should rightly be called something else, and he suggested holophyly. We agree with this perspective, and we follow it in this review (Box 1).

The narrower definition of monophyly by cladistic workers has created confusion and conflict with evolutionary classifiers. The problem is that modern taxonomists agree on accepting only monophyletic groups for maximum information content in classification. This means accepting groups of species that derive from a single common ancestor, as is the case with paraphyly and holophyly. When cladists elected to allow only holophyletic groups in classification, this excluded paraphyletic groups that were accepted by evolutionary workers. This led

to conflict with traditional classifications that had frequently accepted paraphyletic taxa because of shared similarity (e.g., Nordal & Stedje, 2005). Polyphyly, referring to a process that results in a group that derives from three or more ancestors, is unacceptable in classification because a group so configured contains three or more evolutionary lines, which do not share similar character information. This weakens the predictive quality of the group. The same can be said for biphyly (diphyly), i.e., origins of groups from two distinct ancestors. Parallelism is more subtle, as this refers to a group that contains evolutionary lines from a more distant common ancestor (not an immediate one). The predictive quality of a group containing parallelisms should be greater than one of polyphyletic origin, but less than one from monophyly.

## ■ CLADISTIC CLASSIFICATION NEGLECTS IMPORTANT EVOLUTIONARY PROCESSES

Since Darwin, classifications following evolutionary principles attempted to reflect phylogeny in all its dimensions (see Stuessy, 2009b, for detailed discussion): branching pattern (cladistics), divergence within lineages (patristics), degree of observable and measurable similarity, merging (reticulate evolution), and absolute time relationships (chronistics). Evolutionary classification, therefore, has sought to incorporate these aspects into the formal hierarchical scheme. These efforts toward evolutionary classification result in structures of information that are as compatible with the evolutionary process as possible. This results in a classification that has higher information content than one that contains only branching pattern (cladistic) information (Carpenter, 1993). The only negative has been the inability to assess these several relationships quantitatively, which led initially to the phenetic and cladistic schools of classification. This is no longer an issue, as many papers have shown how all aspects of phylogeny can be quantified and integrated (e.g., Stuessy, 1983, 1987, 1997, 2009a,b; Estabrook, 1986; Felsenstein, 2004). We will present methodical approaches later in this paper.

Hennigian and post-Hennigian cladistics have disregarded evolutionary data for the main purpose of constructing the branching pattern. The data of importance become the synapomorphies, whereas autapomorphies are discarded as non-informative. Emphasis on holophyly in a quantitative method of phylogeny reconstruction has resulted in a narrower (and less informative) approach to biological classification. Cladistic principles stress a restrictive hypothesis, that of dichotomous splitting of a lineage into two new lineages, resulting in extinction of the ancestor. Whether other evolutionary processes (e.g., budding and merging) are involved is neither tested, nor verified, nor falsified, but rather neglected a priori (Hörandl, 2010). Statistical tests of tree topologies, e.g., bootstrapping, support tree topologies under the assumption of dichotomies, but they do not test the assumptions themselves. Cladograms are useful tools to formulate specific hypotheses, but because of their theoretical restriction, they are not sufficient to yield robust evolutionary conclusions.

## ■ THE EVOLUTIONARY PROCESS RESULTS IN MANY DIFFERENT TYPES OF NATURAL TAXA

Groups of organisms arise from evolutionary processes. Evolution involves various kinds of processes, however, which result in different kinds of groups. By briefly reviewing these processes, we emphasize that paraphyly is a natural stage in evolution, as is holophyly, and both exist at all levels of diversification.

**Evolutionary groups.**— Evolution comprises descent with modification, and thus is a dualistic process (Knox, 1998). Descent is established by genealogical relationship, and has inherent linearity. Descent transmits not only DNA sequence information but also the whole genetic regulatory network, thus establishing heritable phenotypic similarity from one generation to the next. Modification, however, is more complex, resulting from interplay of variation and external forces of selection. Modification comprises different phenomena, affecting both the genotype and phenotype. It can be a mutation in the DNA sequence, which might be easily traced, but may be selectively neutral. Modification of phenotypes results from the interplay of multiple genes, their expression patterns, and influenced by epigenetic variation. This latter phenomenon, as heritable information not stored in DNA sequences, is important for phenotypic variation that affects ecological interactions and response to selection (e.g., Bossdorf & al., 2008). Both descent and modification, therefore, act together to establish evolutionary groups.

**The bottom-up principle of the origin of natural groups.**— Both descent and modification originate at the populational level. Through reproduction, and by passing on genetic information from one generation to the next, organisms establish descent as a linear coherence through time. Modification, with its variation of genotype and phenotype, also again has its primary source within individuals in populations. The processes within and among populations, therefore, are crucial for any further diversification pattern. Details of these processes are usually ignored in cladistic classifications, which focus on “downward” grouping, i.e., by establishing groups based on logical division and synapomorphy. This represents a fundamental difference between evolutionary and cladistic approaches to forming (and understanding) groups (e.g., Mayr & Bock, 2002). In the real world, natural groups do not originate downwards, but upwards. Speciation requires some degree of isolation, but there are many ways by which this isolation can accrue. Speciation is not simply a process of splitting one species into two, as portrayed by cladistic approaches. Our present knowledge of speciation gives a much more complex picture of group formation (e.g., Coyne & Orr, 2004; see symposium in *Taxon* 59(5)).

Most importantly, diversification processes leading to speciation hardly ever affect a species as a whole, but usually just groups of populations within a species (Hörandl, 2006). The remaining populations, however, may not change. This asymmetrical split is a main source for paraphyly (Rieseberg & Brouillet, 1994). Many speciation processes, in fact, do not result in extinction of the original species (populations), but

**Box 1.** Glossary of terms used in this review.

**Budding:** the origin of a new taxon (population group, species, or group of species), that does not affect the existence and attributes of the parental taxon (stem population group, or stem group of species).

**Clade:** a branch of a cladogram, representing a hypothesis of a holophyletic (= monophyletic s.str.) group.

**Cladistic classification:** a logical ordering system based on descent, synapomorphy, and symmetric divergence.

**Evolutionary classification:** an ordering system based on descent, divergence, and evolutionary similarity (descent is the primary grouping concept, but divergence and similarity are also criteria for formal classification).

**Evolutionary tree:** a diagram of a hypothesis of relationships of taxa, without a priori assumption of processes or relationships, and constructed using defined algorithms.

**Holophyletic:** a group of organisms descended from a common ancestor, and that contains all descendants from this ancestor (= monophyletic sensu Hennig). A holophyletic group excludes the stem group from which the common ancestor arose.

**Merging:** the origin of a new taxon by reticulation between previously diverged taxa (hybridization, symbiogenesis, lateral gene transfer).

**Monophyletic:** a group of organisms that has descended from a common ancestor (includes holophyly and paraphyly).

**Paraphyletic:** a group of organisms that has descended from a common ancestor but that does not include all descendants from this ancestor. A paraphyletic group of species was holophyletic before a younger derivative species (or derivatives) arose from that group.

**Patrocladogram:** a cladistic branching pattern that has been precisely modified by use of patristic distances (i.e., divergences between lineages); a type of phylogram.

**Phylogenetic network:** a diagram representing a hypothesis of reticulate relationships of taxa, constructed by using a defined algorithm.

**Polyphyletic:** a group of organisms that contains descendants from three or more different common ancestors (with two ancestors, biphyletic is the appropriate term).

**Splitting:** the origin into two (or more) lineages by division of the parental lineage. Splitting leads to extinction of the parental lineage.



instead result in co-existing progenitor-derivative species pairs (Crawford, 2010).

**Splitting.** — Only a portion of known speciation processes can be categorized as a split of a species in two or more isolated population groups. Allopatric speciation, whereby, e.g., a geological barrier isolates population groups, does result in a complete disappearance of the original species. Allopatric speciation has been long advocated as the main speciation mechanism, especially in the zoological literature (Coyne & Orr, 2004). This mode of speciation occurs over longer time dimensions, and it divides the ancestral species into more or less equal portions. Allopatric speciation, therefore, fits well the cladistic model of symmetrical divergence, but this is no longer regarded as the predominant mode of speciation, especially in plants (e.g., Rieseberg & Brouillet, 1994). Other evolutionary processes, especially budding and merging, enhance asymmetrical divergence and therefore occurrence of paraphyly.

**Budding.** — Mayr & Bock (2002) coined this term for divergence of a small group of populations, while the rest of the populations remain unchanged. Most obvious are cases of peripatric speciation after geographical isolation of a small group of populations. This is expected to happen mostly after colonizing events by a few individuals, then followed by rapid speciation and adaptation to new environments. Recent evidence from biogeographical studies on both animals and plants suggests that peripatric speciation may be more common than previously thought, since dispersal, even transoceanic dispersal, explains many disjunct distributional patterns (e.g., de Queiroz, 2005; Knapp & al., 2005; Harbaugh & al., 2009; Schaefer & al., 2009; Emadzade & Hörandl, in press; Emadzade & al., in press). Buddings of this kind are often connected to a high amount of phenotypic change in the derivative species, which undergoes drift and adaptive change in the new ecological situation. In contrast, the source populations are neither in any novel environment, nor under any novel selective pressure.

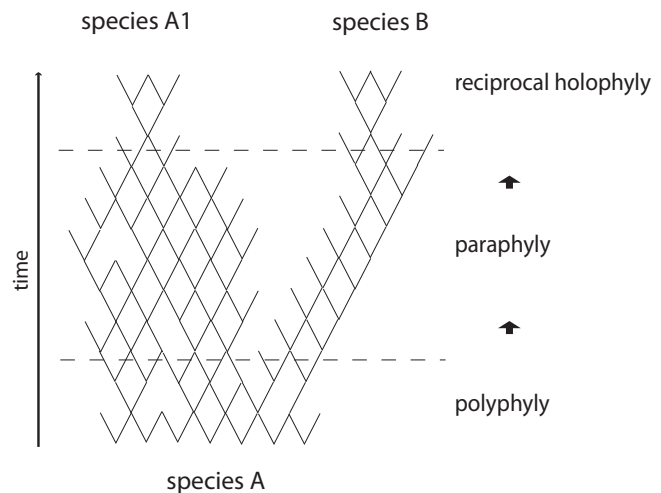
**Merging.** — Hybridization is a potential source for paraphyly via introgression. Alleles from one species may be integrated into the gene pool of another species through interspecific hybridization and backcrossing. A reconstruction of a phylogeny based on an introgressed DNA region will give results incongruent with the general genetic divergence pattern of species. Therefore, depending on the marker used, a species may appear as paraphyletic or even polyphyletic.

Merging of previously diverged species can result in rapid hybrid speciation by transgressive segregation in  $F_2$  and later generations (e.g., Rieseberg & Willis, 2007). This process may result in novel genotypes that are more extreme than their parents and may express novel adaptive traits, allowing rapid speciation into new ecological niches. Hybridization, in combination with polyploidy (allopolyploidy) has often been regarded as a process enhancing speciation by establishment of rapid crossing barriers between cytotypes (Ramsey & Schemske, 1998). Hybrid speciation has long been regarded as a frequent process in plants (e.g., Seehausen, 2004; Soltis & Soltis, 2009), but increasing evidence suggests that it plays an important role in animal evolution as well (Mallet, 2007; Mavárez & Linares,

2008). Merging of previously diverged genomes is potentially a source of a large amount of rapid modification.

Both hybridization and allopolyploidy are major sources for paraphyly, because these processes affect only populations of the new derivative species. Most cases of well documented hybrid speciation provide evidence for the persistence of extant parents. Since hybrid speciation usually quickly establishes crossing barriers, the hybrid derivatives and their progenitors co-exist at the same time. The parents do not undergo a significant change, especially if crossing barriers have been established by polyploidy. If the parental species themselves had a common ancestry (e.g., as sister species), then they will become a paraphyletic group.

**Transitions between evolutionary stages.** — In a temporal framework at the populational level, budding speciation can be seen as a transition of lineages from polyphyly (i.e., reticulating genealogical lineages) to paraphyly to holophyly (Fig. 1). Coalescence models (e.g., Rosenberg, 2003) have demonstrated that the genealogical shape of lineages within a species shortly after divergence most likely consists of multiple ancestral lineages. Reticulate relationships among the lineages keep the species coherent. After establishment of a reproductive barrier in the divergence of some new populations, however, paraphyly of one group of lineages relative to the other occurs. Divergence happens asymmetrically. After a further time period, however, transition to reciprocal holophyly of lineages via lineage sorting and extinction is expected (i.e., lineages of both species now become holophyletic). However, lineage sorting of ancestral polymorphisms by genetic drift or selection into the daughter species may remain incomplete in the case of hybridization, recombination, and large effective population size (e.g., Felsenstein, 2004). Incomplete lineage sorting may also occur if time intervals between species divergence are short relative to those between lineage branching (Rosenberg, 2003; Syring



**Fig. 1.** Transition from initial polyphyly (reticulate genealogical lineages) to paraphyly to reciprocal holophyly of lineages within species during budding speciation. Budding affects a small portion of lineages that speciate rapidly into B, while A remains unchanged; A is paraphyletic relative to B.

& al., 2007; Degnan & Rosenberg, 2009). Incomplete lineage sorting, however, is a major source for persistence of paraphyly of species over long time periods. Coalescence failure has been demonstrated, e.g., in about half of the species of *Pinus* subg. *Strobus* and is expected to occur in woody plant species with similar features (large effective population sizes, long generation times, and high outcrossing rates; Syring & al., 2007).

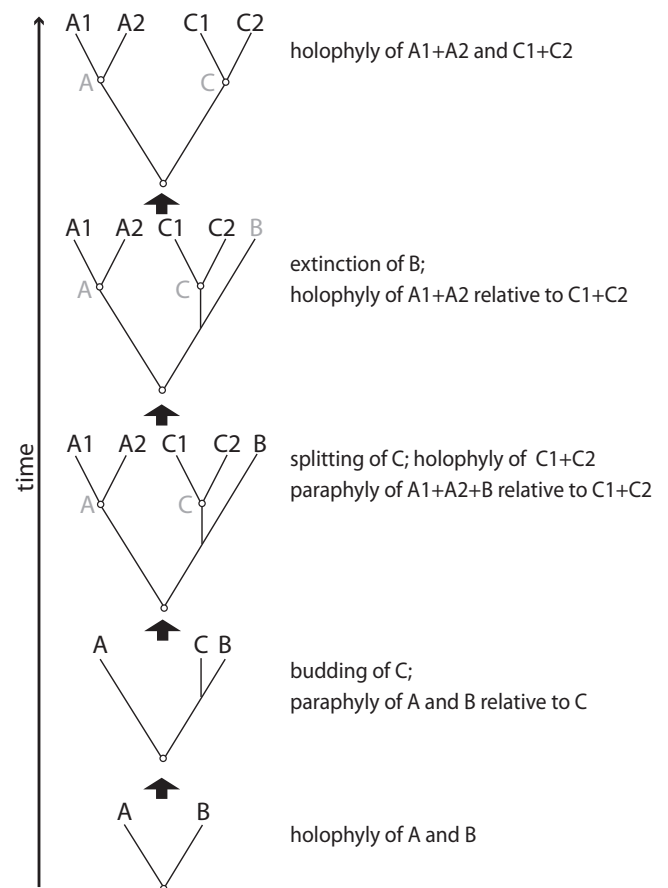
Above the species level, the origin of any higher taxon must be referable to a node from which the group started and further diversified by a series of speciation events. A higher taxon cannot originate from another higher taxon—it can only originate from an ancestral species that belonged to a higher taxon. From the time of completed speciation onwards, reticulation of lineages becomes less frequent because of the predominance of divergence. With reproductive isolation (by definition), reticulation of species becomes less frequent, and with the exception of allopolyploid speciation from wide crosses and symbiogenesis, it is restricted to closely related species (at least for eukaryotes).

The rise of a species within a holophyletic group, therefore, leaves the remaining species unaffected in their genealogy, analogous to progenitor population groups in a budding process. These species become automatically a paraphyletic group. In parallel to speciation processes, reciprocal holophyly can be achieved via extinction of the progenitor species (Fig. 2). In contrast to speciation processes, there is usually no return to polyphyly. The evolutionary stage of taxa above the species level, therefore, alternates mostly from paraphyly to holophyly and back to paraphyly; Fig. 2). Paraphyly above the species level, therefore, is always based on previous holophyly and therefore on common ancestry, while polyphyly is not. The extant paraphyletic group disappears only if all its members have gone extinct. Extinction of extant paraphyletic stem group lineages, in fact, is the only process by which reciprocal holophyly can appear in extant taxa above the specific level (Fig. 3). Holophyletic groups of higher extant taxa, therefore, reflect extinction gaps in what was originally a series of speciation events.

Recent evidence suggests that most major radiations in eukaryotes are due to genome duplications (Van der Peer, 2009) and not multiple symmetrical divergences. Genome duplications are usually followed by waves of diversification and speciation, which may be explained by divergent functions of the duplicated genomes (e.g., Chen, 2007). Genome duplications may have driven major morphological innovations and complexity (Van der Peer, 2009), and are consequently of major importance for modification and establishment of new groups. Since they may act rapidly, they might allow for synchrony of stem and crown groups, potentially also allowing for ecological shifts, and therefore for a long persistence of paraphyletic groups together with their holophyletic derivatives.

Paraphyly therefore applies to all taxonomic levels and to all cases where the evolutionary process leaves a remainder group (of populations or species) that is by itself not affected in its genealogical history. Holophyly is the evolutionary stage that a group achieves after these remainders of lineages or species have gone extinct. Holophyly and paraphyly, therefore,

are only relational stages in the flow of time. In a temporal view, holophyletic taxa have diversified mostly within one time level, whereas paraphyletic groups have diversification spanning various time levels. If we look at these groups retrospectively from the present time, then we observe various groups in different stages. For instance, angiosperms show a paraphyletic stem group of “basal angiosperms” (Archaeangiospermae) with multiple lineages that show angiosperm features and have continued to survive; within this group of “experiments”, the ancestors of “eudicots” (Dicotyledonae) and “monocots” (Monocotyledonae) must have arisen. Monocots and eudicots are holophyletic because at present no other major group has yet emerged out of them. Within the Eudicots, the phylogenetic reconstruction by Chase & Reveal (2009; based on APG III, 2009) suggests that “basal” eudicots represent the paraphyletic stem group that has given rise to “core eudicots”. The great majority of evolutionary processes, therefore, do not result in nicely dichotomous hierarchical groups, because holophyletic and paraphyletic groups exist in parallel. The



**Fig. 2.** Transitions from holophyly to paraphyly to holophyly above the species level. Extinct ancestral species in grey. Paraphyly is a normal stage in the evolutionary process when a new species arises, and it changes to holophyly only after extinction of some (or all) extant paraphyletic stem groups. Holophyly of extant groups of species is, therefore, largely a result of extinction of the paraphyletic transition lineages.

inherent asymmetry of evolutionary processes suggests a dynamic process of continuous parallel emergence of new groups and persistence of old ones. In a review on phylogenetic studies based on mitochondrial DNA in animals, 23% of species were reconstructed as paraphyletic and polyphyletic (Funk & Omland, 2003). In plants, percentages of paraphyletic groups are expected to be even greater because of the higher frequencies of polyploidy and hybridization (Arnold, 1997; Hörandl, 2006).

Recently, Podani (2010) tried to resolve the problem of different time levels by restricting the terms monophyly and paraphyly to phylogenetic trees (which are diachronic, meaning that lineages actually span various time levels), whereas the terms monoclady and paraclady would be used for describing cladograms (which are synchronous and thus confined to one time level; see also Ebach & Williams, 2004). The terminology proposed by Podani (2010) would help disentangle patterns of

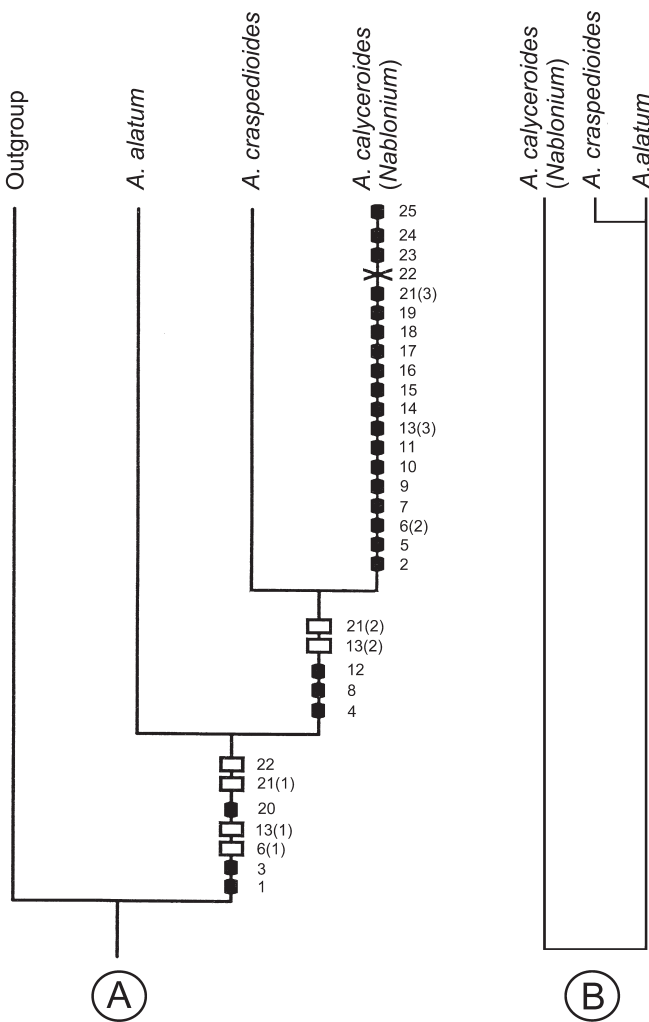
cladograms from underlying phylogenies. Most taxa in contemporary cladistic classifications are regarded as monoclady (as they are derived from clades), but they are not necessarily monophyletic. The new terminology, however, does not overcome the conceptual drawbacks of cladistic principles. We therefore advocate the evolutionary definitions of terms as used in the present paper (see Box 1).

### ■ EXAMPLES OF PARAPHYLY AT DIFFERENT LEVELS OF THE TAXONOMIC HIERARCHY

As an aid to showing the utility of paraphyletic groups in classification, a few examples are provided. These are of different types ranging from the specific level to more inclusive kingdoms.

A conspicuous example at the specific and generic level is the *Ammobium-Nablonium* (*Asteraceae*) complex from Australia. There are three species, two classified originally in *Ammobium* R. Br. (*A. alatum* and *A. craspedioides*) and one divergent in the segregate genus *Nablonium* Cass. (*N. calyceroides*). In a morphological cladistic analysis of this small group (Anderberg, 1990) (Fig. 3A), it was revealed that *N. calyceroides* formed a sister group relationship with *A. craspedioides*, thus rendering the original generic concept of *Ammobium* paraphyletic. On this basis, Anderberg (1990) combined all three species into one genus. The number of autapomorphies leading to *N. calyceroides*, however, was greater than the rest of the character state divergence between the two remaining species. Orchard (1992) pointed to this problem and recommended return to the original classification that recognized two genera (rebutted by Anderberg, 1992, however). With recognition of two genera, *Ammobium* is paraphyletic, but this structure of relationships retains more evolutionary information than with the holophyletic alternative of lumping all species together in a single genus. One might speculate, in fact, that *N. calyceroides* may have speciated out of and diverged rapidly from the parental *Ammobium* complex. Detailed evolutionary studies, especially at the DNA level, would be needed to test this hypothesis.

Many cases have been documented for the origin of a derivative species from out of a progenitor (see recent review by Crawford, 2010). Adaptations to new habitats, new breeding systems, or chromosomal re-arrangements can cause interrupted gene flow, resulting in progenitor-derivative relationships of recently evolved species (Gottlieb, 2004). These relationships reflect an early stage of divergence where the progenitor, which is usually widespread and comprises many populations, coexists with its geographically more restricted derivative species at the same time. Phylogenetically, the progenitor is therefore rendered paraphyletic. Many examples exist, such as the widespread *Layia glandulosa* (*Compositae*) and its derivative *L. discoidea*, a narrow serpentine endemic as confirmed by DNA sequences (Baldwin, 2005). Another case is between *Picea mariana* and *P. rubens* (*Pinaceae*; Perron & al., 2000), whereby nested cladistic analysis of mitochondrial DNA (Jaramillo-Correa & Bousquet, 2003) revealed the progenitor *P. mariana* to be paraphyletic.



**Fig. 3. A**, cladistic relationships among the three species *Ammobium alatum*, *A. craspedioides*, and *Nablonium calyceroides*. Squares = apomorphies (CI = 1); rectangles = apomorphies (CI < 1); X = reversal. Redrawn from Anderberg (1990). **B**, corresponding patrocadogram that shows the strong divergence of *Nablonium* from *Ammobium* (for methodology see Stuessy & König, 2008).



The rapid establishment of crossing barriers by polyploidy at the specific level quickly isolates diploid parental taxa from their polyploid derivatives and can result in paraphyletic parents. Depending on the relationship, the diploids may remain either a paraphyletic group (if they were sister species) or biphyletic (if they were more distantly related). Examples of phylogenetic analyses that reveal parapyly in connection with polyploidy include *Tarasa* (Malvaceae; Tate & Simpson, 2003), *Juncus* (Juncaceae; Roalsen, 2005), *Phragmites* (Poaceae; Lambertini & al., 2006), and *Ranunculus* sect. *Auricomus* (Ranunculaceae; Hörandl & al., 2009). In the latter study, a separate phylogenetic analysis of diploid species explicitly demonstrated how the addition of polyploid hybrid derivatives to phylogenetic trees turns the diploid progenitors into a paraphyletic group. The phenomenon is not restricted to plants; phylogenetic studies on African barbs (Cyprinidae) based on mitochondrial sequences clearly reveal diploid species as paraphyletic relative to their polyploid derivatives (Tsigenopoulos & al., 2002).

Another example of the occurrence of parapyly, and one that has serious conservation implications, are the many endemic plant genera of oceanic archipelagos. It has often occurred that from a large and successful continental genus, one that possesses substantial dispersal capabilities, immigrants have arrived to remote oceanic islands. In isolation, these have diverged rapidly over several million years such that they now appear not only as distinct species morphologically, but also as distinct genera. Molecular phylogenetic analyses often reveal these divergent island lineages to have originated from out of larger continental progenitors. An example in the Robinson Crusoe (Juan Fernandez) islands is the genus *Robinsonia* from out of *Senecio* (Asteraceae; Pelser & al., 2007). A more conspicuous problem prevails in these same islands with *Lactoris fernandeziana*, the sole species of Lactoridaceae, the only family of flowering plants endemic to a volcanic oceanic island. Molecular phylogenetic studies suggest a connection at the generic level with *Aristolochia* (Qiu & al., 1993; Soltis & al., 1997), and this has led to thoughts of submerging *Lactoris* into Aristolochiaceae. Few workers have acted on this suggestion, however, because the morphology of the two families is totally different (Stuessy & al., 1998). If one were to act with conviction based on holophyly, however, Lactoridaceae would disappear into Aristolochiaceae and the archipelago (and world) loses the only angiosperm family endemic to a volcanic oceanic island. This is, in fact, used as the poster plant to attract attention to conservation initiatives in the archipelago. These same taxa, of course, continue to be endemic species and are therefore still worthy of serious conservation attention. The loss of endemic generic (or familial) status, however, greatly lowers their conservation importance. When one multiplies this result in oceanic islands worldwide, the decrease in island endemism at the generic level declines substantially. One has to question the advisability of this approach, particularly because the reason the taxa have been treated as good genera in the first place is because they are highly morphologically divergent from their continental relatives.

Another case in which parapyly plays a useful role is in the basal angiosperms. As emphasized by Stuessy (2010), the basal

angiosperms may represent a series of evolutionary experiments into the angiospermous condition from different seed fern ancestors. A useful concept in classification at our present level of evolutionary understanding is to treat these very divergent early angiosperms as a paraphyletic group, Archaeangiospermae, out of which have come the holophyletic monocots and eudicots. Future evolutionary studies, particularly focusing anew on homologies and finding ties to specific seed fern ancestors may lead to a recommended different hypothesis of classification. In the meantime, the best alternative is to treat the basal angiosperms as a paraphyletic, albeit very heterogeneous group (e.g., class). The alternative of splitting off each basal angiosperm line holophyletically into a small and coordinate higher taxon (Chase & Reveal, 2009) is a less desirable alternative.

Lichenized fungi provide another case of the need for acceptance of parapyly in classification. Molecular phylogenetic studies show clearly that the lichenized condition has occurred multiple times in fungal lines (Gargas & al., 1995), and in fact, some free-living fungi have even had a lichenized ancestry (Lutzoni & al., 2001). The concept of “lichens,” therefore, is clearly a paraphyletic one that describes the symbiosis (mutualism) more than it reflects specific evolutionary ancestry. Few would question the utility of treating lichens as a good taxonomic unit, simply because they possess similar form, physiology, ecology, and symbiosis. Parapyly in this case, therefore, is a useful way of summarizing and classifying this rather odd segment of the living world.

Another classical case of utility of parapyly comes from the oft discussed dinosaur-bird problem. Data now clearly show that modern birds have, in fact, evolved from out of the flying dinosaur line (Zheng & al., 2009). Armed with this information, some workers have suggested formally submerging modern birds into dinosaurs (Bostwick, 2003). Birds become, therefore, simply highly divergent flying dinosaurs. There is nothing to hinder society at large in continuing to call birds, birds (imagine the horror of the local bird watcher’s society having to announce their spring foray to observe the migrating “flying dinosaurs”!). Imagine further the confusion for other scientific disciplines caused by changing the information content of such established terms as “bird” for scientific databases (e.g., the ISI Web of Science). This bears on the conflict of science (in this case holophyly) and society (informal phenotypic evaluation of relationships in nature) as has been pointed out by Yoon (2009). At the professional taxonomic level, the point is that the cladistic classification system ignores the high degree of divergence of birds from dinosaur progenitors. This alternative does not capture the maximum evolutionary information that exists for these groups.

At the deepest levels of time, protists may represent an example for a paraphyletic group (Schlegel & Hülsmann, 2007). The term protist is often used to describe eukaryotes with a unicellular level of organisation, without cell differentiation into tissues. Multicellularity evolved several times out of this paraphyletic stem group, and protists therefore can be assigned to six major eukaryotic super-groups (Adl & al., 2005). These authors refrain from a formal recognition of protists, but argue for an informal use, while Schlegel & Hülsmann (2007)

proposed a paraphyletic taxon Protista. The question remains whether unicellular eukaryotes ever were holophyletic. The chimeric nature of eukaryotic cells originating from Bacteria and Archaea is broadly accepted, but different hypotheses compete for the origin of the nucleus, and for the putative sequence of steps leading to the fully established eukaryotic cell with its included organelles (reviews by Horner & Hirt, 2004; Schlegel & Hülsmann, 2007; Cavalier-Smith, 2010). Extant amitochondriate protists have probably lost mitochondria secondarily, which makes it difficult to reconstruct a “primitive” eukaryote that would have retained ancestral features (Simpson & Roger, 2004). Methodological problems, such as high mutation rates, long-branch attraction, and multiple gene transfer from organelles to the nucleus have so far hampered a robust molecular phylogenetic reconstruction for the basis of the eukaryotic phylogeny (Gribaldo & Philippe, 2004).

### ■ CRITERIA AND METHODS FOR EVOLUTIONARY CLASSIFICATION

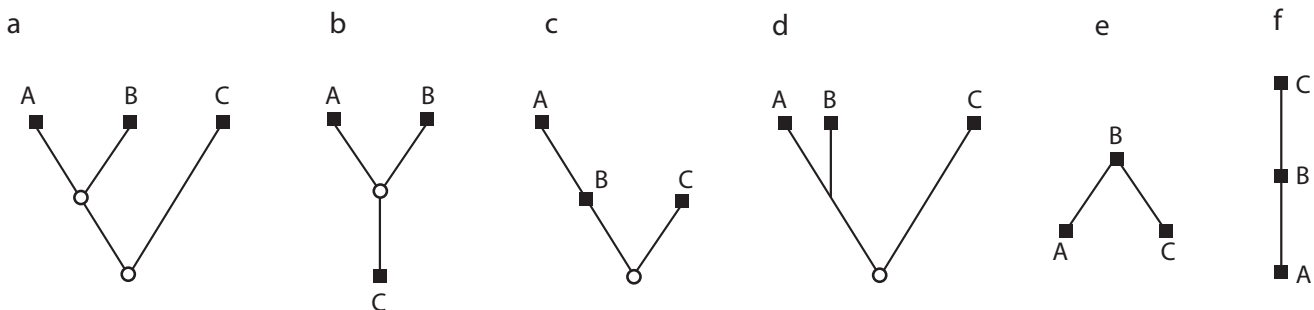
Along with emphasizing the evolutionary significance of paraphyletic groups, the final challenge comes with construction of formal classifications. This involves (1) recognizing evolutionary processes to allow discrimination of holophyletic and paraphyletic groups from polyphyletic ones, and (2) establishing criteria for formal classification. Cladograms, which would include many molecular phylogenetic trees, are not evolutionary trees, but diagrams reflecting character distributions (e.g., Kitching & al., 1998). Cladograms reflect hypotheses of relationships only if based on the assumption of a predominantly symmetrical, mature, divergence process of reciprocal monophyly (Fig. 4a). Only under this restrictive condition can a cladogram reflect relationships correctly. As has already been discussed, however, this is not often the case, and evolutionary trees may differ in their topology from the respective cladograms (e.g., Kitching & al., 1998: 15 ff.; Page & Holmes, 1998: 23–24) (Fig. 4b–f).

To understand the actual evolutionary stage of a group, a detailed analysis of relationships must be carried out, and

this may entail more elaborate theoretical and methodical approaches. Adopting a broader hypothetico-deductive method is recommended. First, explicit hypotheses on the processes that have shaped descent and divergence must be advanced. These hypotheses may be based on an existing classification, a cladogram, a molecular phylogenetic tree, other morphological, karyological, ecological, etc., data or crossing experiments. Second, an appropriate analytical method (or methods) must be selected to test this hypothesis and obtain further insights on the evolutionary processes involved. Third, the results from these analyses will either support the initial hypothesis, or reject it, or give equivocal results. If supportive, one can proceed directly to formal classification. If unresponsive, however, one must consider alternative hypotheses, perhaps involving additional methods of analysis, more data and/or taxon sampling, etc. In the following we will review some presently available methodological approaches for testing specific evolutionary hypotheses.

Incomplete, asymmetrical divergence, e.g., in progenitor-derivative speciation, can be examined by using phylograms or ultrametric trees, which provide a descriptive method for measuring divergence. The patristic distances (divergences within lineages, i.e., the autapomorphies) are visualized in such trees. The only problem is how to use the patristic distance in a precise and objective fashion. The combination of patristic and cladistic distances for cladogram reconstructions can quantitatively assess divergence to aid taxonomic decisions (Stuessy, 1997; Stuessy & König, 2008) (Fig. 3B). Patrocladograms, in particular, can be used to emphasize degrees of divergence by placing highly divergent taxa on separate branches (Stuessy & König, 2008). Patrocladistic analysis can be based both on molecular and morphological data; while molecular divergence can be informative about interruption of gene flow and thus existence of a crossing barrier, morphological divergence may tell us about rapid adaptive change.

In cases of reticulate evolution and incomplete lineage sorting, the assumptions for a simple dichotomous tree phylogeny are also not met (Fig. 4e). In such cases, all types of cladograms give distorted results. Most importantly, such errors cannot be erased by improving sampling, and the distortion may remain



**Fig. 4.** Cladogram (a) and different types of evolutionary trees (b–f). Squares represent extant species (A, B, C), whereas circles represent ancestors. Note that only the relationships in a–d involve hypothetical ancestors. The pattern depicted in the cladogram (a) can result from many different evolutionary relationships (not all possibilities shown); b, only one ancestor involved; c, A is a derivative of B; d, B has budded from A; e, B is a hybrid between A and C; f, A is a progenitor of B, and B a progenitor of C. A cladogram, therefore, reflects only one of many hypotheses of phylogenetic relationships.



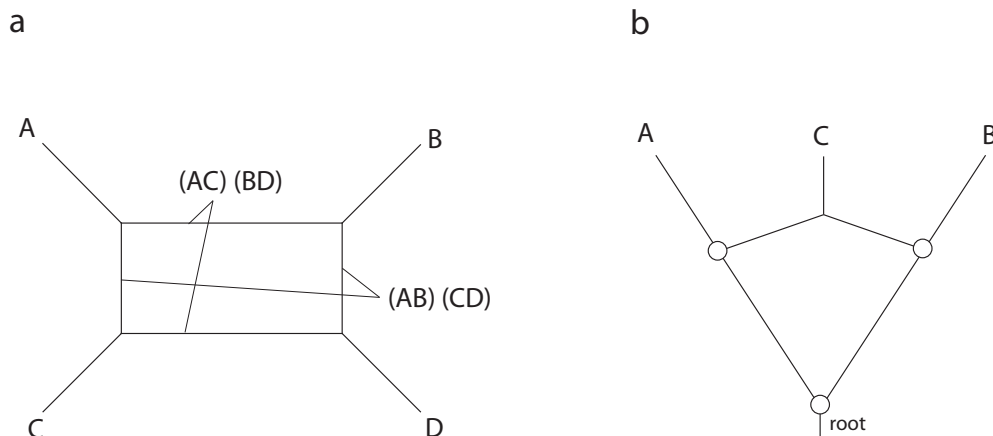
undetected even if tree topologies have high bootstrap or posterior probability support (Delsuc & al., 2005). Gene trees that are incongruent with species trees even might have a higher probability than a gene tree topology that matches the species tree topology (Degnan & Rosenberg, 2009). Clues to reticulate evolution include incongruent phylogenetic tree topologies from different datasets (e.g., nuclear/organellar DNA) and collapse of branches in consensus trees due to conflicting signals (for review see, e.g., Funk, 1985; McDade, 1992).

If relationships are hypothesized to be evolutionarily more complex, phylogenetic network methods may be useful to help visualize relationships of taxa (McBreen & Lockhart, 2006). At the present time Split-Networks and Reticulate Networks are the most popular types of these analyses (Huson & Bryant, 2006; Grünwald & al., 2007). Baroni & al. (2006) presented algorithms for estimating extent of hybridization (minimum number of hybrid events) and time frames of hybridization. By highlighting incompatible phylogenetic signals, splitsgraphs can show deeper evolutionary relationships. Reticulate networks directly offer a hypothesis of reticulate evolutionary history, whereby nodes correspond to ancestral taxa and polygon edges to patterns of descent (Fig. 5). A number of studies have shown the utility of these methods (e.g., Lockhart & al., 2001, Hörandl & al., 2005, Emadzade & al., 2010, in *Ranunculus*; Kloepper & Huson, 2008, on genera of phaeosporic Hyphomycetes; Denk & Grimm, 2009, on *Fagus*; Blösch & al., 2009, in *Melampodium*; Pirie & al., 2009, on Danthonioideae; Grimm & Denk, 2010, on *Platanus*). Statistical tests based on coalescence of lineages may help to disentangle hybridization from ancient incomplete lineage sorting (Peters & al., 2007; Degnan & Rosenberg, 2009; Joly & al., 2009).

Molecular data have been regarded for the past two decades as being very informative regarding evolutionary relationships. It is important to continue to stress, however, that organellar gene trees are not necessarily the same as organismal trees (Doyle, 1992). Frequently a discrepancy arises that molecular phylogenetic trees reveal a group to be paraphyletic, although shared morphological characters suggest holophyly

(e.g., Richter & al., 2009). Such discrepancies deserve special attention. Divergence of DNA sequences, especially of mitochondrial and plastid DNA, is for many reasons not necessarily congruent with the evolution of the respective group of organisms. Incomplete lineage sorting, horizontal transfer, reticulate evolution, chloroplast transfer, and rate heterogeneity all have been recognized as sources of incongruence between plastid/mitochondrial phylogenetic trees and those from the nuclear DNA of the organisms themselves (e.g., Wendel & Doyle, 1998). The increasing number of multilocus analyses has shown the problem of conflicting genealogical histories in different genes. The genealogical shape of gene tree lineages may not reflect the pattern of species divergence because of the presence of multiple ancestral sequences in the populations of diverging organisms (Degnan & Rosenberg, 2009).

Changes in plastid and mitochondrial DNA sequences may be influenced by factors other than descent. Because of the physical proximity of plastid and mitochondrial DNA to electron transfers during photosynthesis and respiration, respectively, organellar DNA is under constant oxidative stress, which can cause various, potentially mutagenic processes, such as DNA lesions, incorrect repair, and various damage tolerance mechanisms (e.g., Allen & Raven, 1996; Dizdaroglou, 1998; Friedberg & al., 2006; Roldan-Arjona & Ariza, 2009). For instance, accelerated evolution of plastid genomes in some taxa of angiosperms may relate to altered or aberrant DNA repair systems (Guisinger & al., 2008, 2010). Recent extensive studies on the diversity of human mitochondrial DNA relate divergence patterns to climatic influence (e.g., Balloux & al., 2009). Another problem is that speciation relies on pre- or postzygotic isolation, but reproductive isolation can have various genetic backgrounds, and is, therefore, not necessarily congruent with genetic differentiation (Coyne & Orr, 2004: 101). Phylogenetic reconstructions based solely on mitochondrial or chloroplast DNA markers, therefore, may distort evolutionary history (Coyne & Orr, 2004: 47). In other words, a group may be holophyletic even though a phylogenetic tree based on organellar DNA might not support this hypothesis.



**Fig. 5.** Phylogenetic networks (splitsgraphs) for analysis of reticulate evolution. **a**, split network; sides of the rectangle represent incompatible splits, indicating that the dataset contains two possible, incompatible groupings; edges do not necessarily correspond to ancestors. **b**, rooted reticulate network of taxa that has originated from a reticulation; edges correspond to ancestors.

Morphological characters frequently are under multigenic control from nuclear genes and their expression patterns. The ABC system of floral organ identity in angiosperms (Coen & Meyerowitz, 1991) may serve as an example of a complex regulatory network that has evolved via multiple independent changes in different components, gene duplications with sub- and neofunctionalization of copies, and changes in expression patterns (e.g., Kramer & Zimmer, 2006; Soltis & al., 2006). Moreover, morphological characters do not act in isolation, as simple synapomorphies; their function relies on combinations (Stuessy, 2004; Hörandl, 2010). Because of high levels of homoplasy, morphological data are in general regarded as less suitable for phylogenetic reconstructions. However, this methodological drawback for cladistic analysis does not disqualify morphological data for classification. The phenotype is important for structure and function, and thus for response to evolutionary mechanisms. Molecular data and phenotypic information, therefore, complement each other—the former for reconstruction of patterns of descent, the latter for recognition of established evolutionary entities.

For a final taxonomic decision, four main criteria should be considered in the following order: theoretical foundation based on natural processes, predictivity, information content, and practicability (e.g., Mishler, 2009). Above the species level,<sup>1</sup> retention of paraphyly and holophyly is essential for the theoretical foundation of taxa through natural processes (common ancestry) and hence for predictivity. Information content and practicability, however, are needed as additional criteria to translate natural taxa into a formal classification. Information content and practicability are dependent on human perception, human logic, terminology, and utility of ordering systems of organisms. These anthropocentric aspects are obviously important for classification, as a global information system for organisms must be provided for the scientific community and for society in general. These principles are violated if classifications abandon paraphyletic taxa that are actually monophyletic s.l., although they may not appear as holophyletic clades in cladograms. Because of shared ancestry, paraphyletic taxa often have high phenotypic similarity and information content. It is no surprise that practice-oriented taxonomists (Brummitt, 2002, 2006, 2008; Farjon, 2005, 2007) and users (Brickell & al., 2008; Yoon, 2009) are hesitant to accept classifications that admit only holophyletic taxa. For a better visualization of the evolutionary status of a class in relation to a tree, “Besseyan cactus trees” (Zander, 2008) or a recently proposed method of mapping a taxon onto a phylogenetic tree (Zander, 2010) can be helpful. However, we do not advocate any automatization in classification of paraphyletic (or holophyletic) taxa; each case has to be judged carefully on its own merits. In view of these many points, we hereby recommend adherence to principles of evolutionary classification, with the following procedural steps:

1 We refrain here from a detailed discussion of species-level classification and below, where phylogenetic principles apply in a different genealogical context (for a recent review see, e.g., Rieppel, 2010).

1. Reconstruct phylogenetic relationships by using appropriate molecular and/or other markers and various analytical tools. Distinguish holophyletic and paraphyletic groups of species as potentially *acceptable* for classification (because of common ancestry) from polyphyletic ones (*unacceptable*).
2. Score phenotypic characters and character combinations of the observed monophyletic (holo- plus paraphyletic) groups. Congruence of phenotypic similarity with descent helps to distinguish similarity arising from paraphyly and similarity resulting from parallel or convergent evolution (polyphyly).
3. Check for evolutionarily meaningful character combinations of holo- and paraphyletic groups, i.e., those that play a major role for evolutionary success, with emphasis on structure and function. Degree of morphological and genetic divergence as measured by patrocadistic methods (Stuessy & König, 2008) (Fig. 3B) is a useful criterion to avoid subjective judgement and overestimation of isolated, although sometimes visually conspicuous characters.
4. Circumscribe taxa according to descent and divergence. Paraphyletic and holophyletic status should be used as features of taxa, describing their evolutionary status, not as criteria for their acceptance in classification (Hörandl, 2007).
5. Choose an appropriate rank. Although genealogical hierarchies are not necessarily the same as Linnaean hierarchies (e.g., Eldredge, 1985), hierarchical systems are essential for efficient communication and high levels of information storage and retrieval, especially flagged hierarchies (with names having endings that indicate rank, e.g., -aceae, -ales; Stevens, 2006).

More recent theoretical and empirical approaches towards an evolutionary classification are collected at <http://www.mobot.org/plantscience/resbot/21EvSy.htm> (edited by R.H. Zander).

## ■ CONCLUSIONS

Some authors (e.g., Adl & al., 2005; Richter & al., 2009; Chase & Reveal, 2009) have argued for a parallel, “informal” naming of paraphyletic groups for practical use and connection to tradition, while reserving formal classification for holophyletic groups only. We reject this approach, because evolutionary classification provides a broader theoretical basis and higher information content for relationships among taxa, and therefore is more appropriate for formal classification.

The time has come to move biological classification to a new level of sophistication so as to capture greater amounts of evolutionary information. We assume that a classification that harbors maximum information regarding evolution should be most predictive for societal needs. Critical to this whole discussion is information—how to define it and how to measure it. There will doubtless be many measures of information possible for use in biological classification, and which one will be

deemed most appropriate by the systematics community must await future comparative investigations. If we are interested only in branching pattern information, and if it is appropriate to assume a bifurcating evolutionary model, then cladistics obviously provides this adequately. For greater evolutionary content in classification, however, more information needs to be captured. Paraphyletic groups routinely originate as part of the evolutionary process, and they, therefore, have an important role to play in classification.

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## ■ LITERATURE CITED

- Adl, S.M., Simpson, A.G.B., Farmer, M.A., Andersen, R.A., Anderson, O.R., Barta, J.A., Bowser, S.S., Bragerolle, G., Fensome, R.A., Fredericq, S., James, T.Y., Karpov, S., Kugrens, P., Krug, J., Lane, C.E., Lewis, L.A., Lodge, J., Lynn, D.H., Mann, D.G., McCourt, R.M., Mendoza, L., Moestrup, Ø., Mozley-Standridge, S.E., Nerad, T.A., Shearer, C.A., Smirnov, A.V., Spiegel, F.W. & Taylor, M.F.J.R. 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *J. Eukaryotic Microbiol.* 52: 399–451.
- Allen, J.F. & Raven, J.A. 1996. Free-radical-induced mutation vs. redox regulation: Costs and benefits of genes in organelles. *J. Molec. Evol.* 42: 482–492.
- Anderberg, A.A. 1990. *Nablonium* is a congener of *Ammobium* (Asteraceae – Gnaphalieae). *Telopea* 4: 129–135.
- Anderberg, A.A. 1992. In defence of the transfer of *Nablonium* to *Ammobium* (Asteraceae–Gnaphalieae), a reply to Orchard. *Telopea* 5: 13–19.
- APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105–121.
- Arnold, M.L. 1997. *Natural hybridization and evolution*. Oxford: Oxford Univ. Press.
- Ashlock, P.D. 1971. Monophyly and associated terms. *Syst. Zool.* 20: 63–69.
- Ashlock, P.D. 1984. Monophyly: Its meaning and importance. Pp. 39–46 in: Duncan, T. & Stuessy, T.F. (eds.), *Cladistics: Perspectives on the reconstruction of evolutionary history*. New York: Columbia Univ. Press.
- Baldwin, B. 2005. Origin of the serpentine-endemic herb *Layia discoidea* from the widespread *L. glandulosa* (Compositae). *Evolution* 59: 2473–2479.
- Balloux, F., Lawson Handley, L.-J., Jombart, T., Liu, H. & Manica, A. 2009. Climate shaped the worldwide distribution of human mitochondrial DNA sequence variation. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 276: 3447–3455.
- Baroni, M., Sempel, C. & Steel, M. 2006. Hybrids in real time. *Syst. Biol.* 55: 46–56.
- Blösch, C., Weiss-Schneeweiss, H., Schneeweiss, G.M., Barfuss, M.H.J., Rebernik, C.A., Villasenor, J.L. & Stuessy, T.F. 2009. Molecular phylogenetic analyses of nuclear and plastid DNA sequences support dysploid and polyploid chromosome number changes and reticulate evolution in the diversification of *Melampodium* (Milleriaceae, Asteraceae). *Molec. Phylog. Evol.* 53: 220–233.
- Bossdorf, O., Richards, C.L. & Pigliucci, M. 2008. Epigenetics for ecologists. *Ecol. Lett.* 11: 106–115.
- Bostwick, K.S. 2003. Bird origins and evolution: Data accumulates, scientists integrate, and yet the “debate” still rages. *Cladistics* 19: 369–371.
- Brickell, C.D., Crawley, M., Cullen, J., Frodin, D.G., Gardner, M., Grey-Wilson, C., Hillier, J., Knees, S., Lancaster, R., Mathew, B.F., Matthews, V.A., Miller, T., Noltie, H.F., Norton, S., Oakeley, H.J., Richards, J. & Woodhead, J. 2008. Do the views of users of taxonomic output count for anything? *Taxon* 57: 1047–1048.
- Brummitt, R.K. 2002. How to chop up a tree. *Taxon* 51: 31–41.
- Brummitt, R.K. 2006. Am I a bony fish? *Taxon* 55: 2–3.
- Brummitt, R.K. 2008. Evolution in taxonomic perspective. *Taxon* 57: 1049–1050.
- Carpenter, K.E. 1993. Optimal cladistic and quantitative evolutionary classifications as illustrated by fusilier fishes (Teleostei: Caesionidae). *Syst. Biol.* 42: 142–154.
- Cavaliere-Smith, T. 2010. Deep phylogeny, ancestral groups and the four ages of life. *Philos. Trans., Ser. B* 365: 111–132.
- Chase, M.W. & Reveal, J.L. 2009. A phylogenetic classification of the land plants to accompany APG III. *Bot. J. Linn. Soc.* 161: 122–127.
- Chen, Z.J. 2007. Genetic and epigenetic mechanisms for gene expression and phenotypic variation in plant polyploids. *Annual Rev. Pl. Biol.* 58: 377–406.
- Chen, E.S. & Meyerowitz, E.M. 1991. The war of the whorls: Genetic interactions controlling flower development. *Nature* 353: 31–37.
- Coyne, J.A. & Orr, H.A. 2004. *Speciation*. Sunderland, Massachusetts: Sinauer.
- Crawford, D.J. 2010. Progenitor-derivative species pairs and plant speciation. *Taxon* 59: 1413–1423.
- de Queiroz, A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol. Evol.* 20: 68–73.
- Degnan, J.H. & Rosenberg, N.A. 2009. Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends Ecol. Evol.* 24: 332–340.
- Delsuc, F., Brinkmann, H. & Philip, H. 2005. Phylogenomics and the reconstruction of the tree of life. *Nature Rev. Genet.* 6: 361–375.
- Denk, T. & Grimm, G.W. 2009. The biogeographic history of beech trees. *Rev. Paleobot. Palynol.* 158: 83–100.
- Dizdaroglou, M. 1998. Mechanisms of free radical damage to DNA. Pp. 3–26 in: Aruoma O.I. & Halliwell, B. (eds.), *DNA and free radicals: Techniques, mechanisms and applications*. London: OICA International.
- Doyle, J.J. 1992. Gene trees and species trees: Molecular systematics as one-character taxonomy. *Syst. Bot.* 17: 144–163.
- Ebach, M.C. & Williams, D. 2004. Classification. *Taxon* 53: 791–794.
- Eldredge, N. 1985. *Unfinished synthesis: Biological hierarchies and modern evolutionary thought*. New York: Oxford Univ. Press.
- Emadzade, K., Gehrke, B., Linder, H.P. & Hörandl, E. In press. The biogeographical history of the cosmopolitan genus *Ranunculus* L. (Ranunculaceae) in the temperate to meridional zones. *Molec. Phylog. Evol.*
- Emadzade, K. & Hörandl, E. In press. Northern Hemisphere origin, transoceanic dispersal, and diversification of Ranunculaceae DC. (Ranunculaceae) in the Cenozoic. *J. Biogeogr.* Doi: 10.1111/j.1365-2699.2010.02404.x.
- Emadzade, K., Lehnbach, C., Lockhart, P. & Hörandl, E. 2010. A molecular phylogeny, morphology and classification of genera of Ranunculaceae (Ranunculaceae). *Taxon* 59: 809–828.
- Estabrook, G.F. 1986. Evolutionary classification using convex phenetics. *Syst. Zool.* 35: 50–570.
- Farjon, A. 2005. *A monograph of Cupressaceae and Sciadopityes*. Kew: Royal Botanic Gardens.



- Farjon, A. 2007. In defence of a conifer taxonomy which recognises evolution. *Taxon* 56: 639–641.
- Felsenstein, J. 2004. *Inferring phylogenies*. Sunderland, Massachusetts: Sinauer.
- Friedberg, E., Walker, G.C., Siede, W., Wood, R.D., Schultz, R.A. & Ellenberger, T. 2006. *DNA repair and mutagenesis*, 2nd ed. Washington, D.C.: American Society for Microbiology.
- Funk, D.J. & Omland, K.E. 2003. Species level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Rev. Ecol. Evol. Syst.* 34: 397–423.
- Funk, V.A. 1985. Phylogenetic patterns and hybridization. *Ann. Missouri Bot. Gard.* 72: 681–715.
- Gargas, A., DePriest, P.T., Grube, M. & Tehler, A. 1995. Multiple origins of lichen symbioses in fungi suggested by SSU rDNA phylogeny. *Science* 268: 1492–1495.
- Gottlieb, L.D. 2004. Rethinking classic examples of recent speciation in plants. *New Phytol.* 161: 71–82.
- Gribaldo, S. & Philippe, H. 2004. Phylogenetics and the phylogeny of eukaryotes. Pp. 133–152 in: Hirt, R.P. & Horner, D.S. (eds.), *Organelles, genomes and eukaryote phylogeny*. Boca Raton: CRC Press.
- Grimm, G.W. & Denk, T. 2010. The reticulate origin of modern plane trees (*Platanus*, Platanaceae): A nuclear marker puzzle. *Taxon* 59: 134–147.
- Grünwald, S., Forslund, K., Dress, A. & Moulton, V. 2007. QNet: An agglomerative method for the construction of phylogenetic networks from weighted quartets. *Molec. Biol. Evol.* 24: 532–538.
- Guisinger, M.M., Chumley, T.W., Kuehl, J.V., Boore, J.L. & Jansen, R.K. 2010. Implications of the plastid genome sequence of *Typha* (Typhaceae, Poales) for understanding genome evolution in Poaceae. *J. Molec. Evol.* 70: 149–166.
- Guisinger, M.M., Kuehl, J.N.V., Boore, J.L. & Jansen, R.K. 2008. Genome-wide analyses of Geraniaceae plastid DNA reveal unprecedented patterns of increased nucleotide substitutions. *Proc. Natl. Acad. Sci. U.S.A.* 105: 18424–18429.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen*. Berlin: Georg Reiner.
- Harbaugh, D.T., Wagner, W.L., Allan, G.J. & Zimmer, E.A. 2009. The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: An example from the plant genus *Melicope* (Rutaceae). *J. Biogeogr.* 36: 230–241.
- Hennig, W. 1962. Veränderungen am phylogenetischen System der Insekten seit 1953. Pp. 29–42 in: Sachtleben, H. (comp.), *Bericht über die 9. Wanderversammlung Deutscher Entomologen, 6.–8. Juni 1961 in Berlin*. Tagungsberichte Deutsche Akademie der Landwirtschaftswissenschaften 45. Berlin: Deutsche Akademie der Landwirtschaftswissenschaften.
- Hennig, W. 1966. *Phylogenetic systematics*, trans. Davis, D.D. & Zangerl, R. Urbana: University of Illinois Press.
- Hey, J. 2001. *Genes, categories, and species: The evolutionary and cognitive causes of the species problem*. Oxford: Oxford Univ. Press.
- Hörandl, E. 2006. Paraphyletic versus monophyletic taxa — evolutionary versus cladistic classifications. *Taxon* 55: 564–570.
- Hörandl, E. 2007. Neglecting evolution is bad taxonomy. *Taxon* 56: 1–5.
- Hörandl, E. 2010. Beyond cladistics: Extending evolutionary classifications into deeper time levels. *Taxon* 59: 345–350.
- Hörandl, E., Greilhuber J., Klimova, K., Paun, O., Tensch, E., Emadzade, K. & Hodállová, I. 2009. Reticulate evolution and taxonomic concepts in the *Ranunculus auricomus* complex (Ranunculaceae): Insights from morphological, karyological and molecular data. *Taxon* 58: 1194–1215.
- Hörandl, E., Paun, O., Johansson, J.T., Lehnebach, C., Armstrong, T., Chen, L. & Lockhart, P. 2005. Phylogenetic relationships and evolutionary traits in *Ranunculus* s.l. (Ranunculaceae) inferred from ITS sequence analysis. *Molec. Phylog. Evol.* 36: 305–327.
- Horner, R.P. & Hirt, D.S. 2004. An overview of eukaryote origins and evolution: The beauty of the cell and the fabulous gene phylogenies. Pp. 1–23 in: Hirt, R.P. & Horner, D.S. (eds.), *Organelles, genomes and eukaryote phylogeny*. Boca Raton: CRC Press.
- Huson, D.H. & Bryant, D. 2006. Application of phylogenetic networks in evolutionary studies. *Molec. Biol. Evol.* 23: 254–267.
- Jaramillo-Correa, J.P. & Bousquet, J. 2003. New evidence from mitochondrial DNA of a progenitor-derivative species relationship between black spruce and red spruce (Pinaceae). *Amer. J. Bot.* 90: 1801–1806.
- Joly, S., McLenachan, P.A. & Lockhart, P.J. 2009. A statistical approach for distinguishing hybridization and incomplete lineage sorting. *Amer. Naturalist* 174: E54–E70.
- Kitching, I.J., Forey, P.L., Humphries, C.J. & Williams, D.M. 1998. *Cladistics: The theory and practice of parsimony analysis*, 2nd ed. Oxford: Oxford Univ. Press.
- Klopper, T.-H. & Huson, D.H. 2008. Drawing explicit phylogenetic networks and their integration into SplitsTree. *BMC Evol. Biol.* 8: 22. Doi: 10.1186/1471-2148-8-22.
- Knapp, M., Stöckler, K., Havell, D., Delsuc, F., Sebastiani, F. & Lockhart, P.J. 2005. Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (Southern Beech). *PLoS Biol.* 3(1): e14. Doi: 10.1371/journal.pbio.0030014.
- Knox, E. 1998. The use of hierarchies as organizational models in systematics. *Biol. J. Linn. Soc.* 63: 1–49.
- Kramer, E.M. & Zimmer, E.A. 2006. Gene duplication and floral developmental genetics of basal eudicots. *Advances Bot. Res.* 44: 354–384.
- Lambertini, C., Gustafsson, M.H.G., Frydenberg, J., Lissner, J., Speranza, M. & Brix, H. 2006. A phylogeographic study of the cosmopolitan genus *Phragmites* (Poaceae) based on AFLPs. *Pl. Syst. Evol.* 258: 161–182.
- Lockhart, P., McLehnanan, P.A., Havell, D., Glenny, D., Huson, D. & Jensen, U. 2001. Phylogeny, dispersal and radiation of New Zealand alpine buttercups: Molecular evidence under split decomposition. *Ann. Missouri Bot. Gard.* 88: 458–477.
- Lutzoni, F., Pagel, M. & Reeb, V. 2001. Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411: 937–940.
- Mallet, J. 2007. Hybrid speciation. *Nature* 446: 279–283.
- Mavárez, J. & Linares, M. 2008. Homoploid hybrid speciation. *Molec. Evol.* 17: 4181–4185.
- Mayden, R.L. 1997. A hierarchy of species concepts: The denouement in the sage of the species problem. Pp. 381–424 in: Claridge, M.R., Dawah H.A. & Wilson, M.R. (eds.), *Species: The units of biodiversity*. London: Chapman & Hall.
- Mayr, E. & Bock, W.J. 2002. Classifications and other ordering systems. *J. Zool. Syst. Evol. Res.* 40: 169–194.
- McBreen, K. & Lockhart, P.J. 2006. Reconstructing reticulate evolutionary histories of plants. *Trends Pl. Sci.* 11: 398–404.
- McDade, L.A. 1992. Hybrids and phylogenetic systematics II. The impact of hybrids on cladistic analysis. *Evolution* 46: 1329–1346.
- Mishler, B.D. 2009. Three centuries of paradigm changes in biological classification: Is the end in sight? *Taxon* 58: 61–67.
- Naef, A. 1919. *Idealistische Morphologie und Phylogenetik*. Jena: Fischer.
- Nordal, I. & Stedje, B. 2005. Paraphyletic taxa should be accepted. *Taxon* 54: 5–6.
- Orchard, A.E. 1992. *Ammobium* and *Nablonium* (Asteraceae, Gnaphalidae)—an alternative view. *Telopea* 5: 1–12.
- Page, R.D.M. & Holmes, E.C. 1998. *Molecular evolution: A phylogenetic approach*. Oxford: Blackwell Sciences.
- Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
- Perron, M., Perry, D.J., Andalo, C. & Bousquet, J. 2000. Evidence from sequence-tagged-site markers of a recent progenitor-derivative species pair in conifers. *Proc. Natl. Acad. Sci. U.S.A.* 97: 11331–11336.
- Peters, J.L., Zhuravlev, Y., Fefelov, I., Logie, A. & Omland, K.E. 2007. Nuclear loci and coalescent methods support ancient

- hybridization as cause of mitochondrial paraphyly between gadwall and falcated duck (*Anas* spp.). *Evolution* 61: 1992–2006.
- Pirie, M.D., Humphreys, A.M., Barker, N.P. & Linder, H.P.** 2009. Reticulation, data combination, and inferring evolutionary history: An example from Danthonioideae (Poaceae). *Syst. Biol.* 58: 612–628.
- Podani, J.** 2010. Monophyly and paraphyly: A discourse without end? *Taxon* 59: 1011–1015.
- Qiu, Y.-L., Chase, M.W., Les, D.H. & Parks, C.R.** 1993. Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbcl*. *Ann. Missouri Bot. Gard.* 80: 587–606.
- Ramsey, J. & Schemske, D.W.** 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Rev. Ecol. Syst.* 29: 467–01.
- Richardson, P.M.** 2006. Species reconsidered: Consequences for biodiversity and evolution. Introduction. *Ann. Missouri Bot. Gard.* 93: 1. [Pp. 2–102 contain the entire symposium.]
- Richter, S., Moller, O.S. & Wirkner, C.S.** 2009. Advances in Crustacean phylogenetics. *Arthropod Syst. Phylog.* 67: 275–286.
- Rieppel, O.** 2010. Species monophyly. *J. Zool. Syst. Evol. Res.* 48: 1–8.
- Rieseberg, L. & Brouillet, L.** 1994. Are many plant species paraphyletic? *Taxon* 43: 21–32.
- Rieseberg, L. & Willis, J.H.** 2007. Plant speciation. *Science* 317: 910–914.
- Roalsen, E.H.** 2005. Phylogenetic relationships in the Juncaceae inferred from nuclear ribosomal DNA internal transcribed spacer sequence data. *Int. J. Pl. Sci.* 166: 397–413.
- Roldan-Arjona, T. & Ariza, R.R.** 2009. Repair and tolerance of oxidative DNA damage in plants. *Mutation Res.* 681: 169–179.
- Rosenberg, N.A.** 2003. The shapes of neutral gene genealogies in two species: Probabilities of monophyly, paraphyly, and polyphyly. *Evolution* 57: 1465–1477.
- Schaefer, H., Heibl, C. & Renner, S.S.** 2009. Gourds afloat: A dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 276: 843–851.
- Schlegel, M. & Hülsmann, N.** 2007. Protists – a textbook example for a paraphyletic taxon. *Organisms, Divers. & Evol.* 7: 166–172.
- Seehausen, O.** 2004. Hybridization and adaptive radiation. *Trends Ecol. Evol.* 19: 198–207.
- Simpson, A.B.G. & Roger, A.J.** 2004. Excavata and the origin of amitochondriate eukaryotes. Pp. 27–53 in: Hirt R.P. & Horner, D.S. (eds.), *Organelles, genomes and eukaryote phylogeny*. Boca Raton: CRC Press.
- Soltis, D.E., Soltis, P.S., Nickrent, D.L., Johnson, L.A., Hahn, W.J., Hoot, S.B., Sweere, J.A., Kuzoff, R.K., Kron, D.A., Chase, M.W., Swensen, S.M., Zimmer, E.A., Chaw, S.-M., Gillespie, L.J., Kress, W.J. & Sytsma, K.J.** 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Missouri Bot. Gard.* 84: 1–49.
- Soltis, P.S. & Soltis, D.E.** 2009. The role of hybridization in plant speciation. *Annual Rev. Pl. Biol.* 60: 561–588.
- Soltis, P.S., Soltis, D.E., Kim, S., Chanderbali, A. & Buzgo, M.** 2006. Expression of floral regulators in basal angiosperms and the origin and evolution of ABC-Function. *Advances Bot. Res.* 44: 484–506.
- Stevens, P.F.** 2006. An end to all things? – Plants and their names. *Austral. Syst. Bot.* 19: 115–133.
- Stuessy, T.F.** 1983. Phylogenetic trees in plant systematics. *Sida* 10: 1–13.
- Stuessy, T.F.** 1987. Explicit approaches for evolutionary classification. *Syst. Bot.* 12: 251–262.
- Stuessy, T.F.** 1997. Classification: More than just branching patterns of evolution. *Aliso* 15: 113–124.
- Stuessy, T.F.** 2004. A transitional-combinational theory for the origin of angiosperms. *Taxon* 53: 3–16.
- Stuessy, T.F.** 2009a. Paradigms in biological classification (1707–2007): Has anything really changed? *Taxon* 58: 68–76.
- Stuessy, T.F.** 2009b. *Plant taxonomy: The systematic evaluation of comparative data*, 2nd ed. New York: Columbia Univ. Press.
- Stuessy, T.F.** 2010. Paraphyly and the origin and classification of angiosperms. *Taxon* 59: 689–693.
- Stuessy, T.F., Crawford, D.J., Anderson, G.J. & Jensen, R.J.** 1998. Systematics, biogeography and conservation of Lactoridaceae. *Perspect. Pl. Ecol. Evol. Syst.* 1: 267–290.
- Stuessy, T.F. & König, C.** 2008. Patrocladistic classification. *Taxon* 57: 594–601.
- Syring, J., Farrell, K., Businsky, R., Cronn, R. & Liston, A.** 2007. Widespread genealogical nonmonophyly in species of *Pinus* subgenus *Strobus*. *Syst. Biol.* 56: 163–181.
- Tate, J.A. & Simpson, B.B.** 2003. Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Syst. Bot.* 28: 723–737.
- Tsigenopoulos, C.S., Ráb, P., Naran, D. & Berrebi, P.** 2002. Multiple origins of polyploidy in the phylogeny of southern African barbs (Cyprinidae) as inferred from mtDNA markers. *Heredity* 88: 458–465.
- Van der Peer, Y., Maere, S. & Meyer, A.** 2009. The evolutionary significance of ancient genome duplications. *Nature Rev. Genet.* 10: 725–732.
- Wendel, J.F. & Doyle, J.J.** 1998. Phylogenetic incongruence: Window into genome history and molecular evolution. Pp. 265–296 in: Soltis, D.E., Soltis, P.S. & Doyle, J.J. (eds.), *Molecular systematics of plants II: DNA sequencing*. Boston: Kluwer Academic Publishers.
- Wheeler, Q.D. & Meier, F. (eds.)** 2000. *Species concepts and phylogenetic theory*. New York: Columbia Univ. Press.
- Willmann, R.** 2003. From Haeckel to Hennig: The early development of phylogenetics in German-speaking Europe. *Cladistics* 19: 449–479.
- Yoon, C.K.** 2009. *Naming nature: The clash between instinct and science*. New York: W.W. Norton.
- Zander, R.H.** 2008. Evolutionary inferences from non-monophyly on molecular trees. *Taxon* 57: 1182–1188.
- Zander, R.H.** 2010. Taxon mapping exemplifies punctuated equilibrium and atavistic saltation. *Pl. Syst. Evol.* 286: 69–90.
- Zheng, X.-T., You, H.-L., Hu, X. & Dong, Z.-M.** 2009. An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. *Nature* 458: 333–336.