

## POINTS OF VIEW

**Paraphyletic versus monophyletic taxa—evolutionary versus cladistic classifications****Elvira Hörandl***Department of Systematic and Evolutionary Botany, Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. elvira.hoerandl@univie.ac.at*

Taxonomy is at its crossroads in choosing criteria for classification of taxa. The debate about recognition of paraphyletic vs. monophyletic taxa and its nomenclatural consequences is continuing and is keenly disputed, as e.g., reflected by recent articles and opinion papers in TAXON (Brummitt, 2002, 2003, 2006; Nelson & al., 2003; Dias & al., 2005; Nordal & Stedje, 2005; Potter & Freudenstein, 2005). Phylogenetic methods and Hennigian principles of classification are nowadays routinely used in systematics, and monophyly is widely accepted as the only criterion for grouping of taxa. On the other hand, facing an accumulation of phylogenetic classifications that are in strong conflict with traditional taxa, proponents of paraphyletic taxa request a consideration of evolutionary processes for classification (e.g., Mayr & Ashlock, 1991; Brummitt, 2002, 2006; Mayr & Bock, 2002).

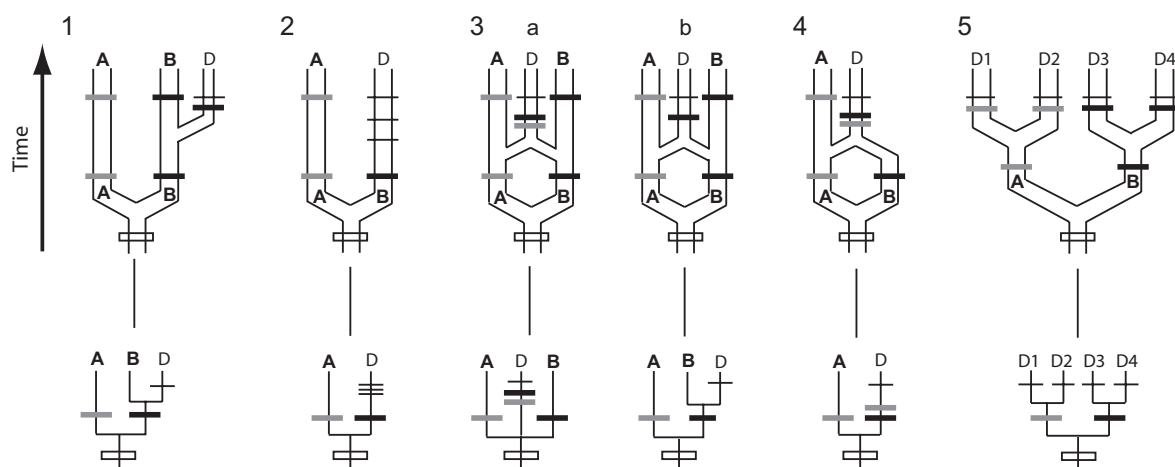
In their recent review, Mayr & Bock (2002) outlined comprehensively the basic conceptual differences of evolutionary (Darwinian) and cladistic (Hennigian) classification. Darwinian classification requests the consideration of two criteria—similarity *and* common descent for classification, which allows a grouping and ranking of taxa according to Linnaean hierarchies. Hennigian classification accepts only a single criterion, i.e., common descent, and the concept of monophyly for definition of taxa.

In this paper, I would like to focus on the question of criteria for grouping of taxa, without explicitly addressing the problem of ranking and subsequent concepts of nomenclature. The incompatibility of Linnaean hierarchy with phylogenetic systematics in the sense of e.g., De Queiroz & Gauthier (1992) and the recently proposed *PhyloCode* (Cantino & De Queiroz, 2004) has been already earlier outlined by e.g., Brummitt (2002). Here I want to show that a strict application of monophyly for grouping of taxa is problematic, because the commonly used tree-building methods result in a too strong abstraction and a too simplified visualization of evolutionary processes.

The inherent problems of these simplifications are manifold. First, proponents of phylogenetic systematics

regard and depict relationships as single lines and define species as basic indivisible units (reasoning that below species level evolution is reticulate and no phylogeny can be applied; e.g., Freudenstein, 1998). This simplification neglects the fact that descent of species and any branching pattern of evolution is constituted and continued by individuals and populations. Consequently, any part of a species can evolve further *without* affecting the rest of the lineage. Freudenstein (1998) depicts this nicely in his phylogenetic tree (his Fig. 1). That is, evolution is a process of entities below the level where cladistics has its starting point. Second, cladistic principles are based on solely dichotomous branching patterns, i.e., the ancestral taxon splits up and no terminal taxon can be at the same time ancestral, that is, logically it cannot exist any more. Here I want to demonstrate that most evolutionary processes result in descendants *without* extinction of the parental group, which results automatically in paraphyly of the latter. That is, in a dichotomous tree reconstruction any group of (younger) descendants destroys the older monophyly of the ancestral groups (see Figs. 1–4). As already outlined by previous authors, speciation processes and consequently natural relationships of lineages can be much more complex than dichotomous branching patterns; neither reticulate evolution, nor anagenetic evolution is well represented by dichotomous trees (e.g., Sosef, 1997; Stuessy, 1997; Brummitt, 2002; Linder & Rieseberg, 2004). Third, phylogenetic relationships are inferred from character state changes of selected characters; increasing information from various types of datasets (morphology, nuclear DNA, organellar DNA, etc.) and a better understanding of character evolution per se have shown that branching patterns of characters of a single data set do not necessarily reflect exactly the relationships of organisms to which they belong. Whereas the first and second items are strongly interconnected and fundamental theoretical problems, applying to any dataset, the third problem is more a methodical one and will be here only very briefly addressed.

Regarding subdivision of species and subsequent branching patterns, more kinds of relationships than



**Figs. 1–5. Five evolutionary processes observed at species level, starting from two sister species A and B (highlighted in bold), and their derivative(s) species D. Note that D can speciate further and constitute a new group, consequently affecting also groups at higher levels of divergence. – In the upper row, phylogenies are constructed to show evolutionary processes in a “streamlike” way, i.e., also allowing non-dichotomous branching, in the flow of time. In the lower row, examples of corresponding tree topologies are shown, as they can result from the observed character state distribution (outgroup not shown). Lines represent unique characters of a derivative, grey and black bars characters of A and B, respectively (shared with D after speciation), the open bars are shared characters of A, B and D. 1, budding from one species with persistence of the progenitor species B; 2, evolution of species B into a derivative species D with extinction of the progenitor (gradual change); 3, hybridization with speciation of the hybrid, with persistence of both parental species; a, the hybrid species combines characters of both parents, resulting in a polytomy; b, the hybrid has just characters of one parent and attaches to this parent in the tree; 4, hybridization with speciation of the hybrid, with extinction of one parental species (hidden reticulation). 5, split-up of both species into each two derivatives with extinction of the progenitors (dichotomy). Cases 1 and 3b make the formerly monophyletic parental species paraphyletic; cases 2, and 4 create no paraphyly, but result in incorrect sister relationships; only in case 5 the cladogram reflects fully the underlying phylogeny.**

dichotomies are possible as exemplified by various speciation processes (e.g., Grant, 1981). Let's start with a pair of species A, and B, that have, for simplicity, a sister relationship and a number of shared characters. A possible case of a speciation process is a split-off or budding (terminology after Mayr & Bock, 2002) of a part of a species, i.e., the parental taxon B does not go extinct (Fig. 1). Within a species, this budding will be usually performed by a few populations or individuals, which undergo a separate evolution (D) resulting in the development of new characters. The evolution of D may be a gradual change, e.g., after geographical isolation via long-distance dispersal, and would reflect a speciation process called anacladogenesis by Stuessy & Crawford (1990). A new lineage D entering a novel niche or adaptive zone, or undergoing bottleneck situations, may also diverge rapidly from the parental lineage B. Novel characters may appear, e.g., after epigenetic changes that may alter the temporal, spatial, and abundance patterns of gene expression and may have heritable and dramatic morphological, physiological, and ecological consequences (Rapp & Wendel, 2005). Rapid speciation may also happen after chromosomal or genomic rearrangements, e.g., after occurrence of autopolyploidy (e.g.,

Soltis & al., in press). Doubling of genomes infers massive and rapid alterations of genomic composition and extensive effects on gene expression, some directly following after onset of polyploidy (e.g., Adams & Wendel, 2005; Comai, 2005). Again, in most cases only a few individuals or populations among the diploid parents undergo this change.

The point is that ecological shifts, polyploidization and epigenetic changes may cause rapid speciation of D, thus leaving B no time for any substantial change. Because of the rapid establishment of reproductive barriers against the parents, there is also no reason why the origin of the new species would directly affect the parental species. Consequently, the parental species B does not become “ancestral”, i.e., extinct, just because of the origin of D, and its shared characters with A are still apparent in the dataset. Such buddings leave the remaining species A and B paraphyletic compared to D in the cladogram. This important mechanism contradicts fundamentally Hennig's (1966) concepts of dichotomous branching where an existing species cannot be ancestral to another one (see also Sosef, 1997).

A corresponding cladogram in Fig. 1 depicts the character states if B remains unchanged. Since D shares

characters with B, the cladogram suggests a “sister” relationship of B and D which is in fact not correct, because it is a progenitor-derivative relationship. B does not exhibit any autapomorphies after budding of D. Most important, B and A will have shared characters—without D, they would be recognized as synapomorphies. Despite their previous common ancestry, they are paraphyletic because of the origin of D and cannot be grouped according to a criterion of monophyly. The only possibility of a monophyletic taxon is A, B, and D, which may be unsatisfactory considering apparent differences in character states. This case is probably common in evolution and reflects what Freudenstein (1998) depicts very nicely in his phylogenetic tree (his Fig. 1), but he fails to see the fundamental difference of his phylogenetic tree to his cladogram; in the former, his species A is at the same time ancestral and terminal, in the latter, species A is terminal and the common ancestor, hypothetical another species, not existing any more. This case is also what Brummitt (2002) discussed and depicts in his Fig. 1 (unfortunately he shows it as a dichotomous diagram, thus weakening his otherwise correct argumentation). Mayr & Bock (2002) provide a couple of examples of such buddings in animals. Since traditional classifications often reflect groupings of A and B because of the apparent shared characters, this leads necessarily to severe conflicts of traditional classifications with monophyletic taxa.

In Fig. 2, the case of a gradual change of one species into a new one is shown, whereby the parental species goes completely extinct, representing a case of anagenetic speciation. B and D have a progenitor-derivative relationship, but without a dichotomy involved. In the corresponding cladogram, derived just from the existing taxa, the derivative will appear as sister to Taxon A. Since B does not exist any more, such cases may remain hidden because the characters inherited from B would appear as an autapomorphy of D. The consequence for the taxonomist may be just that D may appear so different from A because of many autapomorphies that he may not wish to group D with A to reflect the evolutionary processes and differences in character states (e.g., he may wish to classify this as a monotypic genus). If one follows directly the cladogram this causes problems because classifying D at any other rank (within an Linnean hierarchy) makes all other relatives of A (not shown in Fig. 2) paraphyletic. If D is sunk into one taxon with A, the classification after the criterion of monophyly does not allow recognition of the evolutionary processes that have caused the origin of D.

The most complicated cases, and most obvious problems, arise after reticulations caused by interspecific hybridization, and subsequent speciation of the hybrid (Figs. 3, 4). It is not only that a hybrid itself, and conse-

quently all its derivatives, do not form a monophyletic group because the hybrid has not just one but two ancestors (the only monophyletic group is A, B and D). Perhaps even more problematic is the possible impact of the origin of a hybrid species on the parents. If A hybridizes with B, this will happen usually only in a few populations of the species. That is, if the hybrid undergoes speciation, e.g., after allopolyploid origin, or after establishing ecological reproductive barriers after homoploid speciation (e.g., Rieseberg & al., 2003), the diploid parents will persist and remain unchanged. If this reticulation is forced into a dichotomous branching pattern, any tree will fail to depict correctly the natural relationships. Tree topologies including hybrids and parents are in general not easily predictable, depending on the type of characters used, inheritance of characters from the parents, and the expression of these characters (e.g., Rieseberg & Ellstrand, 1993; McDade, 1995; Linder & Rieseberg, 2004 and literature therein). In our simple case, where a hybrid species originates from two parental sister taxa A and B, there are basically three possibilities in a cladogram: (a) a polytomy because of conflicting signals, (b) if the hybrid inherits or expresses just the character of one parent it appears as sister to this parent (the alternative A, D not shown); (c) the hybrid may even appear as sister to the two parental species, if it has a loss of characters shared by A and B (not shown). The polytomy (a) offers just the possibility of grouping A, B and D as a monophyletic group. The second case (b) makes the parents A and B paraphyletic. That is, the dichotomous branching pattern suggests that the terminal taxon B is not the same species as before hybridization, i.e., the origin of D. This implies in case of hybrid speciation, the parental species would become logically “extinct”! Biosystematic and evolutionary studies give evidence that this is simply not the case. Allopolyploidy requires just 1–2 generations for establishment (Ramsey & Schemske, 1998), and again such rapid speciation processes will not affect the parental species. A taxonomist faces again a difficult situation because he cannot group A and B any more, even if they have a common previous ancestor and many shared characters.

The next case (Fig. 4) shows hybrid speciation whereby one parent goes extinct which may happen, e.g., after introgression; consequently, the relationship is again not dichotomous although it may appear so in a cladogram, where the other parent and the derivative will show an incorrect sister relationship. Similar to 2, such relationships may be difficult to reconstruct, because characters that have been inherited from the unknown parent B may appear as autapomorphies in the hybrid species D.

Figures 3 and 4 illustrate just the simple case that A and B have a sister relationship; if the parental taxa are

not closely related, the patterns become even more complex (see e.g., McDade, 1995; Van Raamsdonk, 1998). Reticulate relationships have often been regarded as only important for lower taxa, i.e., on species level, because lineages with higher divergence do not hybridize any more. But, it must be held in mind that any successful hybrid derivative, e.g., an allopolyploid, may speciate further and form a new group independently from its parents. That means, although lineages of high divergence (i.e., higher taxa) do not form reticulations any more, they can well have an *origin* from reticulation events. For higher plants, several authors (e.g., Grant, 1981; Arnold, 1997) have estimated that the majority of taxa are indeed of hybrid origin. The actual number of hybridization events may be much less, because hybrids have speciated further (Arnold, 1997, literature and examples therein). That means, a single effective reticulation event may result in a number of paraphyletic lineages (e.g., Arnold, 1997). Kellog & Bennetzen (2004) show that major genomic changes correlate with the origin of major clades and hypothesize that “groups that we now call families or major clades correspond to major genome rearrangements or polyploidization events”. Consequently, reticulate evolution is in plants, but also in other groups (e.g., fish, bacteria) not at all a negligible matter for phylogenetic reconstruction at higher levels. Under these quantitative considerations it is also unrealistic to demand that species of known hybrid origin should be excluded from phylogenetic analyses.

The last case (Fig. 5) corresponds to the view of a cladogenetic speciation, i.e., both progenitors go extinct, and the derivatives form sister groups. This might happen, e.g., after allopatric speciation. Only in this case the cladogram reflects well the underlying evolution, and only in this case monophyly is a perfect criterion for grouping.

These examples, without being exhaustive, demonstrate that dichotomous branching patterns probably reflect only in a minority of cases the true phylogenies. Budding occurs in all groups of organisms (Mayr & Bock, 2002), and may occur even more frequently in plants via geographical isolation, because only diaspores move, but the parental population remains where it is. I would also estimate that non-dichotomous branching patterns may be more frequent in angiosperms than in other groups of organisms because of the frequent occurrence of polyploidy (estimates range between 40 and 70% of species; Ramsey & Schemske, 1998) and hybridization. Polyploidy is nowadays also traced in many other eukaryotic organisms (recently reviewed by Comai, 2005). Speciation after polyploidization and/or hybridization will result almost necessarily in non-dichotomous branching patterns, i.e., either in budding or in a reticulation (see above).

The increasing information on various kinds of characters has also demonstrated that the evolutionary history of characters used for phylogenetic reconstruction may not always reflect well the evolution of the organisms. Incongruence of nuclear and plastid DNA datasets after hybridization because of different inheritance of markers (e.g., Arnold, 1997), incongruence of gene trees with species trees (e.g., Linder & Rieseberg, 2004), different speed of evolution within DNA regions (e.g., Burleigh & Mathes, 2004), and possible horizontal gene transfer imply that the use of DNA markers is also no guarantee for a correct phylogenetic reconstruction. We observe in our phylogenetic reconstructions dichotomous branching patterns of characters—but a taxonomist wants to understand the relationships of organisms, and finally wants to classify organisms, not just genes or characters. Combining datasets or trees derived from different datasets may increase the phylogenetic signal and provide a better representation of the organisms under study; but in case of incompatible datasets, true relationships of groups may also not be well depicted by producing just a new dichotomous tree from combined datasets.

I want to emphasize that the problem is not the preference of a certain dataset as a basis for classification, but an inherent conceptual problem of tree-building methods. The conflict between traditional classifications and DNA-based classifications rather arises because the former rely almost exclusively on morphological similarities, whereas the latter are almost exclusively being analyzed using phylogenetic tree-building methods.

So far the theory; now to the practice of classification. I do not agree with Potter & Freudenstein (2005) that “we can never know the true underlying phylogeny of relationships” but I would rather say that usage of tree-building methods alone will fail to give insights in the underlying phylogenies. Admittedly, only at lower (species and generic) levels we may have a realistic chance to get insights into the kind of evolutionary processes as depicted in Figs. 1–5. The approach to take evolutionary processes as a basis for the definition of taxa, as demanded by proponents of paraphyletic taxa, requires some knowledge of ancestors for a correct reconstruction of relationships and grouping of taxa (see also Sosef, 1997, his Fig. 2). Common ancestors may be apparent from shared characters, but this will not show the processes involved in the evolution of taxa (see Fig. 1). It is evident, that the deeper the origin of groups lies in the past and the more extinct species are involved, the more uncertainty will be inferred from analyzing data just from the tips of the phylogeny, and the more difficult may be an attempt to reconstruct relationships reflecting specific evolutionary processes. Nevertheless, any evolution of a group out of another group without extinction of

the parental group will make the latter paraphyletic. The implications of non-dichotomous branching for reconstructions of a tree of life should be considered (perhaps it would help to speak of a “stream of life” rather than a tree of life—a terminology that would at least allow to illustrate merging and budding processes).

Different branching patterns may appear in the same lineage, e.g., a widespread species may undergo in one part of its range anagenetic speciation, in another cladogenesis and in a third it can hybridize with another species. This is continued on levels of higher divergence and probably occurs frequently in large groups. In *Ranunculus* s.s., an almost cosmopolitan genus of c. 600 species, c. 40% of them being polyploid, the observed severe conflicts of phylogenetic analyses (Hörandl & al., 2005; Paun & al., 2005) with previous traditional classifications suggest an evolution of many groups after non-dichotomous branching patterns. Phylogenetic analyses using nuclear and plastid datasets plus network methods suggest that some terminal groups have resulted from reticulate evolution (e.g., the water-buttercups, genus *Batrachium* or *R.* subg. *Batrachium*), anagenetic evolution (e.g., *Aphanostemma*, classified as a monotypic genus by previous authors because of several unique morphological features), or budding with ecological shifts (e.g., the alpine *R. montanus*-group, clade VIIIg in Paun & al., 2005, which originated probably from eastern Mediterranean lowland buttercups and turned the extant ones into a paraphyletic group, VIII f). These cases exemplify that various criteria for grouping would have to be applied to reflect the diversity of evolutionary processes in taxonomy.

In this situation, using monophyly alone seems attractive, especially for higher taxa, because it provides a single, objective, logical, reproducible, and efficient criterion, which is from a scientific viewpoint desirable for any classification (see e.g., Stuessy, 1990). Defining taxa after monophyly does not require knowledge of the ancestor which remains always hypothetical, because one can group just the species on the tips of the tree to define a taxon and regard all ancestors as extinct (by rejecting all other than dichotomous branching patterns). Because of their exclusiveness and simplicity, dichotomous trees are easy to visualize and to communicate which make them attractive for human perception.

The big drawback of the concept is that this simplicity fails to reflect the complexity of evolutionary processes involved, simply because evolution is not—or only in a minority of cases—dichotomous. A dichotomous branching pattern just reflects the monophyly of the descendants, but not the *older* monophyly (and similarity) of the parental species (in our examples A and B). Such paraphyletic parental groups do have an historical reality as well as the descendant monophyletic group.

Moreover, dichotomous branching patterns alone fail to reflect anagenetic change as an evolutionary process. In grade-like branching patterns, as it is e.g., observed in Ranunculaceae (Hörandl & al., 2005; Paun & al., 2005), the criterion of monophyly alone offers several alternative options of selecting a larger or smaller clade (each well-supported) for the definition of the genus *Ranunculus* in a narrower or broader sense. Considering branch lengths gives an unequivocal criterion for accepting genera like *Ceratocephala* and *Myosurus* as genera separated from *Ranunculus* s.s. Concluding, taxa classified strictly after the principle of monophyly *alone* are likely to be in many cases just nice logical constructs, or results of subjective decisions, but fail to represent evolutionary processes—which was, ironically enough, the original intention of cladistics by including the concept of descent into classification.

In cases where descendants exist in parallel to their parental groups, a strict application of monophyly as criterion for grouping will in many cases just artificially split up well-defined older monophyletic groups because of the rise of descendants, or force together groups of descendants with parts of older groups (see Figs. 1 and 3b). That is, taxa defined after the criterion of monophyly are not necessarily more “natural” than paraphyletic taxa. If the parental taxa are lumped together with the descendant taxa, the resulting monophyletic taxon will be heterogeneous in many characters and often not easily diagnosable, which will lower the practicability of taxonomies for users. Prominent examples are the break up of the traditional “Reptilia” and the concept of “Avian Dinosaurs” for birds.

An alternative concept of evolutionary “Darwinian” classification was proposed by Mayr & Bock (2002), who requested the consideration of two criteria: “similarity and common descent—and hence the ordered grouping of organisms into classes according to their similarity with their inferred evolutionary descent”. The incorporation of both components avoids using similarities that are a result of parallel or convergent evolution, but allows recognition of similarities of an older parental group which exists in parallel to the derivative group. In practice, that would mean that monophyly would not be a single criterion, but could be alternatively or additionally used with other criteria, which must be then decided case by case. Basically, the difference between cladistic vs. evolutionary classifications is just that the former accepts a single analytical method, and a single criterion for classification, whereas the latter try to incorporate various methods, and accept either a combination or an alternative use of criteria for classification. Whereas the former has the advantage of strict consistency and simplicity, the latter has the advantage of reflecting better the diversity and complexity of evolutionary processes.

Considering these different aspects, I suggest that clades retrieved by phylogenetic analyses should be not used solely as a basis for classification, but should be regarded primarily just as information for a better understanding of relationships. If there is any indication that phylogenies are not dichotomous, researchers should refrain from quick taxonomic conclusions and try first to understand better evolutionary processes leading to such tree topologies, whereby a broad array of analytical methods and datasets, including external evidence, should be used. Considerable progress has been made in understanding and visualizing of reticulations in the last years, including direct network reconstruction or character incompatibility methods (reviewed by e.g., Vriesendorp & Bakker, 2005; McBreen & Lockhart, 2006). For understanding buddings and gradual change, phyletic approaches should be used; displaying branch lengths proportional to character state changes in phylograms is a good starting point and often more informative for relationships than the branching pattern alone. Stuessy (1997) reviewed phyletic approaches and proposed a method of using apomorphic support and apomorphic distance as criteria for classification. An approach of combining cladistic, phyletic, and phenetic methods for reconstruction of phylogenies was proposed by Stuessy (1987). The scarcity of empirical studies, and therefore a broad testing of such methods, is probably just due to the lack of convenient computer programs for rapid analysis; methods to calculate patristic distances are published e.g., by Fourment & Gibbs (2006). Only after analyzing the evolutionary processes involved, the taxonomist may choose the appropriate criteria for grouping the taxa. Such an approach may be more complex and time-consuming than just naming clades, but would probably result in better and more widely accepted classifications.

In conclusion, acceptance of paraphyletic taxa would not at all result in taxa that contain no information or result in possible chaos, as argued by some proponents of monophyly (Dias & al., 2005). I propose here to consider this as an alternative concept for classification. This does not mean to go back to phenetics or mere “tentative” classifications. Phyletic methods are even more evolutionary than cladistic methods (Stuessy, 1990), applying also to network methods (McBreen & Lockhart, 2006). As long as solid analytical methods are used, and reproducible criteria are given for the grouping of taxa, there is no reason to regard alternative classifications as less logical, “unnatural” or “intuitive” with the smell of being non-scientific.

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