

## Glossary of Phylogenetic Systematics

with a critic of mainstream cladism

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This text is a revised translation of a stencilled handout-manuscript by the author for different courses on metazoan morphology, systematics and phylogeny at the Eberhard-Karls-University of Tübingen / Germany, under the supervision of Dr. Gerhard Mickoleit. The definitions and comments refer to Phylogenetic Systematics sensu HENNIG (1959, 1982, 1984), SCHLEE (1971, 1978, 1981), AX (1984, 1988), WILLMANN (1985, 1989) and SUDHAUS & REHFELD (1992), rather than to computer-cladistics and Pattern-Cladism that seem to be more «en vogue» today. I absolutely agree with the recent critic of this mainstream cladism by WÄGELE (1994, 1996a,b) and BORICKI (1996). The presented definitions have passed several years of "evolution", but of course I would be very grateful for further suggestions, amendments and corrections by the readers.

**agamo-species:** A term for groups of primarily or secondarily uniparental (= agamic, apomictic, asexual) organisms, that are morphologically so similar that they have been classified as a single species. These agamo-species represent entities that are fundamentally different from the biospecies of biparental organisms, since the relationships between the members of an agamo-species are exclusively hierarchical, contrary to the generally reticulate relationships within biospecies. Consequently there is no difference between tokogenetic and phylogenetic relationships in all uniparental organisms, and furthermore there exists no particular cohesion by mate recognition mechanisms and gene flow. The only potential mechanism of cohesion might be the ecological concurrence between the individual organisms of an agamo-species. Nevertheless uniparental organisms form clones, that can be discovered by autapomorphies just like monophyletic groups.

**apomorphic (versus plesiomorphic):** A derived character state is termed the apomorphic state. This property "apomorphic" is not generally valid, but always related to the compared character state and the hierarchical level in view: The scales of "reptiles" are apomorphic compared to the smooth and glandulated skin of amphibians, but plesiomorphic compared with the feathers of birds. Hairs are autapomorphic for mammals, but a symplesiomorphy for rodents. Shared derived similarities can be homologous (synapomorphies) or non-homologous (convergences). KLAUSNITZER & RICHTER (1981) suggested the new (synonymous) terms "apotypic", "Autapotypy" and "Synapotypy", since strictly speaking the suffix "-morphic" is only correct for morphological characters. The term "derived" should only be applied to character states, but never to organisms or taxa (taxa that originated from rather young splitting events and have developed numerous apomorphic states should rather be called "modern groups"), since all taxa always have a mixture of plesiomorphic and derived character states (compare living fossils). Considering the frequent phenomenon of reduction or reversals, derived states by no means have to be more sophisticated or more complex than the referring plesiomorphic state. Out of this reason the plesiomorphic state should better not be equaled with "primitive" state.

**biospecies:** A species in the sense of the so-called "biological species concept", as a closed community of reproduction with a closed gene pool (ERNST MAYR: "A species is the most inclusive Mendelian population, sharing a common gene pool, which is reproductively isolated from other populations"). The biospecies is maintaining its cohesion through a common mating system (e.g. "sexual mate recognition system" sensu PATERSON) and is separated from other biospecies through "isolation mechanisms" (sensu DOBZHANSKY). The biospecies concept can of course not be applied to uniparental organisms. A further problem is that the biospecies criterion is null-dimensional, that means it only allows to decide if two organisms that occur together at the same time and at the same place belong to the same species or not, but it does not allow to decide if allochronic populations (populations separated in time) or allopatric populations (populations separated in space) are conspecific or not. The biospecies concept in its original form does not give any clues to the spatio-temporal boundaries of a species.

In Phylogenetic Systematics the spatio-temporal boundaries of a biospecies ("time-biospecies" sensu BRUNDIN) are claimed, by the simple conclusion that if biospecies are no inventions of the human mind (logical classes) but real individual entities of nature (logical individuals) they simply must have spatio-temporal boundaries ("species as individuals" sensu GHISELIN and HULL). The boundaries in time can be regarded in a way as the "birth" and "death" of a biospecies. An important consequence of the theory of Phylogenetic Systematics is that new species can only originate by speciation (splitting of stem-species into two or more new descendant species) but never by a successive phenotypic change of a single evolutionary line, which would mean a gradual transformation of one species into another, by a gradual shift of the gene-frequencies in an undivided gene-pool. The dismissal of a speciation by gradual transformation of species without multiplication of species through splitting, can be easily explained with the following example: A caterpillar that is transforming into a butterfly also remains the same individual through all his life, although its appearance drastically changes. New individuals of butterflies only originate through reproduction of this individual. An individual species terminates either by extinction (extinction of all populations) or by disintegration through speciation (splitting into two or more new descendant species), in which the stem-species of course does not die in a literal sense but it loses its own individuality and hands it equally over to all its descendant species, like a cell that is dividing into two new cells. A stem-species is thus defined as portion of a phylogenetic tree between two successive splitting events. Species that are no stem-species became either extinct before they could produce descendant species or they are still existing in the recent time horizon as potential stem-species which are not yet extinct nor disintegrated through speciation yet ("incomplete species"). According to this view so-called "surviving stem species" (= species that maintain their individual identity after budding of descendant species) are excluded by definition. Since species are recognised as individual spatio-temporal entities of nature, their ontological status as such is absolutely independent of any characters that might be necessary to recognize and distinguish them. Uniting a stem-species with only one of their descendant species, because of

mere phenetic similarity, would be totally arbitrary and would furthermore automatically lead to the formation of paraphyletic groups that are dismissed by Phylogenetic Systematics for good reasons. One-egged twins are also not regarded as the same individual only because they look alike. Like a cell that is dividing into two new cells, a stem-species lives on in all of their descendants, irrespective of their appearance and similarity. Since an individual stem-species cannot maintain its individuality and at the same time being identical with several individual descendant species, its own existence necessarily ends with the splitting event. The well known fact that biparental organisms survive the birth of their offspring without losing their individual existence is no counter example, since the mechanisms of maintaining the individuality and the mechanisms of reproduction are fundamentally different from those of biospecies. The split of a stem-species into descendant species, caused by spatial separation and subsequent divergent evolution, is of course a continuous process (like the division of a cell), and consequently there is a fuzzy zone in which it will always be rather arbitrary to decide if two populations still belong to the same biospecies as subspecies or already constitute separate biospecies. This certain arbitrariness is by no means a weak point of the biospecies concept, or even a proof for the artificial status of species, but a direct corollary of all continuous natural processes.

A related problem is represented by allopatric populations that have retained the potential to interbreed. Such populations might be classified as subspecies (or rather as semi-species) of the same (super-)species (which is of course different from a genuine biospecies) if they are still rather similar and represent a monophyletic group. If they have developed significant differences or do represent a paraphyletic assemblage they should be classified as separate (semi-)species, while the directly superordinated monophyletic assemblage should be classified as a super-species. Super-species are thus monophyletic assemblages of semi-species (eventually including some biospecies too), while semi-species are distinct allopatric populations that have retained the potential ability to interbreed with other such populations. A subspecies is defined as a population within a biospecies that was once separated for a certain period of time and developed distinct characters in this period, but later came in contact with other populations of this biospecies again and is now interbreeding with these populations in a restricted area (hybridisation-zone). These additional terms can be very useful to indicate different stages of speciation. If a continuous morphocline of a character exists between temporally or geographically distant populations of a biospecies, this cline should not be arbitrarily partitioned into "pseudo-subspecies", although this was done quite often in the past (e.g. in case of the chrono-subspecies in paleontology).

Recently several further (cladistic) species concepts were endorsed by cladists of the Anglo-American region, such as the "phylogenetic species concept" (sensu CRACRAFT), and the "monophyletic species concept" or "autapomorphic species concept". In these concepts species are defined either as "smallest units that are 100% diagnosable by a unique combination of characters" (phylogenetic species concept) or as "smallest units with autapomorphies" (monophyletic or autapomorphic species concepts). These concepts are all invalid from the viewpoint of Phylogenetic Systematics, since they are character based, and thus are confusing the tools of discovery of natural entities with the ontological justification of these entities. The "phylogenetic species concept" (sensu CRACRAFT) can at least be regarded as an operational approach (discovery procedure) towards the recognition of hypothetical biospecies, since the interbreeding abilities within most species have to be postulated rather than studied, simply because of the practical obstacles regarding the existence of millions of species on earth. Contrary to the former concept, the so-called monophyletic and autapomorphic species concepts suffer from the severe problem that they exclude the existence of stem-species by definition, since these can neither be monophyletic nor can they possess autapomorphies, since they inherit their "autapomorphies" to their descendant species, so that the former autapomorphies of the stem-species become the autapomorphies of the resulting monophylum and thus become symplesiomorphies of the stem-species. The mentioned cladistic species concepts are not only unacceptable with view to extinct species, but also for recent species, since these are all potential stem-species too.

characters / character states (versus traits): Characters are shared similarities of properties (structures or behaviours) in different organisms, that are recognized and formulated, and that are supposed to be inheritable and homologous. The subdivision of the continuous body of an organism into discrete characters (incl. behavioural characters) will always remain to be rather subjective and optional, although by no means completely arbitrary! Differences between homologous characters in different organisms are called character states. Diagnostic characters (e.g. for keys) can include "primitive" (= plesiomorphic) and derived (= apomorphic) character states, while phylogenetic relationship can only be demonstrated by shared derived character states (synapomorphies). Contrary to the character state, that is only specifying a property, the character itself is not an observation but a hypothesis of homology, since it implies that all included character states are transformations of a shared ancestral state. The term "character" consequently requires a comparison of different organisms; - a single organism does not have characters but only certain properties. The biogeographic distribution, population by parasites or symbionts, the adaptation to certain hosts, habitats or resources, as well as acquired behaviours, do represent distinct properties of organisms, that may even have some correlation with their phylogenetic relationships, but they are no characters according to the above given definition, because they are not genetically inherited. Since they are still more important for evolutionary biology than the particular properties of single organisms, they are often called "traits" to express this difference without using the term "character". Even genetically inheritable features can be traits rather than characters if they are not fixed in a population, since in this case they do not diagnose distinct evolutionary lineages. Such traits should not be used for the reconstruction of phylogenetic relationships, but should be interpreted on the basis of phylogenetic trees that have been reconstructed by the use of genuine characters. This kind of procedure is often applied in biogeographic studies (so-called vicariance-biogeography) and in studies of co-evolution (e.g. of hosts and parasites, or blossoms and pollinators).

chrono-species: A morphological species concept that is unfortunately still very popular in paleontology. Although it is postulated that any time-slice of a chrono-species should reflect a hypothetical biospecies, this species concept has to be dismissed from the viewpoint of Phylogenetic Systematics as being rooted in typology, since the boundaries of these species in time are arbitrarily defined according to selected morphological character states. This species concept allows speciation by budding with surviving stem-species, and consequently is at odds with the basic principles of Phylogenetic Systematics (see biospecies). A chrono-species definitely does not represent a real entity of nature but only an invention of the human mind ("logical class").

cladogram (versus phylogenetic tree): A cladogram is a "phylogenetic argumentation scheme" in shape of a tree-like graphic (dendrogram), which is only specifying the relative degrees of phylogenetic relationship (sister-group relationships) of the analysed taxa as well as their monophyly, based on the evidence of the recognized synapomorphies and autapomorphies.

Contrary to such a cladogram, a genuine phylogenetic tree is also specifying direct ancestor-descendant relationships, just like a pedigree. Although such ancestor-descendant relationships of course exist, there is

unfortunately more or less no possibility to identify an ancestor as such, since these cannot possess any exclusive characters (autapomorphies). A fossil that belongs to the stem-group of a monophyletic group, and is lacking any visible autapomorphies, consequently can either represent a direct ancestor, that is primarily lacking these autapomorphies, or it can be a member of an extinct side-branch of the stem-line, whose autapomorphies simply did not happen to become preserved in this fossil. Only in very rare cases of a continuous and complete fossil record over a considerable range of time at one locality (e.g. in some lacustrine sediments) there might be the possibility to postulate an ancestor-status, provided that no potential descendants are known from the same or even older age, and provided that an allopatric speciation (sister-species) could not be demonstrated. The ground-plans of Phylogenetic Systematics are representing hypothetical reconstructions of the (undiscovered) stem-species.

rule of deviation: During an allopatric speciation through geographic separation of a stem-population, the latter is usually not divided into two populations of similar size (dichopatric speciation), but only a small peripheral population is separated from the remaining population (peripatric speciation). Because of a phenomenon that is generally known as genetic drift the small founder population shows a stronger morphological divergence from the original state than the large rest population that stays more or less unchanged. This "founder effect" was called by WILLI HENNIG the "rule of deviation". The morphological hardly changed rest population cannot be regarded as "surviving stem-species", because of theoretical reasons (see biospecies), and therefore has to be regarded as non-divergent descendant species.

dichotomy principle: Polytomies in a cladogram can have three different causes: Either a real polytomic speciation event (multiple split), or just a simple lack of knowledge about the synapomorphies that could resolve the polytomies into dichotomies, or the polytomies can even result as artefact of a so-called "consensus-method" which is often applied in case of equally supported (equally parsimonious) cladograms of different topology (conflicting evidence). Out of this reason the preference for fully dichotomic trees must be understood as a heuristic principle, that requires that the search for further synapomorphies shall not be discontinued prematurely. The "principle of dichotomy" does by no means imply that polytomic speciations do not at all or do only rarely occur in evolution. This principle is not even essential or necessary for the application of the method of Phylogenetic Systematics. Nevertheless it seems quite likely that from most polytomic speciation events of the past, not more than one or two species have survived till today, since extinction is a much too frequent phenomenon. Because of the fragmentary fossil record these species will often represent the only known descendant species of the referring polytomic speciation event. Therefore most reconstructed speciation events will indeed appear to be dichotomic.

"Evolutionary Systematics": The so-called "Evolutionary Systematics" is a syncretistic approach to biological systematics, which was especially endorsed by ERNST MAYR and SIMPSON. Although the proponents of this approach mostly accepted the Hennigian methodology as adequate technique for the reconstruction of phylogenetic trees, they strongly objected against a strictly cladistic classification, since they wanted to use paraphyletic groups in their classifications. These paraphyla (e.g. "Reptilia") were a direct corollary of their desire to assign a higher categorial rank (e.g. class) to a monophyletic taxon with numerous autapomorphies (e.g. birds), than to its sister-group (e.g. crocodiles), if the latter has retained numerous symplesiomorphies with other groups (e.g. lizards). This desire was justified by the greater "evolutionary divergence" compared to the common ancestor, and the possession of a new "adaptational level". Except the difficulty to define and measure "evolutionary divergence" and "adaptational level", the main problem of this approach is the extreme arbitrariness in the classification and delimitation of paraphyla: Should animals be divided in "Protozoa" (paraphyletic) versus Metazoa (monophyletic), or rather in "Invertebrata" (paraphyletic) versus Vertebrata (monophyletic), or better in "Protostomia" (paraphyletic) versus Deuterostomia (monophyletic); should one likewise divide Vertebrata in "Pisces" (paraphyletic) versus Tetrapoda (monophyletic), or in "Anamnia" (paraphyletic) versus Amniota (monophyletic), or maybe even in non-mammals (paraphyletic) and Mammalia (monophyletic), which curiously was never proposed yet. Even the exclusion of man from the kingdom of animals as separate kingdom (regnum) "Psychozoa" has been proposed and would be absolutely compatible with the principles of "Evolutionary Systematics". The grouping of crocodiles and birds as sister-groups in a monophyletic taxon Archosauria has been dismissed as absurd by evolutionary systematists, while they accepted a group like Deuterostomia without any protest, although it is including such divergent organisms as sea-cucumbers and man. A further critique against Phylogenetic Systematics was the mere conjecture that it shall completely neglect the evidence from symplesiomorphic characters, although they are important homologies too. This statement is of course nonsense, since all homologous characters are recognized and used in Phylogenetic Systematics, and symplesiomorphic characters are therefore not neglected at all, but are recognized on that hierarchical level on which they do represent a synapomorphy (compare apomorphic). A more general problem of "Evolutionary Systematics" is the circumstance that several very different criteria are used for the construction of a classification (phylogeny, divergence, adaptational level), but in the resulting system it is not recognizable which criteria have been used for a particular taxon. Because of the mentioned problems and the theoretical, practical and heuristic superiority of Phylogenetic Systematics, the number of proponents of "Evolutionary Systematics" has strongly declined in the past decades.

ground-plan: The complete set of character states of the last common stem-species of a monophyletic group has been termed the ground-plan of this group. This ground-plan includes all the plesiomorphic states as well as all the apomorphic states (autapomorphies) of this stem-species. The term ground-plan is one of the most important terms of Phylogenetic Systematics, although it was never clearly defined by HENNIG himself. The ground-plan concept is completely different from the typological concept of the "Bauplan". Out of this reason AX (1984) suggested the new (synonymous) term "Grundmuster" (= ground-pattern).

"HENNIG's auxiliary principle": According to this principle a shared derived similarity of a group of organisms has to be regarded as their synapomorphy (thus as a homology), unless the paraphyly of the group can be demonstrated with other characters, that are conflicting to the putative synapomorphy but regarded as stronger evidence by quantity or quality. In cases of structural similarity of a sufficient degree, homology must be assumed, while convergence should never be assumed a priori, but only be postulated on the basis of the total evidence of all available characters (a posteriori). Basically this principle can be regarded as a special case of the principle of parsimony.

heterobathmy: The simple fact that plesiomorphic and apomorphic character states occur in different number and combinations in different groups, because of their different age of origin, was called the "heterobathmy of characters" by WILLI HENNIG. ERNST MAYR called the same phenomenon "mosaic evolution", a term that is frequently misunderstood. It is only because of the heterobathmy of characters that there is the possibility to

reconstruct the past phylogeny with the present pattern of characters. This heterobathmy is caused by an evolutionary process that has been called "additive typogenesis": derived characters did not originate all at the same time but successively one after the other, so that groups that originated from successive splitting events will of course have a different set of these characters (fewer apomorphies if they originated early and more apomorphies if they originated later).

holomorph: The entire set of all morphological, physiological, chemical / molecular, and ethological features of a studied specimen, has been termed the holomorph of this semaphoront by WILLI HENNIG. The "holomorph of a biospecies" (new term!) includes the holomorphs of all its semaphoronts, thus all inheritable features of all ontogenetic instars of both sexes, and in case all morphs (e.g. castes) and all different generations of a heterophasic cycle of generations, including all populations of all generations that existed between the origin and the end of this species.

homology (versus homoplasy): Similar structures or behaviours in different organisms, which are supposed to represent modifications of a single evolutionary novelty in a common ancestor (stem-species) of these organisms, are called homologous characters. Homologies are thus hypotheses about the singular evolutionary origin of certain similarities. Homology is a priorily assumed on the basis of so-called homology criteria (sensu REMANE: basically similarities of a sufficient degree of complexity) and tested by their congruence with other putative homologies and the resulting phylogenetic trees (cladograms). Similar character states are only dismissed as homologies if they are not compatible with other conflicting homology hypotheses (which imply other hypotheses of phylogenetic relationship), that are regarded as stronger evidence because of their greater number (see parsimony) or their higher relative weight (see character weighting). In consequence the question of homology or non-homology can often not be decided on the basis of a singular character, unless this character is so unique and complex that a convergent evolution can be excluded a priorily with sufficient certainty. Example: The wings of bats and birds are not (only) regarded as non-homologous, because of certain anatomical differences, but because both groups are not sister-groups but represent subordinated clades in different groups of terrestrial animals (birds in Sauropsida and bats in Mammalia). If the wings of both groups would be regarded as homologous one would be forced to assume that all other mammals as well as lizards, turtles and crocodiles, have convergently transformed their fore legs from wings into walking legs, which would be a quite absurd idea indeed. On the other hand most biologists would not hesitate to assume a winged ancestor for birds and bats, and thus a homology of their wings, if birds and bats would indeed be sister-groups.

homonymy (= serial homology): Homonomous organs are organs with an identical or at least similar construction ("Bauplan") within a single organism, e.g. the fore leg and hind leg of tetrapods, or the segments of annelid worms. This phenomenon is often termed "serial homology" to indicate that the similarity might be based on a common genetic origin. In molecular biology there is a similar phenomenon because of the frequent existence of multiple copies of genes in a string of DNA. These copies are so to speak "homonomous genes", but have been called paralogous genes, while homologous (s. str.) genes in different organisms have been called orthologous genes.

homoplasy (versus homology): Homoplasy is the most general term for all kinds of non-homologies (see below). All shared character states, that have to be explained on a phylogenetic tree (cladogram) with more than one evolutionary step (multiple origins or losses) are referred to as homoplastic character states. Homoplastic character states are caused by non-homologous similarities (homoplasies), thus either by a non-homology of the presence of a state (convergences) or by a non-homology of the absence (secondary absence) of a state (reductions or reversals).

convergence: Shared derived similarities, that are not based on a singular common origin (= homology), but on an independent origin in different taxa. The following phenomena of convergence have been distinguished:

analogy: Convergent modifications of a non-homologous structure (or behaviour). Analogous organs thus are convergent organs of the same function, e.g. the wings of insects (probably derived from tergal paranota) and the wings of birds (derived from the vertebrate fore legs).

homoiology: Convergent modifications of a homologous structure (or behaviour). The wings of pterosaurs, birds, and bats represent such a homoiology, since they are homologous as tetrapod fore leg, but were convergently modified to flight devices (wings).

parallelism: The term parallelism refers to shared derived (apomorphic) similarities, that are not based on a singular evolutionary origin, but have independently evolved in closely related taxa, and which therefore might be explained with a common genetic predisposition for an evolution of this character state. In cases where a certain character state evolved several times parallel within a monophyletic group, this phenomenon was also referred to as "trends" or "tendencies" (sensu BRUNDIN or HEADS). Example: Within mammals a so-called horizontal mode of tooth replacement is only known from the monophyletic taxon Tethytheria, which includes manatees (Sirenia), elephants (Proboscidea), and the extinct group Desmostylia. Although the mentioned mode of tooth replacement occurs in all three subgroups, it is absent in the most basal representatives of all three subgroups, indicating a triple evolution of this character state by convergence. Such remarkable parallelisms in closely related groups were occasionally regarded as possible evidence for monophyly, in spite of being independently evolved ("underlying synapomorphies" sensu SAETHER). This is of course a rather dubious kind of evidence, although it might be correct in some cases. Basically the term parallelism is just representing a causal explanation for certain cases of convergences. This term is more or less superfluous, just like the distinction between analogy and homoiology, since all these terms refer to the same phenomenon of convergence.

reversal: The secondary presence of an apparently "primitive" character state, which is not homologous with the actual plesiomorphic state. Consequently this state has to be regarded as a derived (apomorphic) condition, that is only looking like a plesiomorphy! Example: The aquatic mode of life of all "fishes" is a symplesiomorphy compared to the terrestrial life of tetrapods, while the aquatic mode of life of whales has to be regarded as a reversal, thus as an autapomorphy of whales. Reversals quite often represent reductions, that are related to a sophisticated mode of life (parasites, cave animals, etc.), e.g. the secondary absence of structures like eyes or legs. Example: Having no legs is a symplesiomorphy of invertebrates, but an autapomorphy of snakes. Besides reductions, reversals can also involve the reappearance of structures or behaviours, that were already completely reduced, or the return to ancient

character states. Both phenomena might be explained in many cases by a reactivation of the preserved, but previously suppressed, genetic information (like atavisms). Convergences can only explain relatively simple structural similarities, since it is very unlikely that identical complex structures can evolve by convergence, e.g. that a marine tetrapod secondarily acquires fins that are truly similar to the fins of a coelacanth (Dollo's rule). Out of this reason reversals are generally restricted to secondary losses (reductions), superficial similarities that are related to a similar mode of life (analogies like the aquatic mode of life in the example), or to the reappearance of relatively simple structures (caused by genetic reactivations or convergences).

"living fossils": This term, which is by no means unproblematic (indeed it is self-contradictory), is often used for recent species or supraspecific taxa that satisfy the following criteria:

- presence of many plesiomorphic character states, compared to the recent sister-group, and generally only few inconspicuous autapomorphies (see heterobathmy)
- existence of only one or few recent species, compared to numerous fossil species of the same clade or at least a similar grade
- relict type of distribution of the recent representatives, often a disjunct distributional pattern
- recent sister-group with relatively numerous species
- apparently an intermediate position between two different recent groups or an extinct group and a recent group, caused by symplesiomorphic similarity with one group and a synapomorphic similarity with the other group (see heterobathmy)

Examples for such "living fossils" are within molluscs the genera *Nautilus* (Nautiloidea) and *Neopilina* (Monoplacophora), within actinopterygid fishes the groups *Cladistia* (e.g. *Polypterus*), *Ginglymodi* (e.g. *Lepisosteus*) and *Halecomorphi* (*Amia*), within sarcopterygid fishes the lungfishes (*Dipnoi*) and the coelacanth (*Actinistia*: *Latimeria*), within lepidosaurs the tuatara (*Rhynchocephalia*: *Sphenodon*), within mammals the *Monotremata*, within arthropods the *peripatus* (*Onychophora*), or within dragonflies the genus *Epiophlebia* ("*Anisozygoptera*"), the family *Petaluridae* (*Anisoptera*) and the genus *Hemiphlebia* (*Zygoptera*). Certain groups of organisms only satisfy some of the mentioned criteria and consequently hardly have been regarded as "living fossils", like for instance all bacteria and all protozoans, or the *Acrania* (*Branchiostoma* = *Amphioxus*) and hagfishes (*Hyperotreta*: e.g. *Myxine*). If one would only look at the skeleton of the arms, man would be something like "living fossils" among placental mammals too, compared to the derived skeletons in bats, whales, ungulates, etc.

logical class (versus logical individual): A group of things (e.g. organisms) that satisfy certain membership criteria, that have been defined by man. Logical classes do not really exist in the physical world, they are just inventions of the human mind. Logical classes do not bear proper names (such as "Canada"), but universal names (such as "country"). Paraphyletic and polyphyletic groups of organisms are such logical classes too.

logical individual (versus logical class): A particular thing that really exists in the outside world, independent from any human recognition ("the moon is still there even if one does not look at it"). Such logical individuals are for instance the Peter-Paul-Cathedral in Rome, the state Canada, the language English, a particular organism (the individual of everyday language), but as well a particular biospecies. Individuals do have a unique origin, a unique fate and a unique end. Individuals can not be defined (like logical classes), but only be discovered, described, and baptized with proper names (*nomina propria*, contrary to the universal names of logical classes). Since monophyletic groups do have a unique origin, fate and end, but lack the internal cohesion that is required if all parts of an individual shall share the same fate (such as in organisms and biospecies), they should rather be called "historical entities" (*sensu* WILEY) than logical individuals.

molecular systematics: A quite unfortunate term that has been introduced for the use of molecular data as characters for phylogenetic analyses. These include methods that are based on overall similarity (Phenetics), like electrophoresis, immuno-distance and DNA-DNA-hybridisation, as well as methods that are based on parsimony (Cladistics), like restriction-site-analysis and sequencing (proteins, RNA, DNA). Actually the term "molecular systematics" is quite misleading, since there exists of course only biological systematics, which is using different methods and different sources of evidence. One could as well coin terms like "osteological systematics" for studies based on skeleton characters, or "behavioural systematics" for studies based on behavioural characters. It has been claimed that molecular data (especially DNA-sequences) are superior to morphological characters, because they are much more numerous, they are easier to define (they are linear rather than multidimensional), and they are representing the basic entity of evolution (the genome). Nevertheless the promises have not been fulfilled yet, and there are only few solutions to old phylogenetic problems that came from molecular evidence, compared to the numerous published "molecular" phylogenies that appear to be quite absurd, e.g. the recent claim that guinea-pigs should not be rodents but the sister-group of camels!

monophyletic group (= monophylum): In a hierarchical system of descent, an ancestor (stem-species) and all of his descendants (descendant species) together form a closed community of descent that is called a monophyletic group (*sensu* HENNIG; = holophyletic group *sensu* ASHLOCK) or monophylum. Monophyletic groups can be discovered (not defined!) by synapomorphies. The term monophyly is always referring to groups of hierarchically reproducing entities (species) and consequently can not be applied to (or within) a single biospecies or even to a single organism. Therefore there exists nothing like a monophyletic or a paraphyletic biospecies, although there are of course numerous biospecies that do possess autapomorphies. The only exception is a monophyletic group of allopatric populations, that are classified as subspecies (they are rather semi-species) within a single (super-)species because of their potential (!) interbreeding capabilities, since in this case the relationships between these populations can be hierarchical too. If such a group of allopatric populations is paraphyletic, it should be splitted up into several (semi-)species, even if they still could potentially interbreed. In case of uniparental organisms the resulting closed communities of descent are usually called "clones".

Monophyla (*sensu* HENNIG) are real spatio-temporal entities of nature, that exist totally independent from our possibilities to discover and distinguish them by certain characters. Since they possess some of the properties of logical individuals, but completely lack the internal cohesion that is usually postulated for the latter, they should be regarded as so-called "historical entities" (*sensu* WILEY). Groups that include a common ancestor and some (but not all) of its descendants, were often called "monophyletic" too (monophyla *sensu* MAYR or REMANE), but these do not really exist in nature (independent from human recognition), but are mere constructions of the human mind (logical classes), that are arbitrarily defined by certain characters. According to

this untenable definition of monophyly, any group of organisms whatever would be "monophyletic", provided that life originated only once on earth. Example: A group including all roses and all eagles would be "monophyletic" too, since they do possess a common ancestor in the stem-species of all eukaryotic organisms. Of course such a group only makes biological sense if all other eukaryotic organisms, that all descended from the same stem-species, are included in this group, which is then representing the monophyletic taxon Eukaryota.

Please note: If a monophyletic group is surrounded with a circle in a phylogenetic tree, only one branch is entering the circle, and none (!!!) is leaving the circle.

outgroup comparison: This procedure is more or less a fitting of new characters into well supported phylogenetic trees (character optimization on a given cladogram). Being based on the so-called principle of parsimony the outgroup comparison represents an indirect method to polarize a new character. The existence of evidence (synapomorphies) for the monophyly of the group in study is essential, as well as the knowledge of some of their closer phylogenetic relatives. If a character has two or more states within the (monophyletic) group in study, the state that is also occurring in the close phylogenetic relatives, which are not members of the monophyletic group in study, is regarded as plesiomorphic state. Example: The monophyly of mammals is well supported by a lot of derived characters (e.g. hairs, milk glands, heterodont dentition, secondary jaw articulation, etc.). It is also undisputed that all other amniote vertebrates (lizards, snakes, turtles, crocodiles and birds) are more closely related to mammals than all other recent organisms. Within mammals there are two different modes of reproduction: egg laying (ovipary) in monotremes (Prototheria) and vivipary in marsupials (Metatheria) and placental mammals (Eutheria). Since ovipary is also the mode of reproduction in the other amniotes (with rare exceptions) and even in most other animals, the ovipary of monotremes has to be regarded as a symplesiomorphy, that cannot demonstrate the monophyly of Prototheria, while vivipary is a shared derived character (a potential synapomorphy), that could demonstrate the monophyly of the taxon Theria (Metatheria and Eutheria). This method of phylogenetic outgroup comparison is something fundamentally different from the so-called outgroup-method in computer-cladism, in which an unrooted most parsimonious tree is calculated and a posteriorly rooted by choice of one of the analysed taxa as the outgroup (often a hypothetical ancestor with all character states coded as "0"). The latter procedure should better be termed "outgroup-rooting" (see Pattern-Cladism).

paraphyletic group (= paraphylum): A non-monophyletic group, that has been defined on the basis of shared "primitive" character states (symplesiomorphies), e.g. "Prokaryota", "Protozoa", "Invertebrata", "Apterygota", "Hemimetabola", "Anamnia", "Pisces", and "Reptilia". Paraphyletic groups do well possess a common stem-species and even include all parts of the phylogenetic tree between this stem-species and the recent representatives, but they do not include all descendant-species of this stem-species. In most cases such paraphyletic groups represent evolutionary "grades", such as fishes or reptiles. Nowadays paraphyletic groups, if retained at all, should be clearly indicated by quotation marks as paraphyla. From the viewpoint of Phylogenetic Systematics paraphyletic taxa have to be strictly dismissed and eliminated from our biological classifications. The unmasking of paraphyletic taxa and their splitting up into monophyla is therefore one of the foremost tasks of Phylogenetic Systematics.

Paraphyletic groups are not only completely arbitrarily delimited and consequently not representing natural entities (see logical individuals versus logical classes), but they even lead to significant misunderstandings and erroneous conclusions, e.g. if it is claimed that "mammals are rooted in reptiles" or that "fishes are the ancestor of tetrapods". Of course there exists nothing like supraspecific ancestors but only individual stem-species! The misleading effect of paraphyletic groups can become even worse if further typological statements are involved, like in the following example: In many current textbooks of biology one can still find statements like "some fishes do possess gills and other fishes do possess lungs", and based on the typological assumption that "fishes are more primitive than tetrapods" one can even find the statement that "the lungs of tetrapods are derived from the air-bladder of fishes", although in reality the lung is representing a "primitive" character, which has been retained in polypterids (Cladistia), lungfishes (Dipnoi) and Tetrapoda as symplesiomorphy, while the air-bladder represents a derived character (synapomorphy) of a rather "modern" subgroup of actinopterygid fishes, which evolved from the pre-existing lungs. Since taxa are commonly used to generalize results that were achieved by the analysis of a few single organisms, it is self-evident that paraphyletic taxa must lead to erroneous generalisations, simply because some of their members are closer related to taxa outside the paraphyletic group than to other taxa within this paraphyletic group. Generalisations can only be expected to be likely correct if they are made for taxa whose members are closer related with each other than to any non-member; - this is only the case in biospecies and monophyla, but not in paraphyla!

Please note: If a paraphyletic group is surrounded with a circle in a phylogenetic tree, there is only one branch entering the circle, but at least one branch is leaving it.

parsimony: The so-called principle of parsimony (also known as "Ockham's Razor") requires that ad hoc assumptions should be minimized as far as possible in scientific explanations of natural phenomena. This means for Phylogenetic Systematics that from the millions of theoretical possible cladograms those should be preferred that minimize the number and/or the weight of necessary assumptions of non-homology (homoplasies). The principle of parsimony is an epistemological principle, and thus should be viewed as a tool, not as a claim that evolution always took the most parsimonious way. This principle is just taking into account that there is no other possibility than parsimony to choose between different alternative hypotheses, that explain singular historical happenings, that can only be reconstructed, but not repeated and tested like scientific experiments. Evolutionary biology in general and Phylogenetic Systematics in particular clearly are historical sciences! Nowadays there exist several software-packages (PAUP, HENNIG-86, PHYLIP and MacClade) for the computer-aided calculation of most parsimonious trees (MPT's) from large data sets (numerous taxa and characters), that can be especially large in case of DNA-sequences as characters. The biggest problem of this computer-cladism is the circumstance that characters are either regarded as unweighted (which means in reality "equally weighted") or that more or less arbitrary discrete weights are assigned to the characters. Since there is no rational way to decide if a character should have the weight 0.3, 1, 17 or 16345, the preference of a most parsimonious tree (in the computer-cladistic sense) which is only some steps shorter than other possible trees appears to be simply nonsense (see character weighting). The subjective choice of characters and the arbitrary delimitation of characters (e.g. lumping or splitting of character complexes) is already representing a (often unreflected) weighting procedure, which makes it quite improbable that all characters have indeed the same weight (= the same probability that they are indeed representing homologies), and it makes it impossible to assign discrete weights to the characters too. Consequently the over-reductionist view of the principle of parsimony in computer-cladistics, as a mere minimization of the number of homoplasies, has to be dismissed as unwarranted formalism that has no place in a science that is striving for the recognition of natural phenomena.

Pattern-Cladism (= Transformed Cladism): A rather new approach to biological systematics, founded by NELSON and PLATNICK ("New York Cladists"), which is claiming to be a further development of HENNIG's Phylogenetic Systematics, but it is differing from the latter in several fundamental points. The central issue of Pattern-Cladism is the conception that a hierarchical order of organisms can be discovered from the pattern of their characters alone, without any recourse to the theory of evolution. This separation of "pattern and process", which are regarded as two opposite aspects of nature which can not both be considered in the biological system, shall avoid an alleged circular reasoning between evolutionary theory and biological systematics, which shall occur if the former is postulated as basis of the latter as it was done by WILLI HENNIG with full intention and good reason. The discovery procedure of pattern-cladistics is a mere computer-aided parsimony-analysis of the character pattern, using a large set of taxa and equally weighted and unpolarised characters. Only that cladogram is accepted, that requires the smallest number of character transformations or steps ("most parsimonious tree" = MPT). The computer is primarily calculating an unrooted tree, that is a posteriorly rooted by choice of one of the analysed taxa as outgroup, and by designating the root between this outgroup and the remaining part of the tree. Only by this procedure of outgroup-rooting (not to be confused with an a priori character polarisation by a true outgroup comparison) and an subsequent most parsimonious optimisation of the characters on the resulting cladogram, the characters finally become polarised and homologised, and are then interpreted in terms of symplesiomorphies and synapomorphies. If an analysis is leading to multiple most parsimonious trees of different topology, a so called "consensus-tree" is calculated that includes all dichotomies ("strict consensus") or all nestings ("Adams consensus") that are common to all MPT's, or at least occur in most of them ("majority rule consensus"). The resulting cladograms are not regarded as graphical representations of phylogenetic relationships (phylogenetic trees *sensu lato*), but as mere synapomorphy-schemes that are understood as graphical representations of the most parsimonious interpretation of the character pattern. The goals of this rather formalistic methodology, that appears to be more similar to Phenetics than to genuine Phylogenetic Systematics, are a theory-neutrality, which shall be very desirable, and an alleged falsifiability (*sensu* POPPER) of the resulting hypotheses of relationship. Unfortunately both goals are dubious and misleading: A theory-neutrality is not desirable at all, since it implies a significant loss of explanatory power, and a falsifiability (which would be desirable indeed, since scientific hypotheses have to be falsifiable according to the philosopher Karl Popper: "The Logic of Science") is beyond reach, since hypothetical reconstructions of singular historical happenings (like phylogeny) can never be falsifiable in a Popperian sense. The only significant difference between Pattern-Cladistics and Numerical Systematics (= Phenetics) seems to be the circumstance that in the former only one of the character states is used as group-defining similarity (the one that is most parsimoniously interpreted as synapomorphy), while in the latter all states (symplesiomorphies, as well as synapomorphies and even convergences) are used as group-defining similarities. Since it is beyond the scope of this glossary to discuss all the erroneous assumptions and epistemological problems of Pattern-Cladism, I refer as central critic to the general arguments against computer-cladism (see character weighting).

Phenetics: A non-phylogenetic approach to biological classification, founded by CAMIN and SOKAL. It is based on the exclusive criterion of overall similarity, without distinction of plesiomorphic and apomorphic character states. The similarity analysis is generally performed by a computerised statistical analysis (cluster-analysis and nearest-neighbour-joining) of a data matrix with the terminal taxa (OTU's = operational taxonomic units) and a large number of unweighted and unpolarised characters (= Numerical Taxonomy). The false goal of Phenetics was a totally theory neutral and allegedly objective procedure for the generation of biological classifications. Fortunately this anti-biological approach does not play any significant role in current systematic biology anymore, maybe with the exception of microbiology, especially bacteriology. Nevertheless WÄGEL (1996a) has recently demonstrated that mainstream computer-cladistics is in several aspects closer to phenetic methods than to genuine Hennigian Phylogenetic Systematics, since there is no a priori polarisation and homologisation of characters, so that symplesiomorphies and convergences can become group-defining characters, as consequence of an over-reductionist application of the principle of parsimony and a blackbox-like application of the computer analyses.

phylogeny (versus evolution): Traditionally the process of evolution was classified into an anagenesis (= transformation of structures and behaviours by mutation and selection, or genetic drift) and a cladogenesis (= multiplication of species by a separation of populations and their subsequent divergent development, including the final development of reproductive isolation mechanisms). Anagenesis is thus referring to the change of properties of populations (biospecies), while cladogenesis is referring to the generation of new distinct biopopulations through speciation. The term phylogenesis was often used as synonym of cladogenesis, but of course also should include anagenesis. The term evolution was mostly used as synonym of "cladogenesis plus anagenesis" too. Nevertheless a definition of evolution as "transformation of organismic properties (anagenesis) including the causal processes like mutation, selection, genetic drift, separation and isolation, as well as annidation" would make much more sense. Phylogenesis is thus best understood as the general process of evolutionary change (anagenesis) together with the general process of speciation (cladogenesis), while the term phylogeny refers to the resulting history of organisms on earth as singular historical fact. Only groups of organisms (biospecies and monophyla) do have a phylogeny, while only properties (e.g. organs or behaviours) do have an evolution. Statements like "the phylogeny of lungs" or "the evolution of horses" consequently have to be regarded as incorrect. The correct statements would be "the evolution of lungs" and "the phylogeny of horses".

phylogenetic relationships (versus tokogenetic relationships): The (generally hierarchical) genealogical relationships between separated biopopulations, biospecies or monophyletic groups (see relationship), contrary to the reticulate genealogical relationships between the individuals within a biopopulation or biospecies.

Phylogenetic Systematics (versus Cladistics): A methodology, described by Prof. WILLI HENNIG, for the reconstruction of phylogenetic trees and the discovery of monophyletic groups by the exclusive use of shared (homologous) derived character states (synapomorphies), as well as the reconstruction of the ground-plans of the discovered monophyletic groups. In case of conflicting evidence the principle of parsimony (in a wide sense, not in the reductionist mainstream-cladistic sense) is used to decide between the alternative hypotheses. Phylogenetic Systematics also advocates the translation of the discovered phylogenetic relationships into a hierarchical classification of organisms, which should exclusively include biospecies and monophyletic groups of such species, but no polyphyletic and paraphyletic groups. Biospecies and monophyla are regarded in Phylogenetic Systematics as real entities of nature (logical individuals), that can be discovered and described, and not as arbitrarily defined logical classes. Like individual organisms these individual entities do have an individual origin, an individual fate, and an individual end. Since the application of Hennigian methods requires entities with hierarchical relationships (see tokogenetic relationships), the basic entity of Phylogenetic Systematics can only be the biospecies, since below the level of the biospecies the relationships become reticulate instead of hierarchical. In the anglo-american region the term "Cladistics" or "cladism" is often used

synonymous with "Phylogenetic Systematics". Because of significant methodological differences between mainstream-cladism and genuine (consequent) Phylogenetic Systematics, the term Cladistics should better be restricted to the computerised generation of cladograms with the principle of parsimony, generally correlated with a dismissal of a priori character weighting and a priori character polarisation. Contrary to Cladistics, which is only aiming at the calculation of most parsimonious cladograms from large data-sets (the resulting tree topologies are often accepted according to a kind of "black box"-principle), the goal of consequent Phylogenetic Systematics is the reconstruction of phylogenetic argumentation schemes, in which all branching points are convincingly supported by strong characters. The main advantage is that the resulting phylogenetic hypotheses as well as the used evidence are presented in a way that makes them open to criticism and discussion.

The so-called "Transformed Cladism" or "Pattern Cladism", founded by NELSON and PLATNICK, is striving to avoid an alleged circular reasoning between evolutionary theory and biological systematics, with the logical consequence that "Pattern-Cladistics", since not being embedded in the total complex of biological theories, is lacking a sound theoretical justification as well as any explanatory power. The reasoning of pattern cladists could be compared with astronomers, that would explore stars as "lights in the sky", without necessarily assuming that they indeed represent distant suns.

plesiomorphic (versus apomorphic): A "primitive" character state, that is taken over from an ancestor without change, is termed the plesiomorphic state. This property is relative (just like apomorphic), since it is depending on the compared character state and the hierarchical level in focus. A plesiomorphic state is only plesiomorphic compared to a derived state, but it can be apomorphic compared to an even more plesiomorphic state. Example: The fore leg of non-flying tetrapods is plesiomorphic compared to the wings of pterosaurs, birds and bats, but it is apomorphic compared to the pectoral fins of "fishes". Shared plesiomorphic similarities can be homologous (symplesiomorphies) or non-homologous (reversals). KLAUSNITZER & RICHTER (1981) suggested the (synonymous) terms "plesiotypic" and "symplesiotypic", since the suffix "-morphic" is strictly speaking only correct for morphological characters. The term "plesiomorphic" or even "primitive" (the latter term should be avoided anyway) should only be used for character states, but never for organisms or taxa (taxa that originated from very old splitting events and have retained a lot of plesiomorphic states should rather be called "ancient groups"), since all taxa always possess a mixture of plesiomorphic and derived character states (compare living fossils).

polarity of characters: The polarity of a character specifies which of its character states has to be regarded as plesiomorphic and which as apomorphic. The polarity can be directly deduced from the stratigraphic or ontogenetic precedence of states, or indirectly deduced with the method of outgroup comparison. Naturally all these criteria and methods might fail, since the fossil record is fragmentary and potentially misleading, and ontogenesis is complicated and can be misleading too (e.g. in case of heterochronies or caenogenetic larval adaptations). Since the most popular method of outgroup comparison is based on a pre-existing knowledge of the phylogenetic relationships, it is not suited as a final criterion of character polarity (problem of infinite regression, also well known as so-called "Münchhausen-Trilemma"). From an epistemological point of view these final criteria are the stratigraphic evidence (the oldest fossils a protozoans and fossil man are rather young) and the ontogenetic evidence (all multicellular organisms develop from a single celled stage), as well as the theoretical conclusion that a scientific explanation of life necessarily implies an evolution from simple to more complicated organisms (as general tendency, not in every particular case!), since a reverse view would imply a creational act by some kind of god.

polyphyletic group (= polyphylum): A non-monophyletic group, that was defined on the base of shared but not homologous character states (convergences). Examples for polyphyletic groups would be a grouping of pterosaurs, birds, and bats as (hypothetical) taxon "flying vertebrates", the old taxon Pachydermata for a grouping of the thick-skinned hippos, rhinos and elephants, or the taxon Haemothermia (recently endorsed by LOVTRUP and GARDINER) for a grouping of haemothermic birds and mammals. All these groups share derived characters (e.g. fore legs developed as wings, thick skin, or haemothermy) but these are not homologous but originated several times by convergence.

Please note: If a polyphyletic group is surrounded with a circle in a phylogenetic tree, there is always more than one branch entering the circle and none, one or several branches are leaving it.

semaphoront: The object of a phylogenetic-systematic study is according to WILLI HENNIG not the individual organism as such, but always only an organism at a certain, relatively short, period of time or even only a point of time in its individual development (ontogenesis). This study object has been termed semaphoront by HENNIG, which means "character bearer". The complete set of characters of a semaphoront has been termed its holomorph. A minor problem of the semaphoront-concept is the simple circumstance that it was mainly developed for morphological characters, while some classes of characters do only exist in the time dimension (e.g. physiological processes, behaviours, and ontogenetic sequences, etc.) (R. SCHOCH. pers. comm.), and other classes of characters even are totally independent from any semaphoront-stage (e.g. sequences of DNA, RNA, or proteins).

sister-groups: Two monophyla or two species, that together form a monophyletic group, thus originated from the same speciation event (mostly dichotomic splits of a stem-species), have been termed sister-groups by HENNIG. AX (1984) suggested the (synonymous) term "adelpho-taxa" which fortunately never became very popular. The discovery of sister-group relationships is one of the foremost goals of Phylogenetic Systematics. Since the fossil record will never be complete, the term sister-group usually only makes sense if it is restricted to recent taxa. The fossil relatives are referred to as stem-group representatives. Example: Crocodiles are the sister-group of birds, while dinosaurs (paraphyletic!), which are closer related to birds than crocodiles, are belonging to the stem-group of birds.

species: One has to distinguish the particular species (individual natural entity; e.g. mankind), the particular taxon (individual hypothesis with designation of a proper name; e.g. the taxon *Homo sapiens*), and the category "species" that is defined by a particular species concept, that defines a set (logical class), which for instance includes all closed reproductive communities (biospecies). The species-taxa are not only the traditional basic entities of biological classifications, but also the most important entities for generalisations in all biological sciences. Unfortunately there exists no species concept, that could be equally applied to all kind of organisms (uniparental as well as biparental). Besides uniparental organisms, the biggest problems concern allopatric and/or allochronic populations, "Rassenkreise", and the boundaries of a species in the time dimension (e.g. the old problem of the "surviving stem-species"). Scientific species names are always binominal, - genus and



species are obligatory categories of the International Rules of Nomenclature. The generic name is written with an initial capital letter, and generic as well as the specific names are generally written in italics in scientific publications. Concerning the species concept in Phylogenetic Systematics see biospecies.

stem-group / stem-group representatives: A group of all the fossil species, that are closer related to a recent monophyletic group than to its recent sister-group, but are older and more basal than the last common stem-species of all recent representatives, has been termed the "stem-group" of a recent monophylum. That means that none of the species of the stem-group is closer related to any recent subgroup of the monophylum. All organisms that belong to the stem-group are referred to as "stem-group representatives" of the recent monophylum. Consequently no recent species can be a stem-group representative, and every fossil species can at best belong to the stem-group of one recent monophylum. To recognize stem-group representatives as such, they have to possess at least one of the autapomorphies of the recent monophylum, but they usually will not possess its complete set of autapomorphies (compare heterobathmy). A stem-group is usually a paraphyletic group, since it is including all fossil relatives that existed between the split of a recent monophylum from its recent sister-group and its division into the recent subgroups. These two events can be quite remotely separated in time; e.g. the origin of the monophylum Mammalia (= Synapsida) is very old (Upper Carboniferous), while its subdivision into Monotremata and Theria (Marsupialia plus Placentalia) is relatively young (Upper Cretaceous). Because of their paraphyletic status stem-groups are not formally named as taxa, but the stem-group concept is still very useful, since it allows a fuzzy phylogenetic classification of fragmentary fossils, of which the precise position in the phylogenetic tree might never been determined with sufficient certainty. Stem-group representatives can be either direct ancestors of the recent monophylum (species of the stem-line = stem-species) or they can belong to extinct side-branches of the stem-line. If stem-group fossils lack any autapomorphies that would identify them as side-branch-species, it is principally impossible to decide if they indeed represent stem-species, that of course never had autapomorphies, or if they are side-branch-species of which the autapomorphies were simply not preserved (absence as artefact). A group of fossil organisms, that was incorrectly united because of numerous symplesiomorphies, but includes representatives of the stem-groups of different recent monophyla, has been termed "false stem-group" by HENNIG (e.g. the Thecodontia, that include stem-group representatives of all archosaurs, as well as of crocodiles and of birds). The monophyletic group of the recent monophylum plus its complete stem-group has been termed the "pan-monophylum" by LAUTERBACH, while the recent monophylum (without its stem-group) has been termed the crown-group by JEFFRIES.

symplesiomorphy (versus synapomorphy): Shared "primitive" (= plesiomorphic) similarities that are regarded as homologous are termed symplesiomorphies. These symplesiomorphies do not represent any evidence for a close phylogenetic relationship (monophyly) of the groups that share these characters. The term symplesiomorphy is only used if one is referring to the shared similarities of several compared taxa, e.g. the presence of legs in all lizards (symplesiomorphy), compared to the secondary absence of legs in all snakes (synapomorphy). Equally the primary absence of feathers and hairs in all groups that have traditionally been united as "reptiles", has to be regarded as a symplesiomorphy of these organisms. A certain problem is the application of the term "homologous" to the absence (primary or secondary) of structures or behaviours, since contrary to other homologies these "absence-homologies" cannot be recognized a priori by similarities of certain features, but only by an interpretation of the total character pattern on a well supported phylogenetic tree (cladogram) using the principle of parsimony (compare reversals). Nevertheless the secondary absence of legs in snakes has to be regarded as "homologous" since it is not regarded as a multiple convergent reduction, but as a synapomorphy of all snakes, that is defined homologous derived similarity.

synapomorphy / autapomorphy (versus symplesiomorphy): Shared derived (= apomorphic) similarities that are regarded as homologous are called synapomorphies, e.g. the presence of hairs in Monotremata, Marsupialia and Placentalia. Such synapomorphies demonstrate the close phylogenetic relationship (monophyly) of two or more species or monophyletic groups. The term synapomorphy is only used if one is referring to several compared taxa. The term autapomorphies (= "Spezialhomologien" sensu REMANE) is used if one is referring to the derived ground-plan characters of a particular monophyletic taxon. Example: Feathers are a particularity (= autapomorphy) of the monophyletic taxon Aves (birds), and a community (= synapomorphy) of all different species of birds (incl. Archaeopteryx).

biological systematics: The aim of biological systematics is the classification of the immense diversity of life into a general reference system, which enables communication about particular groups of organisms and the storage and retrieval of informations about these groups. The entities of this biological classification are of utmost importance for all other biological sciences, since they are used as entities of generalisation for all known biological facts. Systematic biology consequently can be regarded as basis of all biological sciences, as well as their "crown", since it represents the most important integrating discipline which is using the results of all others (evolutionary theory, genetics, ecology, ethology, physiology, morphology, etc.) for the formation of the general reference system. On the basis of the Darwinian theory of evolution, only a consequent phylogenetic-systematic classification is suitable to satisfy the above mentioned claims, since only groups that reflect a true genealogical relationship (biospecies and monophyletic groups and clones) can be expected to allow proper generalisations of results that were achieved by the study of singular sample organisms. Biological systematics therefore should always be understood in terms of Phylogenetic Systematics, because otherwise it would rather represent an art or a kind of book-keeping than a natural science. Charles Darwin himself already remarked in the 13. chapter of his "Origin of Species" that he believes that the arrangement of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural. Since there can only exist one correct phylogenetic tree of life, a consequent phylogenetic (cladistic) classification will finally lead to a more stable classification, which is of course very desirable out of practical reasons.

Although the terms "classification" and "taxonomy" are more or less synonymous with "systematisation", the term classification is frequently restricted to all nomenclatorial matters (naming of new taxa, synonymies, Rules of Nomenclature, etc.), while the term taxonomy is often used in the sense of alpha-taxonomy, that means the description of new species level taxa and their subspecific subdivision. Phylogenetics is mostly understood as the reconstruction of the phylogenetic relationships between such species.

taxon (pl. taxa): A group of organisms that has been formally named with a scientific (Latin or Greek) proper name. In Phylogenetic Systematics only those groups may be named, that reflect real entities of nature, which means closed communities of reproduction with a shared genepool (biospecies) and closed communities of descent (monophyletic groups and clones). These groups are classified according to their phylogenetic relationships in a hierarchical system of superordinated and subordinated taxa (enklaptic hierarchy). The

traditional designation of formal hierarchical ranks (systematic categories), such as "class", "order", "family" and "genus" is arbitrary and unscientific, without any biological meaning, and completely superfluous. Only the species category is objectively defined by a biological criterion (biospecies concept). The other ranks are artefacts from predarwinian typology, in which the Linnean classification originated. The sole objective criterion for the designation of formal hierarchical ranks above the species level would be the absolute age of origin of the referring monophyletic taxa. Although this suggestion by WILLI HENNIG, which of course has a few problems too (e.g. the lack of information about the age of many groups), would offer very promising perspectives (easy storage and retrieval of the age of origin informations, as well as a sound comparability of the taxa in terms of speed of evolution), it unfortunately was completely unsuccessful up to now. The reason for this ignorance seems to be rather a psychological than a scientific one, since the only obstacle was the destruction of the traditional (unscientific) association of certain ranks with certain taxa. Another alternative is to discard formal hierarchical ranks at all, and to subordinate the taxa according to their relative hierarchical position with appropriate indentions in a written hierarchical sequence (eventually supplemented by a numerical code as suggested by HENNIG, 1969):

System of recent elephants with ranks:  
 classis: Mammalia  
 subclassis: Monotremata  
 subclassis: Theria  
 infraclassis: Marsupialia  
 infraclassis: Placentalia  
 ordo: Proboscidea  
 familia: Elephantidae  
 genus: Loxodonta  
 spezie: *L. africana*  
 genus: Elephas  
 spezie: *E. maximus*

System of recent elephants without ranks:  
 (1.) Mammalia  
 (1.1.) Monotremata  
 (1.2.) Theria  
 (1.2.1.) Marsupialia  
 (1.2.2.) Placentalia  
 (1.2.2.1.) Proboscidea  
 (1.2.2.1.1.) Elephantidae  
 (1.2.2.1.1.1.) Loxodonta  
 (1.2.2.1.1.1.1.) *L. africana*  
 (1.2.2.1.1.2.) Elephas  
 (1.2.2.1.1.2.1.) *E. maximus*

tokogenetic relationships (versus phylogenetic relationships): The parental (genealogical) relationships between the individual organisms within a species. Contrary to the phylogenetic relationships between different species, the tokogenetic relationships within biospecies of biparental organisms are not hierarchical but reticulate. In uniparental organisms (agamo-species) the parental relationships of the individual organisms are hierarchical too, so that a distinction between tokogenetic and phylogenetic relationships is not possible. Since synapomorphies can only correctly diagnose monophylic groups if the relationships are strictly hierarchical, the terms "synapomorphic character" and "monophyletic group" cannot be applied to a single biospecies or even within such species. The only exception is a group of allopatric populations, that are classified as subspecies within a single species because of their potential (!) interbreeding capabilities, since in this case the relationships between these populations can be hierarchical too.

Example: Grey mice are reared in a laboratory for several generations. Because of an albino-mutation, one day a white mouse Blondy is born. The albinism is inherited according to the laws of MENDEL to the descendants of Blondy. Finally the laboratory population includes a certain percentage of white mice that are all descendants of Blondy. Although the albinism originated only once in this population, and consequently has to be regarded as derived and homologous, this character cannot be called a synapomorphy, since all white mice do not form a closed community of descent (monophyletic group), that means some white mice are closer related to some grey mice than to some other white mice.

A population of interbreeding biparental organisms, that is separated from other such populations, is developing "genetical exclusiveness" after a sufficient number of generations. This means that at a given point of time every individual member of the population is closer related to any other member of this population than to any individual organism in other populations. For this phenomenon I here suggest the new term "tokophyly" and "tokophyletic". Monophyla and biospecies mostly are tokophyletic, but also populations within a biospecies can become temporally tokophyletic at least.

relationship (versus similarity): It must be distinguished between a mere phenetic relationship, which is based on overall similarity, and a true genealogical relationship, which is based on common ancestry. Furthermore one has to distinguish between horizontal indirect relationship, which is based on shared ancestors (sister-group-relations) and vertical direct relationship, which is based on parental relationships (ancestor-descendant-relations). A confusion of these terms has often led to misunderstandings. Phylogenetic Systematics deals almost exclusively with indirect relationships, since direct ancestors are hardly discoverable out of theoretical and practical reasons (see cladogram versus phylogenetic tree).

The so-called "genetic relationship" (sensu MAYR) means, that two species are regarded the more related the more similar are their genotypes (MAYR: "we do not classify phenotypes but genotypes"). Genetic relationship in this sense is nothing but a phenetic relationship, based on the overall similarity of the genome. This phenetic attitude leads to curious consequences, e.g. one-egg twins would be regarded as closer related with each other than each of them with its parents or children.

In Phylogenetic Systematics the term (phylogenetic) relationship is defined as follows: A taxon A is more closely related with a taxon B than with a taxon C, only if A and B are the descendants of a common stem-species, which is not a stem-species of C. Phylogenetic relationships are therefore defined by the "recency of common descent", thus in exactly the same way as the genealogical relationships (tokogenetic relationships) between individual organisms (the common sense notion of relationship in everyday life). The logical consequence of the above given definition is, that statements about phylogenetic relationships only make sense if they refer at least to three species or monophyletic groups ("three taxa statements"). Statements like "taxon A is closely related to taxon B", which are still common place in biology textbooks, are rather meaningless, if it is not specified compared to which other taxon these two taxa shall be more closely related.

character weighting: The term character weighting is referring to a procedure that is allowing a choice between conflicting hypotheses of homology and monophyly, according to certain weighting criteria, by assigning higher weight to some characters than to other conflicting characters. The object of weighting is not the character as such (indeed true synapomorphies can not have different weights!), but the truth probability of the hypothesis of homology, that is involved in every character definition. Since statements of similarity are the primary cause for all assumptions of homology, the very different degree of complexity of these statements of similarity implies a different truth probability for the resulting hypotheses of homology, and consequently a different weight of the referring characters. The basic rationale behind this statement can be easily explained by the following example: If there are two different pieces of paper, each with an identical single letter written with a typewriter on it, one

would not necessarily assume that they were written by the same person, because the chance that two people independently type the same letter is relatively high (1:26). On the other hand if there would be an identical poem written on these two pieces of paper, one would of course be quite sure that they were derived from the same source, simply because it is unlikely that two persons independently write exactly the same poem. Weighting does not mean that some synapomorphies are better than others, but only that some hypotheses of synapomorphy are more likely to be correct than others. In other words: different weight means different likelihood of convergence. In case of conflicting evidence (otherwise there is no problem anyway) one should of course rather prefer those hypotheses that are supported by stronger evidence (= evidence that is very probably correct) than those that are supported by weaker evidence (= evidence that is more likely to be incorrect). This kind of weighting does not need any knowledge of the evolutionary process, and it does not make any assumptions about it either, since it is exclusively based on properties of the characters and their pattern of occurrence.

The most important criteria for an a priori weighting of characters (a weighting that is preceding the phylogenetic analysis) are the compatibility and structural complexity of the characters. Compatibility refers to the number of conflicting characters, what means that those characters that conflict with fewer other characters are regarded as stronger evidence, than characters that conflict with more other characters. Weighting on the basis of structural complexity means that simple structures that might easily evolve by convergence, or superficial similarities that might be based on an insufficient analysis, are regarded as weaker evidence, than characters that are so complex that they could hardly be non-homologous, and that are so well investigated that the proposed similarity is not just superficial. Since there can be no complexity whatever in the mere absence of something (negative similarities), reductions are normally regarded as rather weak evidence (compare reversals). In molecular biology there is sometimes a further criterion available for a priori weighting, since the different probabilities of certain mutations are known in some cases (e.g. transitions are much more frequent than transversions, which was considered in the so-called transition-transversion-parsimony-algorithm). The most important criterion for so-called a posteriori weighting (weighting on the basis of the result of a phylogenetic analysis) is congruence, which is nothing else than parsimony. This means that characters that are less homoplastic in the resulting cladogram (characters with a CI closer to 1), are regarded as stronger evidence than characters that are more homoplastic (CI closer to 0) and thus imply many convergent origins or many convergent losses. All available weighting criteria should be used to estimate the relative weight of a character.

The representatives of so-called computer-cladism and Pattern-Cladism generally reject character weighting, or at least any sort of a priori weighting, because it shall be a much too subjective procedure. Nevertheless their dogma of (alleged) non-weighting is nothing but a beautiful dream, since the choice of characters and the delimitation of characters already involves so many subjective decisions, that these characters are already strongly weighted as soon as they are chosen and formulated. Furthermore the alleged non-weighting indeed represents an equal-weighting. This is even more problematic since an exactly equal truth probability of all involved homology hypotheses certainly represents one of the least likely cases one can think of. The issue of character weighting of course has most important consequences for the application of the principle of parsimony. The restriction of parsimony to a statistical analysis of the character pattern with a mere numerical minimization of homoplasies ("cladistic parsimony") is not only over-reductionistic, but even becomes rather absurd regarding the highly subjective impact of character choice and delimitation. Since nearly every character complex can be either lumped into a single character (e.g. "vertebrate eye") or splitted into dozens of characters (retina, cornea, iris, ciliary muscle, etc.), a most parsimonious tree can be easily overthrown by a different formulation of the same characters, unless there is no conflicting evidence at all. Objective criteria for the delimitation of characters do not exist and almost certainly never will, because they are impossible out of theoretical reasons, since every subdivision of a continuum like a body always will have to be rather artificial and subjective, and thus more or less optional. Therefore there can only be formalistic arguments but no sound scientific justification for the preference of a most parsimonious cladogram, only because it is a few steps shorter than alternative cladograms. The presented counter-arguments, simple as they are, definitely render any further discussions about parsimony algorithms (e.g. the pro and contra of so-called three-taxon-parsimony), homoplasies indices and consensus procedures absolutely superfluous and ridiculous, even though such issues currently represent the majority of publications in journals like *Systematic Biology* and *Cladistics*. Consequently the principle of parsimony (Ockham's Razor) must be understood in a much broader context, in such a way, that a cladogram that is some steps shorter than other cladograms, but has to interpret complex similarities as non-homologies, is regarded as less parsimonious than a cladogram that is a few steps longer, but treats these similarities as homologies.

The frequently heard argument by dedicated computer-cladists, that an analysis by hand should only be possible in cases of few characters without significant conflicts, while a computer-aided parsimony-analysis shall be far superior in cases of numerous characters with many conflicting evidence, is definitely ill-founded out of the reasons already explained above. Besides all this, a phylogenetic-systematic analysis is not done by hand anyway, but by brain, and therefore should be preferred over a computer-analysis without much brains. The apparent objectivity of computers is misleading, since the most important procedure is not the parsimony-analysis, but the character-analysis (careful study, choice and delimitation of the characters) in which no computers are involved anyway. One should always keep in mind one of the oldest wisdoms of computer enthusiasts: "garbage in - garbage out". Examples for the latter can frequently be found in the literature, which is full of nonsense phylogenies that are based on cladistic analyses of numerous "unweighted" characters. A central problem of computer-cladism is the fact that a parsimony-algorithm can even generate a fully resolved most parsimonious cladogram from an uninformative data set which is only containing very weak and extremely homoplastic characters. This "ability" has even been cherished by computer-cladists as "extraction of a cladistic signal from a noisy data set", while it is in reality nothing but an unwarranted transformation of noise into apparent information (even the best alchemists failed to make gold out of shit). If one cannot find convincing evidence for a phylogenetic tree in a "manual" analysis of a data set, the latter simply does not contain any useful phylogenetic information. Even if a correct tree could be calculated from this data set with a parsimony-analysis, the result would not be useful either, since the branchings are not supported by convincing evidence, what is often the case in published cladograms. Maybe the most fundamental difference between computer-cladistics and consequent Phylogenetic Systematics is, that the former is only striving to get trees from the available data, no matter how, while the latter is carefully searching for convincing evidence (strong characters) to reconstruct phylogenetic trees, that form the basis for other disciplines of evolutionary biology (historical biogeography, co-evolution, evolutionary scenarios, etc.).

#### LITERATURE:

- AX, P. (1984): *Das Phylogenetische System*. Fischer: Stuttgart / New York. 349 pp.  
AX, P. (1988): *Systematik in der Biologie*. Fischer: Stuttgart. 181 pp. (UTB 1502)  
BORICKI, H. (1996): *Evolution und Phylogenetisches System der Chilopoda (Mandibulata, Tracheata)*. - *Verh. naturwiss. Ver. Hamburg, (NF)* 35: 95-226

- FUTUYMA, D.J. (1990): Evolutionsbiologie. Birkhäuser: Basel / Boston / Berlin. xvii + 679 pp.
- HENNIG, W. (1950): Grundzüge einer Theorie der phylogenetischen Systematik. 370 pp. (reprint 1994 by Koeltz Scientific Books)
- HENNIG, W. (1969): Die Stammesgeschichte der Insekten. Kramer: Frankfurt a.M.. 436 pp., 143 figs.
- HENNIG, W. (1981): Insect phylogeny. Wiley: Chichester / New York / Brisbane / Toronto. 514 pp.
- HENNIG, W. (1982): Phylogenetische Systematik. Parey: Berlin / Hamburg. 246 pp. (Pareys Studentexte 34)
- HENNIG, W. (1984): Aufgaben und Probleme stammesgeschichtlicher Forschung. Parey: Berlin / Hamburg. 65 pp. (Pareys Studentexte 35)
- HENNIG, W. (1986): Wirbellose II Gliedertiere. in: HENNIG, W. & MICKOLEIT, G. (eds.) (1986): Taschenbuch der speziellen Zoologie Teil 2: Wirbellose 2 - Gliedertiere. Fischer: Jena und Harri Deutsch: Thun, Frankfurt a.M.. 335 pp.
- KLAUSNITZER, B. & RICHTER, K. (1981): Stammesgeschichte der Gliedertiere. Ziemsen: Wittenberg Lutherstadt. 160 pp. (Die Neue Brehm Bücherei, 541)
- KÖNIGSMANN, E. (1975): Termini der phylogenetischen Systematik. - Biol. Rdsch., 13: 99-115
- MAYR, E. (1975): Grundlagen der zoologischen Systematik. Parey: Hamburg / Berlin. 370 pp.
- MAYR, E. (1967): Artbegriff und Evolution. Parey: Hamburg / Berlin. 617 pp.
- RIEDL, R. (1975): Die Ordnung des Lebendigen. Parey: Hamburg / Berlin. 372 pp.
- RIEPPEL, O. (1983): Kladismus oder die Legende vom Stammbaum. Birkhäuser: Basel / Boston / Stuttgart. 190 pp. (Offene Wissenschaft)
- RIEPPEL, O. (1984): Die Ordnung der Natur. S. 143-167 in: RIEPPEL, O. (1984): Auf Grenzpfaden der Biologie. Birkhäuser: Basel / Boston / Stuttgart. 170 pp. (Offene Wissenschaft)
- RIEPPEL, O. (1985): Muster und Prozeß: Komplementarität im biologischen Denken. - Naturwiss., 72: 337-342
- RIEPPEL, O. (1992): Unterwegs zum Anfang. Geschichte und Konsequenzen der Evolutionstheorie. dtv: München. 269 pp.
- SCHLEE, D. (1971): Die Rekonstruktion der Phylogenese mit HENNIG's Prinzip. - Aufs. u. Red. senckenberg. naturforsch. Ges., 20
- SCHLEE, D. (1978): Anmerkungen zur phylogenetischen Systematik: Stellungnahme zu einigen Missverständnissen. - Stuttg. Beitr. Naturk. (A), 320: 1-14
- SCHLEE, D. (1981): Grundsätze der phylogenetischen Systematik (Eine praxisorientierte Übersicht). - Paläont. Z., 55: 11-30
- SCHMITT, M. (1994): Wie sich das Leben entwickelte - Die faszinierende Geschichte der Evolution. Mosaik Verlag: München. 176 pp.
- SUDHAUS, W. & REHFELD, K. (1992): Einführung in die Phylogenetik und Systematik. G. Fischer: Stuttgart / Jena / New York. 241 pp.
- WÄGELE, J.W. (1994): Review of methodological problems of "Computer cladistics" exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). - Z. zool. Syst. Evolut.-forsch., 32: 81-107
- WÄGELE, J.W. (1996a): First principles of Phylogenetic Systematics, a basis for numerical methods used for morphological and molecular characters. - Vie Milieu, 46(2): 125-138
- WÄGELE, J.W. (1996b): The theory and methodology of Phylogenetic Systematics is still evolving: A reply to Wilson. - Vie Milieu, 46(2): 183-184
- WILLMANN, R. (1985): Die Art in Raum und Zeit. Das Artkonzept in der Biologie und Paläontologie. Parey: Berlin / Hamburg. 207 pp.
- WILLMANN, R. (1989): Paleontology and the systematization of natural taxa. p. 267-291 in: SCHMIDT-KITTLER, N. & WILLMANN, R. (eds.) (1989): Phylogeny and the Classification of Fossil and Recent Organisms. - Abh. naturwiss. Ver. Hamburg, (NF) 28: 300 pp.

Journals that treat theoretical and methodological aspects of Systematic Biology:

Systematik Biology (before: Systematic Zoology / Society of Systematic Biologists  
 Cladistics: The International Journal of the Willi Hennig Society / Academic Press  
 Zeitschrift für Zoologische Systematik und Evolutionsforschung / Paul Parey  
 Journal of Molecular Biology and Evolution / Academic Press