Cladistic analysis or cladistic classification?

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With 8 Figures

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> Ein besonderes Anliegen ist es mir, zu betonen, daß die kritische Auseinandersetzung mit einem Autor dessen Verdienste nicht herabsetzen möchte. Das Gegenteil ist richtig. An unwesentlichen Arbeiten lohnt es sich nicht, Kritik zu üben. Hennig, 1969

The choice of method in a scientific discipline depends to a large extent on the objectives of that discipline. If one wants to determine which of several methods of classifying animals and plants is most productive, one must first clarify one's concept of systematics. Quite rightly, therefore, Hennig begins his *Grundzüge einer Theorie der phylogenetischen Systematik* (1950) with a discussion of the concept of systematics (pp. 1–12). Systematics, he says, is the ordering of the diversity of nature through constructing a classification which can serve as a general reference system. "Creating such a general reference system, and investigating the relations that extend from it to all other possible and necessary systems in biology, is the task of systematics" (Hennig 1966, 7 [id. 1950, 10]).

The task of the creator of classifications, thus, is to find the best possible "general reference system". However, one can and should be more specific: a classification, in contradistinction to an identification scheme, functions as a biological theory (with all the explanatory, predictive, and heuristic properties of a theory) (Mayr 1969, 79–80); it must provide a sound foundation for all comparative studies in biology, and it must be able to serve as an efficient information storage and retrieval system (Mayr 1969, 229–244).

Generalizations in large parts of biology are derived from comparisons. Comparisons of groups, however, are meaningful in evolutionary studies only when such groups are correctly formed, that is, consist of "related" elements. The construction of efficient classifications, is, thus, as stated by Hennig, a prerequisite for sound work in large parts of biology. Warburton (1967) has attempted to specify the criteria on which some classification can be judged to be superior to others in fulfilling the demand to serve as "general reference systems", as sound biological theories, and as efficient information storage and retrieval systems.

The 1930's and 1940's were dominated by the so-called "new systematics". Taxonomists concentrated their attention on the level of species and populations (*microtaxonomy*), which was also the area of principal concern of the newly emerging field of population genetics. The problems relating to the classification of higher taxa (*macrotaxonomy*) were largely neglected. There was, however, a significant minority of workers, particularly among the paleontologists and comparative anatomists, who felt that the seemingly so simple Darwinian credo that classifications should reflect "relationship" or "common descent" raised many unanswered questions. This is

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evident from several contributions to the volumes edited by HUXLEY (1940), HEBERER (1943), JEPSEN, MAYR and SIMPSON (1949), and more specifically from the writings of SIMPSON (1945) and RENSCH (1947). The intellectual ferment of this period led to the formulation of three competing theories of classification during the 1950's and 1960's, each of them claiming to be more objective and a better general reference system than the other two. These three theories, referred to by GÜNTHER (1971, 76) and described in more detail by MAYR (1969, 68–77) will now be characterized. (Unfortunately a considerable number of taxonomists have hardly any theory at all and deal with species and higher taxa purely descriptively, considering classification simply as identification systems.)

The three current theories of classification

a. Phenetic systematics (Phenetics): Organisms are classified, according to this theory, on the basis of "overall similarity". Similarity is calculated from the presence or absence of numerous unweighted characters or character states (SOKAL and SNEATH 1963). This method does not establish groups by inspection, but orders the lowest taxonomic units (usually species) into groups with the help of standardized procedures.

The methods and principles of phenetics have been critically analyzed elsewhere (MAYR 1965, 1969; JOHNSON 1970; HULL 1970).

b. Cladistic systematics (Cladistics)[1]*:* Organisms are classified and ranked, according to this theory, exclusively on the basis of "recency of common descent". Membership of species in taxa is recognized by the joint possession of derived ("apomorphous") characters. Grouping and ranking are given simultaneously by the branching points. (See below for a statement of the reasons why the designation "phylogenetic systematics" for this theory is misleading).

c. Evolutionary systematics: Organisms are classified and ranked, according to this theory, on the basis of two sets of factors, 1. phylogenetic branching ("recency of common descent", retrospectively defined), and 2. amount and nature of evolutionary change between branching points. The latter factor, in turn, depends on the evolutionary history of a respective branch, e. g., whether or not it has entered a new adaptive zone and to what extent it has experienced a major radiation. The evolutionary taxonomist attempts to maximize simultaneously in his classification the information content of both types of variables (1 and 2 above).

The synthetic or evolutionary method of classification thus combines components of cladistics and of phenetics, but in a rather different manner. It agrees with cladistics in the postulate that as complete as possible a reconstruction of phylogeny must precede the construction of a classification since groups that are not composed of descendants of a common ancestor are artifical and of low predictive value. More generally it agrees also with the cladists in the careful weighting of characters. It rejects, however, the "divisional" process of classification ("downward" classification), which is most evident in the cladists' definition of "monophyletic". Evolutionary classification rejects most of the conceptual axioms of phenetics, but agrees with it in the actual procedure of grouping by a largely phenetic approach. However, in contrast to the unweighted approach of the pheneticists, it bases its conclusions on the careful weighting of characters.

The method in which cladistic and phenetic components are combined was originated by DARWIN (see below).

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[1] The nouns cladism and cladistics have been used interchangeably. Since the ending "-ics" corresponds to that of phenetics, systematics, and genetics I now prefer to use cladistics.

Is cladistics the best theory of classification?

The cladists are sincerely convinced that their theory produces the best classifications. HENNIG, for instance, states "that the claim of phylogenetic systematics for primacy among all possible forms of biological systematics has never been refuted even in the slightest" (1971, 9). GÜNTHER (1971, 38) likewise states: "W. HENNIG has elaborated and substantiated his theory of phylogenetic systematics to such an extent that it can be considered as irrefutable". GÜNTHER (l. c., p. 76) furthermore claims that, among the three prevailing conceptualizations of biological systematics, it is only the consistently phylogenetic (genealogical) concept which permits drawing phylogenetically unequivocal conclusions. Similar statements can be found in the writings of BRUNDIN, CROWSON, NELSON, SCHLEE and other cladists. GRIFFITHS, for instance, states that HENNIG's method "provides the only theoretically sound basis for achieving an objective equivalence between the taxa assigned to particular categories in a phylogenetic system" (1972, 9).

Considering this conviction of the superiority of their method cladists are genuinely puzzled "why there are nevertheless so many systematists who have not (or only with reservations) committed themselves to phylogenetic systematics" (HENNIG 1971, 9). HENNIG answers his own question by implying that it is simply insufficient familiarity with the objectives and methods of cladistics which has been in the way of a more general adoption. GÜNTHER, on the other hand, believes that it is the unavailability or neglect of three sets of facts which have prevented the more general application of cladistics: (1) the lack of sufficient available distinguishing characters, (2) the uncertainty as to which characters are ancestral and which derived, and (3) the difficulty of a clear recognition of convergences (1971, 77). In other words, both of these authors feel that empirical rather than conceptual reasons are responsible for the delay in a more rapid adoption of cladistics.

Is this conclusion really justified? Does a purely genealogical arrangement answer the demands of a "best classification"? Indeed, how do we determine which of several alternate classifications is the best?

There has long been agreement among the theoreticians of classification that in most cases those classifications are "best" which allow the greatest number of conclusions and predictions. MILL (1874, 466–467) expressed this, one hundred years ago, in the statement:

"The ends of scientific classification are best answered when objects are formed into groups respecting which a greater number of general propositions can be made, and those propositions (being) more important, than could be made respecting any other groups into which the same things could be distributed."

The opponents of cladistics claim that cladistic classifications do not satisfy MILL's criterion of a "best classification". The number of evolutionary statements and predictions that can be made for many holophyletic[2] groups (like birds and crocodilians) is often quite minimal, consisting ultimately only of a list of the synapomorphies. Indeed, the cladistic theory of classification would seem to suffer from several fundamental conceptual flaws.

The argument cannot be settled without a searching analysis of the theory (including all the underlying assumptions) on which cladistics is based.

There are many indications that most cladists have never given serious consideration to alternative theories of classification, particularly to the theory of evolutionary taxonomy. For how else could HENNIG (1971, 7) have classified the evolutionary

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[2] A holophyletic group contains all the descendants of a stem species.

taxonomists in one group with those taxonomists who work without any theory at all? (See also BRUNDIN 1972, 111). Other cladists, in their arguments, proceed as if phenetics (classification simply based on similarity) is the only alternative to cladistics. Even GRIFFITHS (1972, 18) who clearly distinguishes between the three methods of classifying argues in his actual defense of cladistics only against "morphological-phenetic classifications." Objections to the cladistic theory are being brushed aside as being due to inconsistencies or as having a purely psychological basis (GÜNTHER 1971, 38).

There can be no hope for a meeting of the minds until the cladists face up to criticisms of their opponents and attempt to refute them, point by point. GRIFFITHS (1972) is the only cladist who has even attempted such a refutation.

In contrast to the flood of defenses of cladistics published in recent years (by BIGELOW, BRUNDIN, CRACRAFT, CROWSON, GRIFFITHS, GÜNTHER, HENNIG, KIRIAKOFF, NELSON, ROSEN, SCHLEE and others) there has been only a limited amount of critical analysis of their theory. SIMPSON (1961) and myself (1969) have dealt with it *en passant* in major textbooks. There have been several short critical book reviews, and certain specific points (like the definition of "monophyly") were criticized by ASHLOCK, COLLESS, FARRIS, GUTMANN, JOHNSON, MICHENER, PETERS, and others. But DARLINGTON's papers were really the only serious attempt of a broad criticism of cladistics. Even his criticism deals more with the application of cladistics to biogeography than with the underlying basic assumptions. Indeed DARLINGTON himself states that his criticism "is not a general consideration of cladism" (1970, 1). It is the objective of the present critical analysis to fill a serious gap in the taxonomic literature.

The components of cladistics

It is most important for the understanding of cladistics to realize that it actually consists of two quite different sets of operations:

1. the reconstruction of the branching pattern of phylogeny through *cladistic analysis*,
2. the construction of a *cladistic classification* based on this branching pattern.

The first of these two operations is important and largely unobjectionable. It is the second one which has encountered widespread criticism and will be carefully analyzed in the ensuing pages, with particular attention to the claim of the cladist that a classification should be a mirror image of the branching pattern of the phylogeny.

Reconstruction of the branching pattern of phylogeny (cladistic analysis)

The cladistic analysis starts from the basic assumption that a sound classification cannot be constructed without a thorough understanding of the phylogeny of the given group. The evolutionary taxonomist agrees, on the whole, with this assumption. All phylogeny, except in cases of reticulate evolution, is strictly genealogical. HENNIG is quite right when he states: "Phylogenetic research as biological science is possible only if it adopts the discovery of the genealogical relation of species as its first objective" (HENNIG 1969, 33).

But how is one to proceed if one wants to reconstruct the phylogeny of a group? As HENNIG has stated (1969, 19), this method rests, in the last analysis, on the simple realization "that all differences and agreements between various species originated in the course of phylogeny. During the splitting of a species its characters are transmitted to the daughter species either changed or unchanged". HENNIG is fully aware that all that can be inferred by this method is the sequence of splits but not at all their absolute chronology.

HENNIG has emphasized, and quite rightly so, that a phylogeny does not need to be based on fossils but can be inferred from a careful comparative analysis of morphological characters. This thesis is well substantiated by the classification of the Recent mammals. Our ideas of their relationships, based on a study of their comparative anatomy, have in no case been refuted by subsequent discoveries in the fossil record. On the other hand, the fossil record is entirely indispensable for the determination of absolute chronologies.

The most important step in the cladistic analysis is the attempt to separate characters into ancestral (plesiomorphous) and derived (apomorphous) characters. Only the latter are considered legitimate evidence for relationship, and taxa are therefore based on the joint possession of derived characters (synapomorphies). (For a consideration of the value of symplesiomorphies in the process of ranking see p. 118). Neither HENNIG nor any of his followers has claimed that this important principle was new when proclaimed by HENNIG: "The observation that taxa should only be characterized by apomorphous (derivative) conditions in their ground plan is, of course, by no means new and to many people seems self-evident" (GRIFFITHS 1972, 21). To mention only one example, TILLYARD's classification of the Perlaria (1921, 35–43) was based on this principle. In fact, one can say that most of the better taxonomists of former eras had applied this principle, as is quite evident from a study of their classifications.

Nevertheless, HENNIG deserves great credit for having fully developed the principles of cladistic analysis. The clear recognition of the importance of synapomorphies for the reconstruction of branching sequences is HENNIG's major contribution. The cladograms which can be constructed with the help of this method are as important for the evolutionary taxonomist as they are for the cladist. I have previously (MAYR 1969, 212–217) called attention to the extreme value of this method for the delimitation of taxa. The relative time sequence of the various branching points which the cladogram provides is of great value in many studies, particularly in zoogeographic ones, as HENNIG himself has demonstrated for the diptera of New Zealand (HENNIG 1960).

Cladistic analysis and cladistic classification

There is little argument between cladists and evolutionary taxonomists about the cladogram which results from the cladistic analysis. The argument arises over the relationship of such a cladogram to the classification that is to be based on it. Cladists assume that a one-to-one relationship exists between cladogram (phyletic diagram) and classification. The cladogram, once it is constructed, provides so to speak automatically also the classification. A cladogram and a classification are for the cladist merely two sides of the same coin. The evolutionary taxonomist, on the contrary, believes that a mere branching pattern cannot convey nearly as much interesting information as an evolutionary classification which takes additional processes of evolution into consideration (see below).

Traditionally, the first step in the classification of animals taken by the practicing taxonomist has always been the delimitation by inspection of seemingly "natural" groups. At first these are frankly based on the apparent "similarity" of the included species, that is on phenetic criteria. When HENNIG first proposed the cladistic method (1950) virtually all major higher taxa of animals were already known. He, therefore, automatically adopted the traditional method of taxonomy, of ranking and regrouping animal taxa which other authors had previously delimited. The validity of these provisional groups is subsequently tested in traditional taxonomy against a whole series of additional criteria, such as the homology of characters (similar and dissimilar ones), the presence of synapomorphies, the chronological relation to similar groups, an absence of conflict with the fossil record (when available), an absence of convergence (= spurious similarities), a meaningful geographic distribution, etc. The more experienced a taxonomist is, the more quickly and thoroughly he can undertake these tests. (The classifying procedure of the pheneticist is drastically different). Once established, a classification is thus constantly improved by the process designated by HENNIG (1950) as "reciprocal illumination", which, as HULL (1967) has shown, does not involve circular reasoning. Indeed, the method is nothing more than another application of the hypothetico-deductive approach (POPPER 1959, 1963), so commonly used in all branches of science and particularly (since DARWIN) in biology. As soon as a new (or improved) classification is proposed, it will generate new information which, in turn, will lead to a reanalysis and possibly an improvement of the classification. This traditional approach to classification was followed without serious criticism during much of the 19th and 20th centuries.

Unfortunately this approach by trial and error is sometimes rather inefficient and has led to frequent changes in classifications. Again and again the hope was therefore expressed for a more reliable approach. The better taxonomists agreed on two minimal conditions, the crucial importance of the right choice of characters (a point DARWIN already had emphasized), and the necessity of basing taxa on numerous characters. But this still left much uncertainty.

It was HENNIG's novel proposal simply to translate the cladogram into a hierarchical classification and thus do away with all the previous uncertainty. The proposal to construct a classification directly from the cladogram, however, does not convey the entire theory of cladistic classification. For this reason it would be highly desirable to present a detailed exposition of the entire theory in all of its ramifications, but this is rather difficult. Not only is HENNIG's original work (1950) written in a rather turbid style, but some of his earlier theses seem to be no longer maintained in more recent publications. Furthermore, some of his followers, like BRUNDIN, SCHLEE, and GRIFFITHS, seem to have added postulates which, although perhaps implicit in the original theory, were not explicitly made by HENNIG himself. Nevertheless, the major theses and postulates of cladistics have been stated sufficiently often to permit their enumeration. I shall try to list the more important ones, preferably by direct quotes from the works of cladists. I suspect that my listing is neither complete nor that each of the postulates is adopted by every cladist. However, I hope that this list can serve as a convenient basis for the ensuing analysis.

These are the more important postulates of cladistics (page reference in parenthesis refers to the more detailed discussion below):

1. that all taxa should be "monophyletic", with this term redefined in a novel way, in conflict with the traditional definition of this term (p. 103);
2. that the term phylogenetic be restricted to the branching (cladistic) component of phylogeny (p. 100);
3. that relationship be measured in terms of "recency of common descent", i. e., narrowly genealogically (p. 101–103);
4. that "there is only one dimension in phylogeny and that is the time dimension" (BRUNDIN 1966). Consequently, the splitting of phyletic lines (as reconstructed from the joint acquisition of derived characters) is admitted as the only legitimate evidence in the construction of classifications. To consider also similarities or the relative amount of ancestral (plesiomorphus) characters would lead to a "syncretistic system" which "robs the combination of any scientific value" (HENNIG

1966, 77). He quotes with approval BIGELOW's (1956) statement: "Classification must be based on one or the other (on "overall resemblance" *or* "recency of common ancestry" ...), not on both, if philosophical confusion is to be avoided" (HENNIG, l. c.) (p. 102, p. 123);

5. that the categorical rank of a taxon is automatically given by the absolute geological age of the stem species, or (in a less rigorous formulation) by the "relative age" of the stem species (p. 114). (See also CROWSON, p. 251 and disclaimer by GRIFFITHS [1972, 10, 16]);
6. that species can be delimited in time by two successive events of speciation (p. 109);
7. that the splitting of lines is always a dichotomy, resulting in the production of two sister groups (p. 109);
8. that "homology ... is usually defined in terms of common origin in time" (GRIFFITHS 1972, 17). (This is simply not true. Except for the ancestor-descendant relationship, the concept of homology is completely independent of the time dimension. No other cladist has made such a claim. HENNIG himself adopts REMANE's (1952) concept of homology);
9. that "basically" all classifications should be horizontal classifications, valid only for a given time period (HENNIG 1950, 259) and that therefore the same taxon might be given different categorical rank in different geological periods (p. 115).

Objections to the theory of cladistic classification

The basic postulate of the cladistic theory, a complete congruence of cladogram and classification, can be satisfied only by making numerous assumptions and redefinitions and by ignoring numerous facts of evolution and of phylogeny (broadly defined). This results in major theoretical and practical shortcomings which will now be analyzed, point by point, in three major and a number of subordinate sections.

1. Arbitrary decisions

In order for their method of classification to work, cladists have to make a number of arbitrary decisions, involving a redefinition of well known terms, a re-interpretation of adaptive evolution, and the proposal of a new species definition. When these arbitrary decisions are rejected, very little support for cladistic classification remains.

a. Redefinition of well known terms

A large part of the controversy between cladistics and its opponents can be ascribed to the fact that the cladists have given an entirely new meaning to a number of widely used evolutionary terms which in a rather different sense had been in essentially consistent usage for about 100 years. The transfer of well known and universally understood terms to entirely new concepts cannot fail to produce confusion. This is particularly true for three terms: *phylogeny*, *relationship*, and *monophyletic.*

Phylogeny

Since the days of DARWIN and HAECKEL the term phylogeny has been applied to all aspects of descent. Any article or book in the last 100 years that has used the term phylogeny (and its adjective phylogenetic) has used it comprehensively for all phenomena revealed by Stammbaumforschung. The Collegiate Dictionary of Zoology, for instance, defines it as "1. Evolutionary relationships and lines of descent in any taxon. 2. The origin and evolution of higher taxonomic categories" (PENNAK 1971, 395). But HENNIG now attempts to restrict this term to a single aspect of phylogeny, that of branching. He states, "We will call 'phylogenetic relationship' the . . . (genealogical) relations between different sections (in the diagram), each bounded by two cleavage processes in the sequence of individuals that are connected by tokogenetic relations" (1966, 20). Or, "We have defined the phylogenetic relationships . . . as those segments of the stream of genealogical relationships that lie between two processes of speciation" (l. c. 29). SCHLEE (1971) defines phylogeny as "the origin of taxa, that is that part of evolution which is designated as its cladistic component."

HENNIG's definition and use of the term phylogenetic is clearly in conflict with the previously universal use of the term phylogenetic. His diagrams are cladograms and not at all phylogenetic trees which by the lengths and angles of their branches convey far more information than a cladogram. It would only aggravate the confusion if HENNIG's specialized theory of classification would continue to be designated as "phylogenetic" classification.

GISIN (1964) has proposed to designate HENNIG's method by the term "genealogical" classification, since genealogical (kinship) relationships are an important aspect of the HENNIG method. Unfortunately, the designation "genealogical" does not differentiate cladistics from certain other types of classification, because any classification in which each taxon consists of species that are derived from a common ancestor is a genealogical classification. DARWIN was, therefore, quite right in stating that evolutionary classifications are genealogies. In any phylogeny in which hybridization does not occur (and this is the case in nearly all animal phylogenies) there can be only one genealogy, because each speciational event is unique. This unequivocality of the branching component of phylogeny is rightly emphasized by the cladists. However, even an unequivocal genealogy can usually be converted into a number of different classifications. And this is where evolutionists and cladists have a parting of their ways. Those who allow for a different weighting of different adaptational processes and events (e. g., by giving greater weight to the occupation of a major adaptive zone) may arrive at a very different classification from someone who uses branching as his only basis (as do the cladists), even though the genealogies on which both base their classifications are identical. Since the term "genealogical" does not discriminate between evolutionary and cladistic classifications, I prefer the term "cladistic" for HENNIG's method because it applies to it unequivocally and not to any other system of classification. Furthermore, it conforms to the terminology proposed by RENSCH (1947) and CAIN and HARRISON (1960). It is the only term which accurately conveys the emphasis of the HENNIG method on branching and on branching alone.

When employed in phylogeny the term "genealogical" is obviously used in a somewhat generalized sense, with "taxa" corresponding to the "individuals" of a conventional genealogy. The only alternative would be to classify "generations" of individuals. This, indeed, would be logically impeccable, but useless for purposes of biological classification.

Relationship

The term relationship has been used in the systematic literature in many different senses. Recourse to a dictionary is of no help, since it lists extremely diverging definitions. The term relationship (or affinity) was widely used in the 18th century taxonomic literature, long before the evolutionary theory was adopted. For most authors, at that period, it simply meant similarity. Yet, even today, the term relationship is being defined in many different ways.

Pheneticists, in the beginning, were operating on the basis of the assumption that the phenotype accurately reflects the genotype and that an unweighted determination of "overall similarity" allows a correct determination of relationship. They are no longer as dogmatic about this as they were in 1963, but relationship still means similarity to them. The shortcomings of this interpretation have been pointed out by MAYR (1969) and many others.

The cladists go to the other extreme and restrict the term relationship to designate kinship in a strictly genealogical sense. According to HENNIG "the measure of phylogenetic relationship is the relative recency of common ancestry" (1966, 74). Relationship between two species is measured by the number of branching steps which separate them from the common ancestor (HENNIG 1950, 129). When CRACRAFT (1972, 381) claims that the cladistic method "is the best one available for determining relationships in a relatively unambiguous fashion", he has fallen victim to a circular argument because he uses the highly specialized definition of relationship of the cladists. To repeat, relationship for the cladist is genealogical kinship. But cladistic kinship alone, for an evolutionist, is a completely one-sided way of documenting relationship, because it ignores the fate of phyletic lines subsequent to splitting.

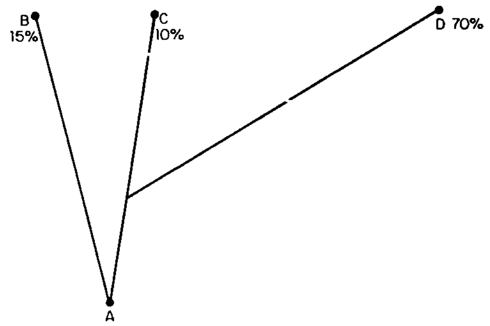
Let me explain. Since a person receives half of his chromosomes from his father, and his child again receives half of his chromosomes from him, it is correct to say that a person is genetically as closely related to his father as to his child. The percentage of shared genes (genetic relationship), however, becomes quite unpredictable, owing to the vagaries of crossing over and of the random distribution of homologous chromosomes during meiosis, when it comes to collateral relatives (siblings, cousins) and to more distant descendants (grandparents and grandchildren, etc.). Two first cousins (even two brothers, for that matter) could have one hundred times as many genes in common with each other than they share with a third first cousin (or brother) (among the loci variable in that population). The more generations are involved, the greater becomes the discrepancy between genealogical kinship and similarity of genotype, even though all these relatives still derive their genes from the gene pool of a single species.

In phylogeny, where thousands and millions of generations are involved, that is thousands and millions of occasions for a change in gene frequencies owing to stochastic processes, recombination, selection, and genetic revolutions, it becomes quite meaningless to express relationship only in terms of the genealogical kinship.

In addition to the cytogenetic processes there are also numerous aspects of selection which can result in a highly unequal degree of genetic change in different lines of descent. One of several phyletic sister lines may enter a new adaptive zone and there become exposed to severe novel selection pressures. As a result it will diverge dramatically from its cladistically nearest relatives and may become genetically so different that it would be biologically misleading to continue calling the sister groups near relatives. Yet being the joint descendants of a stem species they must be designated sister groups. And being sister groups they must be coordinate in rank, i. e., according to cladistic theory, they must have the same absolute categorical rank in the hierarchy (HENNIG 1966, 139). This decision ignores the fact that one is still very much like the stem species while the other has evolved in the meantime into a drastically different type of organism.

This situation is best illustrated by a diagram (Fig. 1). There will be a maximal genetic difference of 25 % between the genomes of B and C, but of 60 to 70 % between C and D. The cladist will say that C is more nearly related to D than to B, the evolutionist and the pheneticist that C is much closer to B than to D.

This independence of adaptive shifts from phyletic splitting is the reason why the evolutionary taxonomist adopts a very different definition of relationship. To him



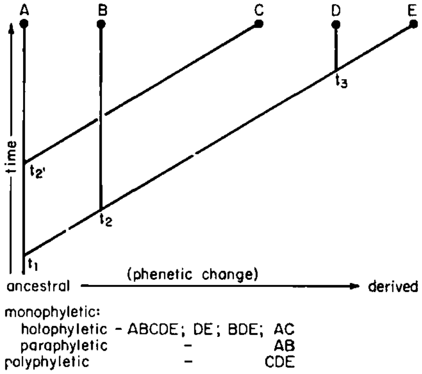


Fig. 1 (left). Inferred percentual difference from ultimate ancestor (A). Taxon C is more closely related to B than to D, even though it shares a more recent common ancestor with D. – *Fig. 2 (right).* Taxon C, through parallel evolution, has become more similar to D and E than to A with which it shares a nearer common ancestor. The converse is true for B (After ASHLOCK 1969)

relationship means the inferred amount of shared genotype, it means gene content rather than purely formalistic kinship. For what is of primary interest in a taxon, its evolutionary role, its system of adaptations, and all the correlations in its structure and characters, is ultimately encoded in its genotype.

Since distant relatives cannot be analyzed genetically and since a purely additive analysis of a complex system of adaptations would be quite meaningless anyhow, it is necessary to infer degree of genetic relationship on the basis of indirect evidence. In this approach use is made of every available clue, but primarily of the combined evidence from phyletic branching and from a carefully weighted phyletic analysis. The evolutionary taxonomist believes that an approach which superimposes a carefully weighted phenetic analysis on a preceding cladistic analysis is better able to establish degree of relationship than either a purely cladistic or an unweighted phenetic approach. And a classification based on such a multiple-based determination of relationship will be more reliable and more predictive than one based on one-sided criteria. The criteria which have to be employed to make such weighting meaningful have been discussed elsewhere (MAYR 1969, 217–228). These criteria permit measuring something that is more than mere "overall similarity."

Convergence, parallelism, and mosaic evolution, all these evolutionary phenomena underline the importance in evolution of the underlying invisible genotype. A diagram (Fig. 2) will illustrate the difficulties created by the concealed potential of the genotype. If species C owing to its concealed genotype acquires by parallel evolution very much the same characters as D and E, even though it branched off from the line leading to A, it would seem legitimate to classify it with D + E. The cladist would presumably call a taxon composed of C + D + E polyphyletic as if the similarity were due to convergence. Phenotypically, indeed, C + D + E form a polyphyletic group. Many evolutionary phenomena indicate the existence of a concealed genotype which cannot be read out completely and directly from the visible phenotype. Most of our difficulties with apparent polyphyly are due to the manifestations of such a concealed genotype.

Monophyletic

The traditional procedure of taxonomy is to recognize a higher taxon "intuitively", that is on the basis of shared characteristics, evolutionary role, etc. As HENNIG stated it (1966, 146): "Taxonomy can begin its grouping task with the assumption that the degree of similarity between species corresponds with the degree of their phylogenetic kinship," an assumption to be thoroughly tested subsequently. There is thus agreement between HENNIG and the traditional taxonomist that the characterization and delimitation of groups has primacy in the classificatory operation (See above, w. 98). This primacy is confirmed by GRIFFITHS (1972, 7) who proposes "that the phylogenetic system should be expressed by revision of the traditional Linnaean system rather than by proposal of a separate classification."

Not until a taxon is established provisionally does the taxonomist ask whether it is truly a "natural" taxon, composed of species that are each other's closest relatives. One of the ways to satisfy this condition is to ask whether all members of the taxon have descended from a common ancestor, that is whether the taxon is monophyletic. The term monophyletic is a qualifying adjective for a noun, the noun *group* (or *taxon*). Among possible groups (and taxa) there are some which we can identify as being monophyletic. It is a distinctly "retrospective" term (MAYR 1969, 75). For this reason the term monophyletic, ever since HAECKEL, has been applied to groups which satisfied two conditions: 1. the component species, owing to their characteristics, are believed to be each other's nearest relatives, and 2. they are all inferred to have descended from the same common ancestor. The second qualification is needed to exclude unnatural groupings due to convergence.

When this traditional definition of monophyletic is applied to taxa, difficulties are rarely encountered: birds are monophyletic, crocodilians are monophyletic, and reptiles are monophyletic. The concept as such is entirely unambiguous, even though its application encounters occasional difficulties, as in the therapsid-mammalian transition (SIMPSON 1961, 124–125; but see CROMPTON and JENKINS 1973).

HENNIG has created enormous confusion by adding to the traditional definition of a monophyletic taxon the following qualification: "... and which includes all species descended from this stem species." This definition is the inevitable consequence of the elimination of all consideration of adaptive evolution from HENNIG's concept of phylogeny. Since birds and crocodilians (excluding all other living reptiles) are derived from a common ancestor, his method forces the cladist to recognize a taxon for birds and crocodilians together, even though this is a useless assemblage. HENNIG has transferred the qualification "monophyletic" from the taxon to the mode of descent. From a retrospective principle he has made monophyly a prospective criterion. This ignores, indeed it quite deliberately conceals, the most interesting aspects of evolution and phylogeny, those of adaptive radiation and the invasion of new adaptive zones (further discussed below under Grades).

His definition of monophyletic forces HENNIG to add another term to the phyletic terminology: *paraphyletic*[3]. A taxonomic group is paraphyletic if it has given rise to specialized side-lines which are not considered part of the group. For instance, the Reptilia are – for HENNIG – a paraphyletic group, because certain Reptilia were the stem mothers both of other reptilia and of the birds (and the same is true for the stem species that gave rise to the mammalian branch). To designate groups as paraphyletic strikes me as a purely formalistic approach. It is of no relevance whatsoever for the relationship between crocodilians and other reptiles to know that the branch leading to the crocodilians (the archosaurian lineage) produced an offshoot which eventually became the class Aves. The animal taxonomist does not classify a logician's schemata or diagrams, but actually concrete groups of organisms. It is of no relevance for our

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[3] HENNIG designates a group as *paraphyletic* if the similarity of the composing taxa is based on symplesiomorphy. For instance, the Reptilia are a paraphyletic group, in contrast to the archosaurians (crocodilians and birds) and the therapsids (mammal-like reptiles and mammals), which are holophyletic.

judgment on the biological classification of the crocodilians whether or not a side branch gave rise to a drastically modified daughter group.

To take the traditional term monophyletic and transfer it to a new concept for which it had never been used before is contrary to sound language practices and to principles of scientific terminology. It strikes me as ludicrous when HENNIG's adherents criticize their opponents for an "illogical usage of the word monophyletic." If one wants to have a term for "the aggregate of all groups descended from a common ancestor," one must coin a new term. ASHLOCK (1971, 65; 1972) has recognized this quite clearly and has proposed for it the term "holophyletic." This corresponds to "monophyletic" as used by HENNIG in contrast to the traditional usage.

No cladist seems to have noticed some of the consequences of the redefinition of the term monophyletic. It forces him to abandon upward classification as traditionally practiced by the empirical taxonomists ever since DARWIN and even earlier, and replace it by "downward" classification. Although starting from entirely different premises, the cladist has methodologically returned to the "divisional" method of classification that was dominant from Cesalpino to Linnaeus. His criterion of division is of course very different from that of the adherents of ARISTOTLE's logical division, but the principle of classifying of both schools (cladists and logicians) is very much the same.

It may sound like a platitude to say that when classifying one ought to deal with entities which one has in front of himself. The pheneticist and evolutionist classify species and genera in this manner. Not so the cladist, who deals with the unknown quantities produced by phylogenetic splits. It is implicit in his principles that he is forced to make the prediction that sister lines derived from a stem species will have sufficiently similar evolutionary fates so that the resulting sister groups can be ranked at the same categorical level (= are coordinate). The case of the birds and crocodilians is a particularly convincing illustration of the thousands of occasions where this prediction does not come true. It is the abandonment of the principle of upward classification, dominant since DARWIN, and its replacement by ARISTOTLE's downward classification which is the fatal flaw in the philosophy of cladistic classification.

Those who would adopt the three terms *phylogeny*, *relationship*, and *monophyletic* in their new aberrant Hennigian definitions are forced to adopt drastic changes in the whole theory and practice of phylogeny and classification as compared to the traditional. It is quite true that one can operate in an entirely logical manner within the framework set by these new definitions. However, as GHISELIN has pointed out so often, one can operate in an entirely logical manner on the basis of totally wrong premises. Many, if not most, of the claims of the cladists go back to the consequences of their new definitions of these three terms.

b. The neglect of the dual nature of evolutionary change

DARWIN saw clearly that speciation involves two independent processes. One is the acquisition of reproductive isolation, a prerequisite of prevention of the hybridization between the two incipient species. The other one is the acquisition of niche differences resulting in "divergence of character" in order to overcome the effects of competition (DARWIN 1859, 111).

What is true at the level of the species, is equally true in macroevolution. We can distinguish two processes of evolution, that of the splitting of phyletic lines and that of the invasion of new adaptive niches and major adaptive zones by phyletic lines. Any theory of classification which pays no attention to the tremendous range of difference between shifts of phyletic lines into minor niches and into entirely new adaptive zones, is bound to produce classifications that are unbalanced and meaningless. But such a neglect of different kinds of phyletic evolution is precisely what the cladistic method demands.

The cladist proceeds in the construction of his classifications as if the splitting of lineages were the only phylogenetic process and as if all such splits were equivalent. All splits have equal weight for the cladist, just as all characters have equal weight for the pheneticist. His exclusive preoccupation with splitting has been confirmed by HENNIG on several occasions, but will be documented here only by the following quotation: "Decisive is the fact that processes of species cleavage are the characteristic feature of evolution; they are the only positively demonstrable historical processes that take place in supra-individual organism groups in nature." (HENNIG 1966, 235). This leads HENNIG to the claim that his method is the only one that gives historically correct answers.

The cladist states openly that branching is the only aspect of phylogeny of interest to him. That some of the resulting lineages may enter entirely new adaptive zones and then become extraordinarily different from other, more conservative lineages, is considered by him as irrelevant; if removed from the common ancestor by the same number of speciational steps they all will have to be given the same taxonomic rank. Cladistics treats any apomorphous character like any other. Those taxa are combined which have the greatest number of joint apomorphies (as being derived from the same stem species). So far as I can judge from the cladistic literature, no weighting of apomorphies is undertaken, and derived characters which signify entrance into an entirely new adaptive zone (as in the case of the birds) are given no more weight than the joint apomorphies of birds and crocodiles (which distinguish these living archosaurians from other living reptiles). The acquisition of minor specializations are given the same weight as major adaptive innovations. That some events in adaptive evolution are far more important than others is completely ignored. This is, perhaps, the most significant difference between cladistic and evolutionary classification.

It is evident that the cladist reveals great ambivalence in the treatment of divergence. He pays lip service to the fact that there are differences in the rate of evolution in various communities of descent, but does not draw any of the obvious conclusions from this observation. Neither HENNIG nor BRUNDIN nor any of their younger followers (i. e. SCHLEE, NELSON, GRIFFITHS) pays even the slightest attention to these differences in rates mentioned by HENNIG when they construct classifications. They likewise entirely ignore various other important evolutionary phenomena such as the existence of "grades" and of highly specialized side lines, all the phenomena of mosaic evolution, and all causal factors in evolution. How rapidly a new branch diverges, how it changes in relation to the "sister group", how many additional characters it acquires, which new adaptive zone it has invaded, etc., all these are questions which the cladist hardly ever mentions. By considering only genealogical distance the cladist acts as if he assumed that all lines diverge in an equivalent manner and that genealogical distance corresponds to genetic distance. By claiming that branching is the only historical process of consequence, he denies that other aspects of evolutionary change such as rate of evolution, adaptive radiation, the occupation of new adaptive zones, mosaic evolution, and many other macroevolutionary phenomena are eligible for the term "historical process."

Both components of phylogeny are potentially of equal importance for the evolutionary taxonomist, and both must be judiciously considered in the construction of classifications. Splitting as well as phyletic change occur simultaneously in evolution, but in most groups either one or the other process predominates at a certain geological period. Whenever there is massive splitting, such as, for instance, during the speciation of the 50,000 or 100,000 species of weevils (Curculionidae), or of the several thousand species of *Drosophila,* phyletic divergence is relatively insignificant. Among the invertebrates, and more specifically among the arthropods, there are numerous higher taxa in which abundant speciation has occurred without any impact on the basic morphology and without any shift into a new adaptive zone. All the species of these assemblages are repeated variations on a theme. This is in strong contrast to such memorable episodes in the history of the world as was the origin of the vascular plants, the angiosperms, the chordates, the vertebrates, the terrestrial tetrapods, the reptiles, or the birds.

RENSCH (1947), HUXLEY (1942, 1958), and SIMPSON (1959b, 1961), particularly, have emphasized the importance of these levels of adaptation, designated by HUXLEY as *grades*. All members of a grade are characterized by a well integrated adaptive complex. The successful evolution of a phyletic lineage toward and into a new adaptive zone is characterized by the stepwise acquisition (mosaic evolution) of a series of novelties to adapt it (and its descendants) to its new position in the ecosystem. Subsequently the basic new type of this phyletic line may undergo little evolutionary change but experience instead abundant adaptive radiation as a result of bountiful speciation and various modifications in the basic adaptive theme of the grade. In the history of the vertebrates we know many such cases of the formation of successful new grades such as the sharks, the bony fishes, the amphibians, reptiles, birds, and mammals. Each of these is characterized by a certain type of adaptation to the environment (BOCK 1965), regardless of the amount of cladistic break-up within the grade. It results in a great deal of loss of information to ignore the adaptive component of evolution expressed by the concept of grade and to limit one's attention only to the splitting of lines. But this is precisely what the cladists are doing.

Actually, the existence of minor and major grades is one of the most interesting phylogenetic phenomena, even though it is a phenomenon which we are still unable to understand adequately. Why is there so often such a uniformity of type within a higher taxon? There is a rich diversity of species of parrots but all of them from the smallest pygmy parrot or lorikeet to the largest cockatoo or macaw are charactersti-cally parrots. And so it is in many, if not most, higher taxa. The reptiles represent a well defined grade between the amphibian level and that of the two derivatives of the reptiles, the birds and the mammals.

SIMPSON, in his various publications (1953, 1959b, 1961) has repeatedly discussed the contrast between clades and grades. Crocodiles have a more recent common ancestor with birds than with lizards. They belong, thus, to the same clade as birds but they do not belong to the avian grade, but rather to that of the reptiles. To which of these two aspects of evolution shall we give primacy? There are literally thousands of similar dilemmas in the evolution of animals and plants. For instance, the African apes (*Pan*) have a more recent common ancestor with man (*Homo*) than with the orang (*Pongo*). However *Pan* belongs to the same grade as *Pongo*, very different from that typified by man. The better the fossil record becomes known, the more often one encounters such dilemmas. To the evolutionary taxonomist the existence of grades seems often more significant and more meaningful biologically than the mere splitting of phyletic lines. How little some of the cladists appreciate the biological significance of grades is illustrated in a comment by BRUNDIN (1972, 111) who designates groups such as the reptiles as "timeless abstractions."

One senses two reasons for the deliberate neglect of evolutionary divergence by cladists. One is that this factor cannot be measured precisely and unequivocally. Indeed, rates and degrees of evolutionary divergence can usually be inferred only by extrapolation or other indirect approaches. Yet, by appropriate weighting (MAYR 1969, 220–228) one can draw meaningful probabilistic inferences, which, although not entirely precise, are far more valuable than the advice to ignore evolutionary divergence altogether. A second reason is that cladists seem to think that they have to make a choice, in the delimitation of taxa, between basing them *either* on branching points *or* on degrees of evolutionary divergence. They fail to appreciate the added amount of information by utilizing *both* sources of evidence.

Cladists, when criticized for the neglect of evolutionary divergence, try to defend themselves by referring to HENNIG's *deviation rule* "When a species splits, one of the two daughter species tends to deviate more strongly than the other from the common stem species" (1966, 207). The establishment of this rule, say the cladists, proves that they do not ignore phyletic evolution. Several aspects of this rule are remarkable. First of all, it is in flat contradiction to HENNIG's assertion that splitting is the only historical process in phylogeny. Unequal deviation is a historical process which – as such – is independent of splitting. Secondly, although the deviation rule was pronounced by HENNIG already in 1950 (p. 111) and confirmed in 1966 and 1969 (p. 43), and although it is in principle adopted by most cladists (e. g. BRUNDIN 1972, 108), it seems to play no role whatsoever in the construction of any of their classifications. The dendrogram illustrating the deviation rule (1950, Fig. 25) is one of HENNIG's very few diagrams in which the angles of all clades are not the same. One almost gets the impression that it is the whole purpose of the deviation rule to permit cladists to defend themselves against the accusation of having ignored evolutionary divergence altogether. For the consequences of the deviation rule are completely neglected. They would become obvious, if the process of unequal deviation were to occur after each step of speciation. Then it would become evident how important phyletic divergence is. For instance, if one of the newly arisen "sister groups" is very much like the parental group or even identical with it (as implied by HENNIG 1966, 59) while the other deviates strongly, the terminology "sister groups" is no longer applicable since one now deals with a continuing parental group from which a daughter group has split off (HENNIG 1966, Figs. 14, 15). But beyond this formal objection there is the much more serious one that a greatly accelerated rate of divergence in one branch (one sister group) while subsequent branches of the other sister group diverge only slightly, would lead in time to such an unbalance of the system as to destroy completely the usefulness of the dichotomous cladogram. Such asymmetric branching happens in evolution very frequently and is easily accommodated in the classifications of the evolutionary taxonomists but fits only very awkwardly (if at all) into the cladistic classifications.

Some of HENNIG's followers have recognized these contradictions. SCHLEE (1971, 5, 30, 37) sees rather clearly that the deviation rule is dispensable: "It neither forms an argument for the justification of HENNIG's method nor a prerequisite for the work with HENNIG's principle." SCHLEE adds a mysterious interpretation by HENNIG himself (l. c. 6): "that the 'deviation rule' must be understood in a special genealogical sense, but not in a morphological-biological sense." Actually, the opposite is true: in a strict genealogical sense, there can be no deviation. If there is an unequal deviation, it must be in "a morphological-biological sense." Such morphological deviation is the normal situation in phylogeny. Whenever there is a splitting of phyletic lines, almost invariably one line will diverge more rapidly and more widely than the other, in fact, one of them may not change at all. The complete neglect of the frequent occurrence of this process is one of the fatal errors in the translation of the cladistic analysis into a classification.

Since the consideration of grades in classification is sometimes referred to in the cladistic literature as a typological approach, I would like to call attention to a somewhat different usage of the term typological (typologisch) in the American and the German literature. Typological in American usage is a straight synonym of essentialistic, referring to the abstraction of an underlying *eidos* (essence) and the neglect of the existence and importance of variation. In the German phylogenetic literature

Typus or Bauplan is also an abstraction, representing either the inferred ancestral "type" or the "ideal" Bauplan of a major taxon. To recognize the reptiles as a legitimate taxon, means recognizing a generalized reptilian Bauplan, and is then referred to as a typological approach. The emphasis in the German usage is on the typological philosophy of idealistic morphology. Typological in the German usage often also implies "phenetic" (broadly defined). The confusion between the two concepts of "typological" is well illustrated in a discussion by SCHINDEWOLF (1967).

c. A purely formalistic species definition

HENNIG's species definition in his original treatise (1950) is concerned only with the delimitation of species in the time dimension. A species is simply the distance between two branching points of the phylogenetic tree (p. 111). This concept is retained in his 1966 book (pp. 56–65). For instance: "The limits of the species in a longitudinal section through time would consequently be determined by two processes of speciation: the one through which it arose as an independent reproductive community, and the other through which the descendants of this original population ceased to exist as a homogeneous reproductive community" (p. 58). Although the last words of this definition have a slight flavor of the biological species definition, the diagrams in which it is illustrated (particularly his Fig. 15, p. 60) show how purely formalistic HENNIG's species concept is. For instance species B and D_1 differ in no way from the stem species A, but must be called different species, because C and E had in the meantime branched off this stem. In contrast species D_2 is different from species D_1 ("morphologically" says HENNIG, but his argument would be the same if they were "reproductively" isolated), but must be called the same species, because no branch had budded off from this stem in the meantime.

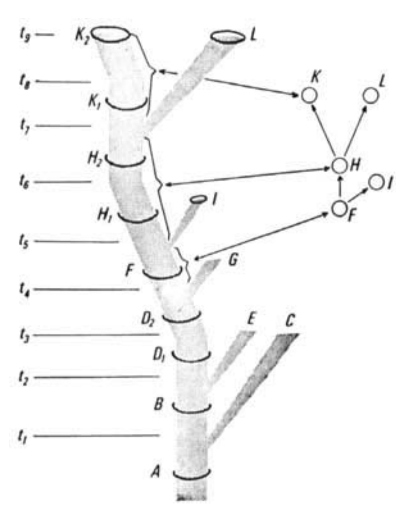

Fig. 3. The relation, according to HENNIG, between branching and speciation (From HENNIG 1966, Fig. 15)

I am calling attention to HENNIG's species concept, not because it is the decisive capstone in the HENNIG theory (it is *not*, HENNIG's own claims notwithstanding), but merely to give another example of the arbitrariness and purely formalistic nature of the major components of HENNIG's cladistic theory. HENNIG's species concept is so obviously unbiological and unrealistic that it has been rejected by numerous recent critics. PETERS, for instance, refutes HENNIG's formulations very effectively (1970, 28–30), showing that among all the possible properties of species their duration in the time dimension is the least meaningful. CAIN (1967, 412) also exposes the biological meaninglessness of HENNIG's formalism.

HENNIG's concept of the process of speciation is strongly affected by his species concept. The various possibilities implied in HENNIG's discussions can be formulated as three alternatives:

A. Parental species eliminated by

1. the splitting of the mother species into two daughter species (dichotomy), or
2. the simultaneous splitting of the mother species into more than two daughter species, or

B. Parental species continuing
3. after the origin of one of several side branches from the essentially unchanged phyletic mainline.

In his 1950 book HENNIG allows only for alternative 1. and among cladists this is still the favored alternative because it fits most easily into the cladistic scheme. Cladists are not unaware of alternative 3. but find a formal solution which does away with this inconvenient phenomenon. If a species *a* throws off a species *c*, species *a* will have to be called species *b* from the branching point on, in order to satisfy the cladistic postulates, even when *b* is biologically quite indistinguishable from *a*. In kinship studies, writes HENNIG (in SCHLEE 1971, 28): "the question of the biological identity of different species from different chronological horizons becomes totally irrelevant." This illustrates well to what extremes the dogmatic formalism is carried by HENNIG. Because, no matter what he says, if *a* and *b* are biologically identical, then they simply are not different species but the same species from which species *c* has branched off at some time. And this is of critical importance for the discrimination between sister and daughter groups. HENNIG's solution is thoroughly misleading. The production of a side branch, a new phyletic lineage, does not change the parental species.

Dichotomy or not. Modern speciation studies permit us to determine at which relative frequency alternatives 1. and 2. occur. All the indications are that a simple dichotomy into two daughter species is not the rule. Polytypic species almost invariably have more than two subspecies. Far better evidence is provided by superspecies which consist of groups of allospecies. In North American at least 48 (= 40 %) of 126 superspecies of birds have more than two allospecies (MAYR and SHORT 1970). Among 94 Northern Melanesian superspecies 61 (= 65 %) are non-dichotomous, containing three to 13 allospecies (MAYR and DIAMOND in press). The dichotomous "standard" is also refuted by all species-rich genera and by the frequency of clusters of sibling species. What is usually found in speciation studies is that the maternal species undergoes relatively little evolutionary change while numerous daughter species bud off at the periphery. HENNIG himself is not unaware of this situation as shown by his presentation of geographic variation in the snake *Dendrophis pictus* in which the large central population is surrounded by six peripherally isolated populations (HENNIG 1966, Fig. 16, p. 61). It is increasingly realized by biologists (MAYR 1942, 1963) that peripheral budding is the most frequent process of speciation, even though most of these daughter species are extremely short-lived. Under these circumstances I fail to comprehend the logic of NELSON's (1971, 374) assertion: "The use of dichotomous speciation as a methodological principle is required before an hypothesis of multiple speciation is even tentatively acceptable".

The difference between splitting and budding might seem a purely semantic one, if it were not for the fact that the cladists base such far-reaching conclusions on the postulate of consistent dichotomy. DARLINGTON (1970, 2–4) has presented an incisive critique. Even some cladists are beginning to abandon the principle of obligatory dichotomy (e. g. SCHLEE 1971, 27), but they have not yet faced up to the consequences this poses for their theory of sister groups. If a non-dichotomous split has produced three or four independent phyletic lines, it would mean that each of the resulting groups has two or three different sister groups rather than a single one. Many of the discussions of sister groups found in the cladistic literature would become meaningless under these circumstances.

In his *Stammesgeschichte der Insekten* (1969) HENNIG recognizes a number of higher taxa which consist of more than two sister groups. However, he emphasizes that this is a purely provisional arrangement, acceptable only "as long as the exact relationships are still uncertain."

The role of *extinction* is greatly underestimated in the cladistic constructions. Pairs of related taxa (HENNIG's sister groups) are indeed frequently encountered. Their existence, however, is usually due to the extinction of numerous intermediate phyletic lines rather than to a peculiar process of speciation, i. e., the splitting of a mother species into two daughter species. There is little evidence that this occurs frequently, and none whatsoever that this is the universal process of phylogeny.

d. The mode of origin of higher taxa

His phylogenetic theory forces the cladist to propose an unrealistic mode of origin for higher taxa. Since he recognizes branching as the only phylogenetic process, he has to give his branching points two properties: they are the origin of new species and also of new higher taxa. This arbitrary assumption in no way corresponds to the facts, as correctly pointed out by DARLINGTON (1970, 2). Speciation, that is the acquisition of reproductive isolating mechanisms between populations, and the acquisition of phylogenetically significant new apomorphous characters are two largely independent processes. The study of groups of sibling species and of most species-rich genera shows that the acquisition of reproductive isolation is often (if not usually) without effect on the morphological criteria that a taxonomist or evolutionary biologist would associate with the origin of new higher taxa. It is the exception rather than the rule that one of the daughter species acquires during speciation a character which is of potential significance for the characterization of a new higher taxon. The appearance of new apomorphous characters is correlated with the invasion of new niches and adaptive zones rather than with speciation (SIMPSON 1956b; BOCK 1965). The occurrence of phylogenetic dichotomy, thus, becomes more plausible when it is divorced from speciation, because the probability that several daughter lines shift simultaneously into the same new adaptive zone is small. It is, however, not nil, since a change of climate and vegetation or the arrival of a new predator may, indeed, cause a simultaneous identical shift in several related lines.

Probably more frequent and potentially more troublesome is the occurrence of the simultaneous acquisition of the same apomorphous characters in different lines in a cluster of sister groups, let us say the descendants of a highly polytypic superspecies. Extinction often provides a practical solution to this dilemma. The evolution of a new higher taxon from the line initiated by the new species is a later event, representing the second phylogenetic process, evolutionary divergence, and has nothing to do with splitting as such. It is a misleading formulation to say that higher taxa split. The evidence for this assertion is this: A higher taxon is a collective assemblage, which comprises numerous species and lesser evolutionary lines. Very few of them ever diverge to the extent that they form a separate higher taxon. But every once in a while one of these lesser branches diverges to such an extent that it must be removed eventually as a separate higher taxon.

Two aspects are important: The "Adam" of the new phyletic line almost invariably belongs to the ancestral taxon. The first member of the phyletic line that eventually led to the birds (long before *Archaeopteryx*) was presumably an otherwise rather conventional dinosaur, but with feathers or feather-like scales. Is a single derived character enough to throw such an "Adam" into the new taxon which will eventually emerge from his lineage? Paleontologists have long been concerned about this problem, which has been discussed in great detail by SIMPSON (1961 and elsewhere).

ASHLOCK (1971, 67) makes the sensible suggestion that the delimitation of the ancestral taxon against the derived taxon should be arrived at as follows: "The unique innovations found in the living members should be traced through the available fossils and the break placed somewhere between the first appearance of one of these characters and the first appearance of all of them . . . The specific assignment of the boundary

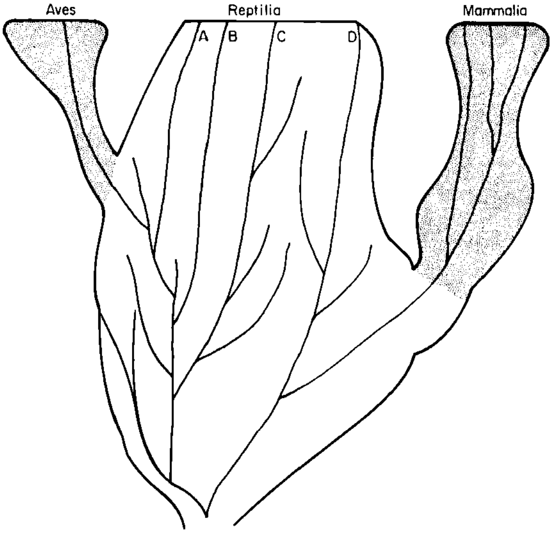

Fig. 4. The independence of the emergence of the avian and mammalian grades from the branching pattern of the reptilian grade. A (= crocodilians) belongs cladistically with the Aves, but is still a characteristic member of the reptilian grade. The origin of birds and mammals does not affect the categorical status of the reptilian branches from which they arose.

should be phenetically determined, weighting characters if appropriate, so as to establish attainment of the grade of the derived group." He admits that failure of preservation of the soft parts and an absent fossil record may make this task difficult, if not impossible, but in principle this is certainly the appropriate procedure.

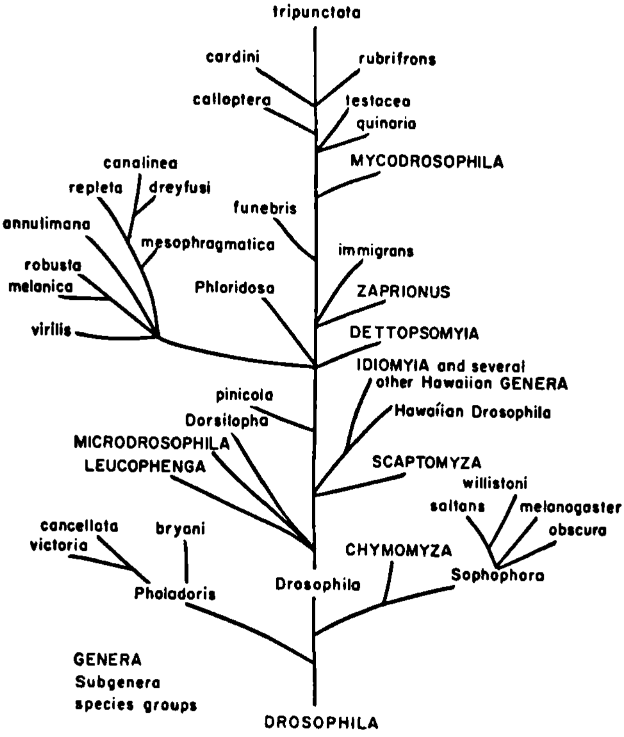

Fig. 5. The origin of specialized derivative genera from within the Drosophila phyletic tree (From Throckmorton 1965)

The other important conclusion is that the origin of a side branch is of no evolutionary consequence for the main branch (except for possible competition). For instance, the Class Reptilia, a well characterized grade of tetrapods, has existed since the Carboniferous and survives in four living orders. Some time in the Triassic one of the numerous reptilian side branches (the cynodonts among the therapsids) evolved into the mammals and a little later another one gave rise to the birds (Fig. 4). A rigid application of their dogma forces the cladists to break up the reptilian grade into many separate "classes" and to designate particular reptilian lineages as the "sister groups" of birds and mammals. The fact that no one would place the crocodilians outside the reptiles, if birds did not exist, reveals how artificial and arbitrary this procedure is. The essential unity of the reptiles is best illustrated by the continuing argument among paleontologists as to which particular orders of reptiles are most closly related to which others.

One of the major sources of the cladistic difficulty is the assumption that the origin of any new higher taxon requires the disappearance of the parental taxon. Even though there is massive evidence that many, if not most, higher taxa are lateral derivatives (side branches) of other taxa that had existed long previously and have continued to exist long after the split, his particular formalism forces the cladist to make such unrealistic claims as: "The stem species belongs neither to one nor to the other (daughter) group (to which it has given rise): it cannot be assigned to either of the two" (HENNIG 1969, 33).

How unsuitable this cladistic approach is can be demonstrated best by the study of a richly diversified group which is still in existence and actively speciating. The modern family of Drosophilidae represents such a case (Fig. 5). In this higher taxon one has such rich information from morphology, chromosomes, behavior and other characteristics that one can reconstruct the probable phylogeny with a considerable degree of reliability. The resulting dendrogram shows that several specialized genera originated from various locations within the *Drosophila* dendrogram. The origin of a specialized side line, to which one accredits separate generic status, affects in no way the taxonomic status of the main line of *Drosophila* which continues as the genus *Drosophila*. This is not a unique case. The origin of multiple side lines, each specializing in a somewhat different way while the major stem group continues essentially unchanged, is a very common occurrence in phylogeny.

2. A misleading conceptualization of ranking

The process of classification consists essentially of two steps, 1. the *grouping* of lower taxa (usually species) into higher taxa, and 2. the assignment of these taxa to the proper categories in the taxonomic hierarchy (*ranking*). The considerations which govern these two processes are quite different from each other (MAYR 1969, cap. 10). The cladists, following the erroneous assumption that phylogeny is a unitary process (consisting only of branching) assert that classifying likewise is a single-step procedure and that the grouping of taxa simultaneously also supplies their rank. Traditionally the rank of a taxon is determined by such criteria as degree of difference, uniqueness of the occupied adaptive zone, or amount of adaptive radiation within (MAYR l. c. 233). According to cladistics rank is given automatically by time of origin, and the same rank must be given to sister groups.

This erroneous conclusion is reinforced by HENNIG's frequent confusion of the terms taxon and category. In 1950 such confusion was excusable because up to that time no terminological distinction had been made. By 1966 when the difference had been made abundantly clear by numerous writers, the confusion was no longer defensible. Yet, even in 1966 (pp. 77–83) HENNIG speaks of the "reality and individuality" of categories, when he means taxa, and this confusion thoroughly obfuscates his discussion of the ranking procedures. The whole process of classification is based on the clear discrimination of *taxon* and *category:* zoological groups (taxa) have "reality" in nature because taxa names like birds, butterflies, or bats, are unambiguously names for clearly distinguishable groups. It is equally evident that the ranking of these taxa in the Linnaean hierarchy of taxonomic categories is rather arbitrary and often highly controversial. What one author considers a tribe, a second may call a subfamily, and a third a family or even superfamily. (See below, p. 122).

Hennig, unfortunately, believes (or at least originally believed) that a knowledge of branching points would permit him to determine the categorical rank of a taxon. He utilizes two criteria: the geological age of the branching point (leading to the nearest sister group) and the number of subsequent branching points. He has stated this without reservations at numerous places in his writings. For instance, the taxa in the hierarchy "are subordinated to one another according to the temporal distance between their origins and the present; the sequence of subordination corresponds to the 'recency of common ancestry'" (1950, 83). "... in the phylogenetic system ... the absolute rank order cannot be independent of the age of the group since ... the coordination and subordination of groups is by definition set by their relative age of origin" (1966, 160).

Both of Hennig's criteria have been frequently criticized. Peters (1970), for instance, recognizes that among two evolutionary lines, which evolve at the same rate, one might give off a large number of side branches, while the other might maintain a monolithic singularity. It would make no sense to grant a higher rank to the frequently branching line than to the non-branching line. After all, branching and evolutionary divergence are two independent processes. Hennig and some of his followers now speak occasionally of "relative chronological age" instead of "absolute geological age" but in 1966 Hennig still maintained that the location of the branching point on the geological time scale determines categorical rank (Fig. 6).

Accordingly, taxa that originated from a split in the pre-Cambrian are ranked as phyla; between Cambrian and Devonian as classes; between Mississippian and Permian as orders; between Triassic and Lower Cretaceous as families; between Upper Cretaceous and Oligocene as tribes; and in the Miocene as genera. Hennig continues "then the mammals would have to be called an order ... the Marsupialia and Placentalia would have to be downgraded to families, and the 'orders' of the Placentalia would be tribes" (p. 187). Similar statements can be found in the writings of other cladists. For instance: "Species are to be ranked 1. according to their relative time of origin or 2. such that sister groups are given equal rank" (Nelson 1972, 366). "Relative age" is a term frequently referred to in the cladistic literature but no one has yet proposed an operational method of determining relative age.

If one would really rank taxa on the basis of their (geological) time of origin, one would be forced to adopt an entirely unbalanced system. Since the genus *Lingula* originated earlier than either the class Aves or the class Mammalia, one would have to place *Lingula* (and other contemporary, still surviving genera) into higher categories than birds and mammals. Even a cladist would presumably rather be inconsistent than go to

Geological time periods		Categorical rank
VI	*Miocene*	*Genus*
V	*Oligocene* *Upper Cretaceous*	*Tribe*
IV	*Lower Cretaceous* *Triassic*	*Family*
III	*Permian* *Mississippian*	*Order*
II	*Devonian* *Cambrian*	*Class*
I	*Precambrian*	*Phylum*

Fig. 6. The assignment by Hennig of categorical rank on the basis of the absolute geological age of the stem species (From Hennig 1966, Fig. 58 and text p. 187)

such extremes. The discussions of Griffiths (1972, 10) and Crowson (1970, 250–254) reveal their difficulties.

Curiously, Hennig has cited the classification of parasites as support for the cladistic method (1950, 261–269). He confirms that "host group and group of parasites must be given the same systematic rank ... when a group of parasites, which is restricted to a certain host group, originated simultaneously with it, perhaps in the manner that the stem species of the group of parasites lived as parasites in the host group" (l. c. 265). And yet, as Osche (1961) has pointed out, the chronology of parasites and their hosts actually refute the cladistic method. It is highly probable that many vertebrate parasites originated at the same geological period as their host taxa. This would necessitate, if one were to follow Hennig strictly, that a genus of cestodes be raised to the rank of a family or order because it parasitizes a family or order of vertebrates or reciprocally that the host taxon be reduced to the rank of a genus. It would also mean that the superfamily Ascaroidea of the nematodes be given the same categorical rank as the class Cestoda because the stem species of both taxa are believed to have invaded the vertebrates at the same time.

The more carefully phylogenies are studied the more difficulties for the Hennig principle of ranking are discovered. Various auxiliary devices proposed by Hennig do not improve the situation. By assuming branching to be a regular process, with an approximately even rate, Hennig believes that the number of species contained in a taxon provides an approximate measure for its age: "Monophyletic groups with large numbers of species cannot be very young" (1966, 182). Recent evolutionary researches have clearly demonstrated that this conclusion does not hold. The correlation between age of a taxon and number of contained species is extremely loose. The Hawaiian drosophilids, a clearly monophyletic group, is not only very recent (probably less than 4 million years old) but also extremely rich in species (at least 600 to 800). Most of the species flocks of African cichlid fishes are likewise very young, a product of the last couple of million years. Most families of rodents, rich in species, are geologically much younger than most of those families of mammals that contain only two or three genera. The monotremes with four to five species are as old or older than the eutherians with more than 3,000 species (Peters 1970, 31). Well known types of marine invertebrates go back 300 to 400 million years without ever having produced rich species flocks.

Hennig and his supporters claim that the great merit of the cladistic method is that it provides non-arbitrary definitions of the higher categories. Griffiths (1972, 16), for instance, praises Hennig for having proposed a logically unobjectionable definition "in terms of the age of origin of the stem species." I have shown above how unrealistic this proposal is and how utterly it fails to provide a sound procedure of ranking. Invertebrate paleontologists, who can demonstrate extremely different evolutionary fates for different phyletic lines (derived from the same stem species) have frequently pointed out to what unbalanced classifications the cladistic method of ranking would lead. Simpson (1961, 142–144) likewise has described what the application of this principle would do to vertebrate classification. Crowson (1970, 260) admits "If phylogenetic classification proceeds usually by dichotomous divisions, and very unequal ones at that, it will necessitate the usage of many more categories [and taxa names] than were needed for older, 'formal', systems." Simpson is fully justified in calling such classifications "completely impractical." Hennig himself (1969, 10) now realizes that this method leads to an absurd scale of ranking and has abandoned in his book on the phylogeny of insects any attempt to provide categorical ranks for the higher taxa. But what method of classification is this which cannot rank higher taxa?

3. Operational neglect of evident facts

Many aspects of phylogeny create difficulties for cladistics. Hennig and his followers are not unaware of these facts and occasionally discuss them freely. However, they ignore these difficulties in the construction of their classifications or at least they offer no operational instructions on how to cope with them. I have referred to this already in the discussion of the "deviation rule" (see above) in which the unequal divergence of phyletic lines is acknowledged, but without drawing the obvious consequences for classification. Other facts that are neglected are the following.

a. The difficulty of determining the direction of evolutionary sequences

Taxa are constructed by Hennig on the basis of synapomorphies (derived characters). The direction of the evolutionary change must therefore be determined for each character sequence. Sometimes it is easy to make such a decision, in many other cases it is quite difficult. Hennig is well aware of this problem and has formulated four rules (1950, 172 ff.) which help to determine which of several alternate characters are more ancestral and which derived. Most of these rules, reformulated by Peters and Gutmann (1971, 242), are based on practices that go back to Darwin or even earlier periods. Peters and Gutmann (l. c. 256) emphasize correctly that any formalism in phylogenetic research (including cladistics) tends to lead to superficial and often unreliable conclusions. It must be replaced by a far more biological attitude toward the morphological evidence. The phylogenetic reconstruction must be based on an analysis of function and adaptive significance, such as is practised in evolutionary morphology (Bock 1965, 1969). I refer to the essay of Peters and Gutmann (l. c.) for a very perceptive statement of this weakness of cladistics. Their considerations make it obvious that the magnitude of an adaptive innovation is of the utmost importance in classification, a fact consistently ignored by the cladists.

b. The discrimination between parallelism and convergence

The common possession of the same character in two different taxa may have one of four possible causes (Mayr 1969, 202):

1. *Plesiomorphous similarity.* The sharing of characters with an ancestor (see the cladistic literature for more precise specifications).
2. *Synapomorphous similarity.* The unique sharing of characters derived from a stem species, e. g., all birds, but no other organisms, have feathers.
3. *Similarity due to parallelism.* Characteristics produced by a shared genotype inherited from a common ancestor.
4. *Similarity due to convergence.* These can be either convergent acquisitions (wing in pterodactyls and bats) or convergent losses (leglessness in snakes and worm lizards).

To discriminate between these four possibilities is not nearly as easy as it may sound, because all that is accessible to the student of phylogeny are phenotypes, while phylogeny actually consists of a change in genotypes.

The traditional recipe for the discrimination between parallelism and convergence is the analysis of homology. Cases where a homology between characters can be established, that is a derivation from the equivalent character in the common ancestor, are the result of parallel evolution. Similarities in non-homologous characters are the result of convergence (Bock 1963, 1967). To follow this recipe in practice, is, however, very difficult, not only because the establishment of homology is often fraught with difficulties (Hull 1967), but also because in distant relatives the line between parallelism and convergence is often not sharp (For a discussion of parallelism see also

Simpson 1961, 103–106). Osche (1965) has given a perceptive analysis of the difficulties caused by the potentialities of the hidden genotype.

Cladists pay little attention to the various possibilities: "In deciding whether corresponding characters of several species are to be regarded as synapomorphies, convergences, homologies, or parallelisms we must determine whether the same character was already present in a stem species that is common only to the bearers of the identical characters" (Hennig 1966, 120). Contrary to Hennig's claim this does not permit a discrimination between the four possibilities but only between synapomorphy on one hand and the other three on the other hand. Here and elsewhere (for instance l. c. 121) Hennig is quite outspoken in his lack of interest in making a distinction between parallelism and convergence (see also Peters 1972, 168). And yet such a distinction is of crucial importance in deciding degree of relationship between taxa.

Taxa are classified in cladistics on the basis of the presence or absence of derived characters. Indeed Hennig has emphasized repeatedly that nothing counts in classification but such characters. Unfortunately, only part of the genotype is expressed in the visible phenotype and yet the hidden part of the genotype is often as important for the future evolution of a phyletic line than that which is revealed in the visible phenotype. Hennig (1950, 176) himself has shown that a potential for stalked eyes is widespread among the acalyptrate dipterans but is realized only in scattered species and genera. A secondary jaw articulation originated at least 14 times independently in the class Aves (Bock 1969). In the genus *Drosophila* the repeated manifestation of concealed potentialities is extremely frequent (Throckmorton 1962, 1965). There is hardly a higher taxon known in which such derived characters do not occur scattered through the system. In any particular case the presence or absence of the character is not in the least determined by the presence or absence of the character in the common ancestor. To be sure the genotype of the common ancestor has the potential for the development of this character but its realization is unpredictable.

When such an independent realization of incipient tendencies occurs with several characters, there is no way to determine in what sequence these derived characters were acquired in different lines and in what sequence the various related lines branched from each other. This can be shown in a diagram (Fig. 7). The only way the cladist can cope with this problem is to say that it will disappear if one takes enough characters. Unfortunately this is not necessarily true. Usually there are not enough such characters available and, when only few are available, the decision will have to be made on the basis of careful, weighting, often hardly distinguishable from being arbitrary. To imply that there really is not much difference between convergence and parallelism (Hennig 1966, 121) reveals a peculiar reluctance to come to grips with one of the major weaknesses of the cladistic system. These are not purely theoretical problems. The recent effort by Inger (1967) and of Kluge and Farris (1969) to arrive at a satisfactory phylogeny of the anurans depends to a considerable extent on decisions concerning the relative primitiveness of various characters.

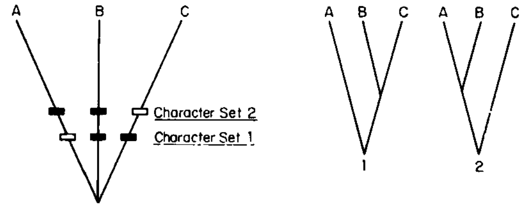

Fig. 7. Contradictory information provided by different sets of characters owing to mosaic evolution. According to character set 1 the lineages B and C form a sister group to A; according to character set 2 the lineages A and B form a sister group to C

Griffiths (1972, 24–26) has a lengthy discussion on the question of whether or not convergence poses a serious problem for cladistics. He is surely on safe grounds in his belief that highly complex characters or character combinations are not apt to be acquired independently in unrelated phyletic lines. (For a critique of the complexity criterion see PETERS 1972, 168–170). However characters (even rather complex ones) can be lost independently in different lines and rather simple characters can be acquired convergently. Unfortunately GRIFFITHS misinterprets DARWIN in the following sentence: "Doubts have been raised about the validity of DARWIN's distinction between 'adaptive' and 'non-adaptive' characters for purposes of evolutionary evaluation, and I therefore do not employ such a criterion" (p. 25). Actually DARWIN makes no such distinction. He speaks only of *ad hoc* specializations which indeed have low phyletic weight and can be acquired convergently. This is what CRACRAFT (1972) has overlooked in his recent discussion of ratite evolution. If several groups of running birds lose their power of flight independently, acquire large size and specialize entirely in running, one would expect them to acquire the ratite complex of characters even if the stem species of this assemblage did not have these characters. This consideration is quite independent of the question whether or not the families of birds which lost their power of flight were a closely-knit group of related genera or only distantly related to each other. Potentially the same objection applies to acquisition of diving adaptations by *Hesperornis*, grebes and loons. The arguments of the cladistic school do not weaken the validity of DARWIN's warning against relying too much on *ad hoc* specializations (see also MAYR 1969, 220, 223).

HENNIG believes that one can distinguish convergence (and parallelism) from synapomorphy by "taking into account as many characters as possible" (1966, 121). This is true in principle, but often impossible to implement. SCHLEE (1971, 23) lists some additional criteria which, indeed, are quite helpful. However, when well established phylogenies are carefully analyzed, it becomes obvious that an unequivocal decision can only rarely be reached. Owing to a very scanty fossil record of insects, as compared, for instance, to that of mammals, the insect taxonomists are not nearly as aware, as they ought to be, of the frequency of parallelism. For instance "within the most advanced group (of therapsid reptiles), the cynodonts, several mammalian features (e. g., dentary-squamosal jaw articulation, loss of alternate tooth replacement, complex occlusion, and double-rooted check teeth) are known to have evolved independently in several phyletic lines" (CROMPTON and JENKINS 1973, 138). Most workers also accept that the incorporation of the quadrate and articular into the middle ear must have occured independently in therian and non-therian mammals. The frequency of the independent acquisition of identical adaptations in birds, for instance a secondary jaw articulation (BOCK 1959) or various specializations in different lines of woodpeckers (BOCK and MILLER 1959), or of independent phyletic advances in *Drosophila* (THROCKMORTON 1965) highlight the difficulties (see BOCK 1967 and PETERS 1972, 168).

More disturbing is the fact that cladists, when actually constructing classifications, never seem to come to grips with the difficulties caused by parallelism and convergence. They simply ignore them.

c. The information content of ancestral characters

Cladists rightfully criticize the adoption of "mere similarity" as the only criterion of taxon delimitation, but so have evolutionary taxonomists for many years. GHISELIN (1969b), SIMPSON (1961) and myself (1969) have consistently pointed out the pitfalls of basing a classification entirely on similarity, particularly (as proposed by the pheneticists) on unweighted similarity. However, this does not justify going to the other extreme by rejecting all consideration of similarity in the construction of a classification. To do so would result in the loss of a great deal of taxonomically important information. After all similarity, when properly evaluated, is an important index of the amount of shared genotype and is the basis for the determination of homology. Cladists completely ignore this and as a result overlook the fact that the retention of a large number of ancestral characters is just as important an indicator of "relationship" (traditionally defined) as the joint acquisition of a few "derived" characters.

Two extremes have been proposed with respect to the relative importance of conservative (ancestral) and advanced (derived) characters. The cladists consider only the latter, while it is sometimes said that it is the study of conservative characters which is most apt to reveal relationship. The evolutionary taxonomist is convinced (and has acted on this basis for the last 100 years) that one must evaluate information from both types of characters in order to be able to construct a sound classification. Nothing could be further from the truth than the claim that "primitive similarities contain no phylogenetic information" (CRACRAFT 1972, 383).

Let me illustrate this with two examples: There are three major families of living gallinaceous birds. Among these the Megapodiidae have the greatest number of primitive characters while the Phasianidae have the greatest number of derived characters. The South American Cracidae are intermediate. They share a few derived characters with the advanced Phasianidae but a far greater number of primitive characters with the Megapodiidae. Traditionally, because they seemingly share to such a large extent the same genotype, the Cracidae have been said to be more closely related to the megapodes than to the Phasianidae. As a cladist, however, CRACRAFT (l. c. 283) insists that the Cracidae are "more closely related" to the Phasianidae because they share with them a few derived characters. I consider this to be a misleading statement. In the aggregate of their characters Cracidae are obviously much closer to the Megapodiidae than to the Phasianidae. To know that the Phasianidae branch off the same branch that leads to the Cracidae is important, but only part of the evidence that leads to a classification.

Let me cite another example which HENNIG has recently used in order to illustrate the superiority of the cladistic approach (1971, 12–14) (See Fig. 8). In the Canadian amber of the Upper Cretaceous two fossil diptera were found which show relationship to two modern families, to the Phoridae, a cosmopolitan family with some 2,500 species, and to the Sciadoceridae with two Recent species, both in the southern continents. In which of the two Recent families should one place these fossils? The original

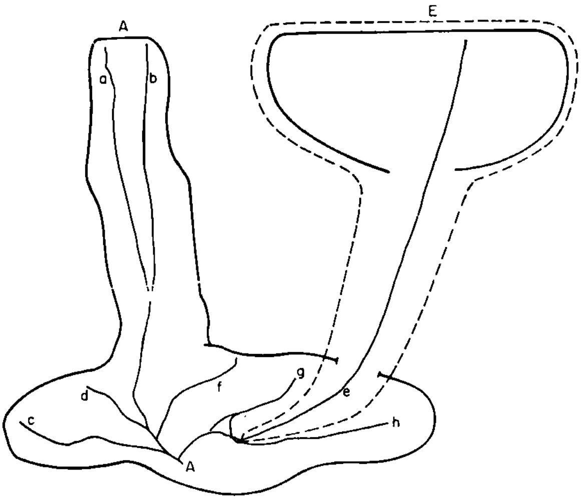

Fig. 8. Two different interpretations of the taxonomic assignment of fossil flies. According to the traditional interpretation (solid outline) the fossils (e) belong to the Sciadoceridae (A); according to the cladistic interpretation (broken outline) they belong to the Phoridae (E). a–h = sublines of the Sciadoceridae with varying evolutionary potentials, most of which (c, d, f, g, h) have become extinct.

describers of the fossils (McAlpine and Martin 1966) acknowledged distant relationship with the Phoridae but placed the fossils in the Sciadoceridae because they are far more similar to species of that family than to any recent Phoridae.

The two Canadian fossils (*Sciadophora* and *Prioriphora*) differ from the living Sciadoceridae consistently only in a single apomorph character, the absence of a discal cell. In two other apomorph characters (absence of anal cell, dorsal arista) the recent Sciadoceridae are variable. One of the two Canadian fossils (*Prioriphora*) acquired some additional phorid-like apomorph characters (e. g., loss of proscutellum, apically enlarged palpus, insertion of R_{4+5} far from the wing tip, m_1 not joining m_2) but in all these characters the other Canadian fossil (*Sciadophora*) retains the plesiomorph (Sciadoceridae-like) condition. Although the Canadian fossils (as a group) show one or two derived characters, they agree in the majority of their characters far better with the living Sciadoceridae than with the Phoridae. In particular, they lack the additional fusion and reduction in the length of wing vein r_3 and the loss of the second basal cell. Also in typical phorids the coxae and femora are stouter and the whole habitus is stockier.

In this case, and in several others I have studied, the entire cladistic re-classification rests on one or two characters. This is implicitly nothing but a return to a "single-character classification." In spite of their exhortations to base classifications on the holomorph (= totality of characters), in practice virtually all dichotomies in classifications are based on exceedingly few characters, often a single character pair. This has been rightly criticized by Darlington (1970, 17).

d. Mosaic evolution

As far as ancestral versus derived character states are involved, cladistics assumes that once "evolution" has "decided" to give one phyletic line a primitive character state and the "sister group" the derived character state, this difference will be perpetuated forever. In many instances, this is, indeed, the case. In many others, and this is completely ignored by the cladists, the potential for the derived character exists in all daughter lines of the original ancestor, as I have just pointed out, but is realized in the various daughter lines irregularly and at different rates, leading to parallel evolution. The claim "if derived character states can be identified, then monophyletic lineages can be constructed" (Cracraft 1972, 381), is clearly not justified.

Cladists have not been able to overcome the difficulties caused by mosaic evolution. Yet it is not true (as has been claimed) that they believe that dichotomies create primitive and advanced *groups*. They realize, like all good taxonomists, that most groups possess a mixture of primitive and derived characters. Even the most primitive group of living mammals, the monotremes, have a number of derived characters.

However, a difficulty is created by the fact that newly acquired characters are sometimes lost again in subsequent evolution. Such a double apomorphy (= secondary primitiveness) would be masquerading as a plesiomorphy. Although some cladists are aware of this possibility, I do not recall that it was ever taken into consideration in the construction of cladistic classifications.

Darwin and classification

Evolutionary taxonomists have long been convinced that they strictly follow Darwinian principles of classification by giving equal consideration to branching *and* to phyletic change. As Simpson (1961, 52) has said: "Evolutionary taxonomy stems explicitly and almost exclusively from DARWIN" (See SIMPSON 1959a, for a more detailed discussion of DARWIN's theory of classification). In recent years cladists have tried to claim DARWIN for their side and NELSON has gone so far as to state: "If, indeed, there is a cladistic school DARWIN is its founder and chief exponent" (1971, 375). He has referred to cladistics as "the DARWIN–HENNIG classification" (1972, 370). Is there any justification in this claim?

DARWIN's *Origin* (1859) was the first major publication to propose evolution through common descent, at that time an entirely novel concept (quite different from LAMARCK's concept of evolution). Genealogical language quite naturally played an important role in this volume. Like the modern evolutionary taxonomist (see above, p. 99) DARWIN started out on a strictly genealogical basis: "The arrangement . . . must be strictly genealogical in order to be natural." Since any group of animals can have only one genealogy, as we have seen above, DARWIN's postulate is an axiom for any evolutionary taxonomist. However this was only the first step for DARWIN, because he continues: ". . . but that the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is *expressed by the forms being ranked under different genera, families*, sections, or orders" (1859, 420) (See also GHISELIN 1969a, 84). It is significant that DARWIN at this point refers back to his famous diagram in the fourth chapter (opposite page 116). Here he shows that three congeneric Silurian species (A, F, and I) evolved into 15 modern genera. These represent three "sister groups" derived from the three Silurian genera. The descendants of A and of I now constitute distinct families or even orders (p. 125). "But the existing genus F 14 may be supposed to have been but slightly modified; and it will then rank with the parent genus F; just as some few still living organic beings belong to Silurian genera" (p. 421). No more explicit statement could be wished for to refute the claim that DARWIN was an exponent of cladistic classification.

GHISELIN and JAFFE (1973) have shown how frequently DARWIN in his classification of the Cirripedia deviated from a cladistic classification: He places *Alcippe* in the Thoracica even though it is on the Abdominalia stem; *Pachylasma*, on the branch leading to the Balaninae, is included with the Chthamalinae; *Pollicipes* gives rise to the Lepadidae (with which it is included) and biphyletically to the stalkless cirripedes (Verrucidae and Balanidae). He could have adopted none of these classifications if he had followed the cladistic definition of monophyly. In each case DARWIN established what the cladists would call a paraphyletic group.

In contrast to NELSON's is BRUNDIN's claim (1972, 107) that the HENNIG method had revealed the "weaknesses of current neo-Darwinistic theory." No other cladist makes such claims. There are several indications in BRUNDIN's writings that he fails to comprehend the Darwinian theory. Does he perhaps believe in some sort of orthogenesis, as implied by the statement: "The evolutionary process is far more orderly than admitted by the neo-Darwinists of today" (l. c. 119)?

Cladistic objections to the methods of evolutionary (combined) classification

GRIFFITHS (1972, 16) has stated that the "combined" (= evolutionary) grouping should be rejected because it "raises serious logical difficulties." HENNIG, furthermore, has claimed repeatedly that a "synthetic" (1971, 11) or "syncretistic" (1966, 77) systematics is unable to elaborate a consistent system ("robs the combination of any scientific value") and leads to serious error. GRIFFITHS (1972, 15–17), however, is the only author who has tried seriously to enumerate and classify what he considers to be the shortcomings of the evolutionary method. In order to minimize future misunderstandings, let me attempt to refute some of his objections.

GRIFFITHS states that I reject the endeavor to achieve "an unequivocal correspondence between phylogeny and classification above the species level" (l. c. 16). On the contrary, I object to HENNIG's narrow definition of phylogeny, which forces the cladist to neglect at least half of the information which phylogeny provides. It is my contention that the traditional method of classification reflects phylogeny to a far greater extent than HENNIG's.

GRIFFITHS further states that it is impossible to measure rates of evolutionary change accurately. Correct! Perhaps it is inappropriate to say a classification should reflect "rates of evolution." However, a classifier should not and can not ignore the *results* of highly uneven rates of evolution. Even if it should be impossible to compare numerically the (slow) rate of evolution between the stem species and the modern crocodilians with the (rapid) rate between the same stem species and the modern birds, every beginner can see how much more drastically the birds differ from the common ancestor than the crocodilians. To ignore this altogether, because it can not (yet) be measured accurately, would seem a poor escape from a difficulty.

A third objection is that the evolutionists fail to provide an objective definition of the categories above the species level. Their definition compares very unfavorably, claims GRIFFITHS (1972, 7–8) with "HENNIG's proposal to define categories above the species level in terms of the origin of the stem species of the member taxa." GRIFFITHS forgets that HENNIG has traded biological meaning for a hoped-for logical consistency. As DARWIN showed (see above), the modern descendants of two Silurian sister species may be, biologically speaking, respectively an order and a genus. To give them the same categorical rank to satisfy HENNIG's formalistic definition may be logically impeccable, but is simply wrong biologically. HENNIG himself, in the mean, time, has abandoned the claim to be able to give a non-arbitrary definition of the higher categories and refrains from placing higher taxa of insects into categories (see above, p. 115). GRIFFITHS' objections to the evolutionary criteria of ranking are based on the special cladistic definitions of monophyly and phylogeny. They become invalid and irrelevant when these definitions are rejected.

It is sometimes stated that the evolutionary taxonomists fail to provide definitions for categories. This is not correct. All I have emphasized is that the species category is the only category for which a non-arbitrary definition is possible. Both SIMPSON (1961) and I (1969) have provided formal definitions for the higher categories, even though for reasons we have stated such definitions have limits to their usefulness.

These are GRIFFITHS' specified criticisms. More generally the cladist criticizes the evolutionary taxonomist for failing to provide simple criteria for making decisions in classification. It would seem to me that the nature of the material precludes a simplistic approach. The number of variables that must be considered in the construction of a classification is so large that simple methods will not work. This is the reason why the evolutionary taxonomist carefully weights the evidence and uses his judgment in arriving at conclusions. He asks what role a higher taxon plays in the economy of nature. He considers the nature of the adaptive break-through which gave rise to the taxon (PETERS 1972). In short, he insists on approaching his material as a biologist and evolutionist, rather than looking for automatic answers. In the short run this may create difficulties and uncertainties, but who would want to question that a classification, which utilizes all potentially available information, is more informative, more predictive, and indeed more truly reflecting past evolution than a classification which arbitrarily restricts itself entirely to the information provided by the branching pattern?

Synopsis

A sound classification of a group of organisms can not be devised without a well considered reconstruction of its phylogeny.

One component of such a reconstruction is an establishment of the branching pattern of the various phyletic lines, and the design of a cladogram. HENNIG has demonstrated that this can be done in a relatively unequivocal manner by classifying characters into apomorphous (derived) and plesiomorphous (ancestral) characters.

The high information content of derived (apomorph) characters was appreciated by many taxonomists long before HENNIG, but never sufficiently stressed, and, in fact, entirely ignored by some authors. The emphasis on the proper weighting of synapomorphies, under the impact of HENNIG's cladistic theory, has been a healthy development in systematics.

It would require an impartial analysis to determine how many recent improvements in the classification of fishes, insects, and other groups were the result of a rigorous application of cladistic analysis. CRACRAFT (1972) has recently asserted that application of the cladistic method would revolutionize avian taxonomy. However, after 12 pages of discussion, he failed to produce even a single case in which he could demonstrate that the currently accepted classification was wrong. All he was able to show was that a classification based only on branching points is sometimes different from a classification in which phylogenetic divergence is given primacy. The case of the fossil Sciadoceridae (see pages 119–120 above) is another illustration of a change in classification, but not necessarily an improvement. The reasons why the cladistic method cannot show more achievements should be obvious from the previous discussion.

Cladistic grouping encounters many difficulties even if we exclude unacceptable decisions in ranking. For instance, very often there are not enough apomorphous characters available, or else there is doubt as to which of two alternative character states is ancestral and which is derived, and, finally, owing to mosaic or parallel evolution, there may be conflict between the information provided by different apomorphous characters.

As valuable as the cladistic analysis is, it does not automatically provide a classification. By making use of only one of the two available sets of phylogenetic data, cladistics produces classifications which are less able to serve as general reference systems than evolutionary classifications, because they have a poorer information content. Evolutionary taxonomists, by weighting the information from both sources, arrive at classifications which may be criticized as being more "subjective", but which reflect evolutionary history more accurately and are therefore more meaningful biologically. The cladist believes that the simple adding up of synapomorphies will provide the correct classification, so to speak, automatically. The evolutionary taxonomist, in contrast, feels that only a careful weighting of all the evidence will reveal meaningful degrees of relationship, in the sense of inferred genetic relationship. He feels, furthermore, that a classification must pay attention to major adaptive events in evolutionary history, like becoming terrestrial or airborne, since these are of greater importance for the ranking of taxa than the mere splitting of phyletic lines. JOHNSON (1970) and MICHENER (1970, 20–22) are other systematists who have recently stated the case in favour of evolutionary (synthetic) systematics.

GRIFFITHS (1972, 17) has proposed that if one wants to express the effects of different degrees of evolutionary divergence in different phyletic lines, one should for this purpose construct an entirely separate classification, in other words that one should have several (or at least two) sets of classifications. This proposal strikes me as altogether impractical. PETERS and GUTMANN (1971, 256) likewise reject the purely formalistic approach of the HENNIG school and demand that it be replaced by a biological attitude toward the morphological evidence. This includes giving due consideration to the size of adaptive breakthroughs.

An eclectic classification which considers with equal care the branching points in phylogeny and all aspects of phylogenetic divergence would seem the best way to generate biologically meaningful classifications, permitting the greatest number of broad generalizations. DARWIN's advice to use both these sources of information was adopted by the most successful classifiers of the last 100 years.

In conclusion, it is evident that, no matter how useful cladistic analysis is, it cannot be automatically translated into a classification.

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In a field as difficult and controversial as the theory of classification no one can expect to be always right. I would be completely gratified if my analysis were to contribute to a clarification of the issues.

Summary

Three theories of classification compete with each other at the present time, each claiming to be best suited for meaningful and reliable classification. One of these, HENNIG's theory of cladistics, uses the "recency of common descent" as the primary criterion for the delimitation and categorical ranking of taxa.

The opponents of cladistics, however, raise the objection that one must make a difference between cladistic analysis and cladistic classification. Admittedly, since every natural group (taxon) must consist of closest relatives, it is indispensable in the delimitation of such a group to make sure that all members are derived from a common ancestor, that is that the group is monophyletic. HENNIG's method of classifying characters in plesiomorphous and apomorphous ones is excellently suited to lend precision to an unequivocal determination of the common ancestor. HENNIG's cladistic analysis is thus an important contribution to systematic methodology.

The possibility of converting the results of such analysis directly into a classification, as is demanded by the cladists, is however questioned by many systematists. Categorical rank ("family," "order," etc.) of a taxon is determined according to cladistic theory by the branching point of the dendrogram, and so-called sister groups must be given the same categorical ranking. This means that the branching point fixes irrevocably the categorical rank of subsequently evolving taxa without any consideration of evolutionary events that happen later (except branching).

Such a "downward" classification is unable to take into consideration the sometimes rather drastically different fates of several phyletic lines that are derived from the same common ancestor. A group which had invaded an entirely new adaptive zone (as for instance, the birds) is given the same rank as a sister group (like the crocodilians) which had remained in the ancestral adaptive zone. Cladistics classifies exclusively on the basis of branching points instead of an evaluation of the characteristics and adaptive complexes of taxa. The characters of taxa are taken into consideration only as far as this is necessary for the determination of the branching points.

The redefinition of three widely-used technical terms, phylogenetic, relationship, and monophyletic, by the cladists has caused a great deal of confusion in the literature. There is no reason to abandon the traditional definitions.

Multiplication of species is not a dichotomy in every case and in periods of intensive speciation it occurs sometimes that three or more sister groups originate simultaneously.

The new diagnostic characteristics of a phyletic line emerge often only long after the original branching-off from the ancestor. A downward classification is misleading in such cases. It is unrealistic to separate the older taxa of a new phyletic line from the parental group as long as they are still joined to it by the common possession of critical characters. It is equally unrealistic to act during classification as if the occurrence of a sidebranch resulted in the extinction of the main line.

It leads to striking contradictions if one determines the categorical rank of a taxon on the basis of the absolute geological time that has passed since the original branching. Only a slight improvement is achieved by accepting "relative" age as criterion.

The occurrence of parallel evolution, of convergence, and of mosaic evolution is on the whole not considered in the classifications of the cladists. The information content of plesiomorph characters is likewise ignored. As a result the information content of cladistic classifications is greatly reduced.

The traditional method of classification, according to which both processes of phylogeny, branching, and subsequent divergence are considered equally, is the method which was proposed by Darwin in 1859 and was used by him in his own systematic works, for instance in his monograph of the Cirripedia.

The objections which have been raised by the opponents of cladistics lead to the conclusion that it is not possible to translate the results of a cladistic analysis, that is the cladogram, directly into a classification.

Zusammenfassung

Kladistische Analyse oder kladistische Klassifikation

Zur Zeit werden drei Theorien der Klassifikation unterschieden, von denen jede behauptet in der Lage zu sein, das beste „allgemeine Ordnungssystem" schaffen zu können. Eine dieser Theorien ist die kladistische Theorie, von W. Hennig begründet, die den Abstand von der nächsten gemeinsamen Stammart (Vorfahren) als Maßstab für die Abgrenzung und kategorische Eingliederung von Taxa annimmt.

Die Gegner der kladistischen Klassifikation erheben dagegen den Einwurf, daß man zwischen kladistischer Analyse und kladistischer Klassifikation unterscheiden muß. Da jede natürliche Gruppe (Taxon) aus engsten Verwandten bestehen muß, ist es für die Abgrenzung einer solchen Gruppe unerläßlich nachzuweisen, daß alle Mitglieder von einem gemeinsamen Ahnen abstammen, d. h. daß die Gruppe monophyletisch ist. Hennigs Methode, Merkmale in plesiomorphe und apomorphe zu trennen, ist hervorragend geeignet, die eindeutige Bestimmung des gemeinsamen Vorfahrens zu präzisieren und die anzuerkennenden Gruppen einheitlicher zu gestalten. Hennigs kladistische Analyse ist somit ein wichtiger Beitrag zur systematischen Methode.

Die Möglichkeit, die Ergebnisse dieser Analyse unmittelbar in eine Klassifikation zu übersetzen, wie es von den Kladisten vorgeschlagen wird, wird jedoch von vielen Systematikern bezweifelt. Der kategorische Rang ("Familie", „Ordnung" usw.) eines Taxons wird gemäß der kladistischen Theorie durch den Zweigpunkt des Stammbaumes bestimmt, und sogenannte Schwestergruppen müssen in dieselbe Kategorie eingereiht werden. Das bedeutet, daß der Verzweigungspunkt unwiderruflich den kategorischen Rang der später entstehenden Taxa festlegt, ohne Rücksicht auf später erfolgende Evolutionsgeschehnisse.

Solch eine „Abwärts-Klassifikation" kann die unterschiedlichen Geschicke der mehreren Deszendenzlinien, die von der gemeinsamen Stammart abzweigten, nicht berücksichtigen. Eine Gruppe, die in eine völlig neue Adaptationsebene eingewandert ist (wie z. B. die Vögel), wird genauso behandelt, wie eine Schwestergruppe (wie z. B. die Krokodile), die in der ancestralen Adaptationszone verblieben ist. Statt Taxa aufgrund ihrer Merkmale und Adaptationskomplexe zu klassifizieren, klassifiziert die Kladistik ausschließlich aufgrund der Verzweigungspunkte. Sie berücksichtigt die Merkmale der Taxa nur so weit, als das für die Erfassung der Verzweigungspunkte nötig ist.

Die Umdefinierung der drei wohlbekannten Fachausdrücke phylogenetisch, Verwandtschaft und monophyletisch durch die Kladisten hat viel Verwirrung in der Literatur verursacht. Es besteht kein Grund, die traditionellen Definitionen aufzugeben.

Artbildung ist nicht notwendigerweise eine Dichotomie, und in einer Periode von intensiver Artbildung können manchmal drei oder noch mehr Schwestergruppen entstehen.

Die charakteristischen neuen Eigenschaften einer Stammlinie treten oft erst lange nach der ursprünglichen Abzweigung in Erscheinung. Eine Abwärts-Klassifikation ist in diesen Fällen irreführend. Es ist unrealistisch, die älteren Taxa einer neuen phyletischen Linie von der Elterngruppe zu trennen, solange sie mit ihr noch durch gemeinsamen Merkmalbesitz verbunden sind. Ebenso unrealistisch ist die Annahme, daß das Abzweigen einer phyletischen Linie die Stammlinie sozusagen auslöscht.

Den kategorischen Rang eines Taxons aufgrund der absoluten geologischen Zeit seit der ursprünglichen Abzweigung zu bestimmen, führt zu großen Widersprüchen. Das „relative" Alter als Maßstab anzunehmen ermöglicht nur eine geringe Verbesserung.

Das Vorkommen von paralleler Evolution, von Konvergenz und von Mosaikevolution wird in den Klassifikationen der Kladisten im allgemeinen nicht berücksichtigt. Der Informationsgehalt plesiomorpher Merkmale wird gleichfalls ignoriert. All das mindert den Informationsgehalt kladistischer Klassifikationen.

Die traditionelle Methode der Klassifikation, die die beiden Vorgänge der Evolution, Verzweigung und nachfolgende Divergenz gleichmäßig berücksichtigt, ist diejenige, die Darwin 1859 vorschlug und in seinen eigenen systematischen Arbeiten (z. B. in der Monographie der Cirripedia) benutzte.

Die Einwürfe, die von den Gegnern der Kladistik erhoben werden, deuten darauf hin, daß man eine Klassifikation nicht einfach aus dem Ergebnis der kladistischen Analyse, d. h. dem Kladogram ablesen kann.

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The systematics and evolution of the phylum Phoronida

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With 23 figures

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The phylum Phoronida consists of two genera (*Phoronis* and *Phoronopsis*) and some eleven species, exclusively marine and entirely free-living. This phylum must be considered as primitive Deuterostomia (ZIMMER 1964; EMIG 1973b). Phoronid taxonomy has been studied by several authors (BENHAM 1889; CORI 1890; SELYS-LONGCHAMPS 1907). CORI (1939) listed sixteen species, omitting *Phoronopsis californica*, but his account is unsatisfactory and does not make any mention of the degree of morphological variation. Since then *Phoronis pallida* has been described by SILÉN (1952) and *Phoronis bhadurii* by GANGULY and MAJUMDAR (1967). The dubious validity of some species has been commented on by SILÉN (1952) and MARSDEN (1959), but at this time the taxonomy of *Phoronida* obviously needs revision. The author (EMIG 1971b) studied the degree of variation of all taxonomic characters and concluded that several species can be considered as synonyms owing to the variability of many of these features (Tables 1, 2). In the present work study of several of these characters is completed or confirmed.

I. Taxonomic characters

Phoronid taxonomy is based on external and internal anatomy, the latter being studied by means of serial cross sections. The characters are listed and discussed below.

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