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On the ■ Phylogenetic Classification

[Pp. 499—524, 2 text-figures]

O klasyfikacji filogenetycznej

О филогенетической классификации

Abstract. An axiomatization of the logics of phylogenetic classification, based largely on HENNIG's theory of cladism, is presented. It is shown that in principle two different methods can be employed for the purpose of phylogenetic classification, both of which are presently used. The first one, the quantitative approach is, essentially, the one employed in numerical taxonomy. The second one, the qualitative method, involves an evaluation of the phylogenetic importance of various sets of taxonomic characters. It is the one most widely used at the time being, and it may lead to correct results, but mistakes cannot be excluded.

In the last section are discussed the implications for the species concept of the view propounded.

'only a clear statement of how the conclusions were arrived at can disclose the causes of divergent opinions'

(H. SZARSKI, 1962, p. 195)

'phylogenetic... classification is possible only through the use of precise, non-arbitrary conventions'

(G. NELSON, 1973, p. 359)

'do we wish to classify organisms, or the classifier's response to organisms?'

(M. T. GHISELIN, 1966, p. 213)

Recent years have witnessed a lively debate on the issue of phylogenetic classification instigated, in particular, by the theory of cladism published by

HENNIG (1966). This work has met with enthusiasm in some quarters, with coolness and rejection in others, but of late the trend seems to be directed towards the former alternative (cf. NELSON, 1972). Although HENNIG's book is distinguished by an unusual stringency for biological treatises it is still very difficult to read, and if I understand him correctly, it seems that he has not in every instance drawn the ultimate consequences of his own premises. This, at least, is the result I have come to when trying to axiomatize the theory (LØVTRUP, 1973; 1974).

Since this work was completed, I have had the opportunity to think more about the problem, particularly on the application of the theory in practice. In the present paper I am going to present the outcome of my endeavours, once again in axiomatic form. I presume that it may be considered a very ambitious undertaking to state a biological argument in this way. However, if biology is to be an explanatory, as contrasted to descriptive, empirical science, then biological thinking must obey the laws of deductive logic. I do not doubt that a majority of biologists agree with, and adhere to, this postulate. If this is the case, the only difference between an axiomatic and a non-axiomatic presentation is that in the former case it is much easier to discover the errors committed by the author and also to pinpoint exactly which premises are in dispute.

In order to give a consistent statement of my views I cannot avoid repeating some of the axioms and premises from my earlier work, but to save space the discussion is reduced to a minimum. For further details I must therefore refer the reader to the mentioned publications.

CLADISM

I shall begin by stating two methodological premises which form the basis for all phylogenetic research. These are:

- (I) All animals*, living and extinct, have a common phylogenetic origin.
- (II) Barring convergence, the varying degrees of similarity obtaining with respect to the properties possessed by various animals are expressions of phylogenetic kinship.

These premises, asserting that phylogenetic evolution is a reality and phylogenetic classification a possibility, are endorsed by most, if not all, biologists. But in order to proceed beyond this stage it is necessary to introduce a number of further axioms, all concerned with phylogenetic classification. The first axiom states:

* The present axiomatization is stated with reference to animals; this does not imply that I do not believe that the other living organisms have undergone phylogenetic evolution, nor does it exclude that the present theory may be of interest for others than zoologists.

(A 1)* Animal classification involves the distinction and naming of classes of animals, defined by certain properties which are possessed by all members of a set.

The classification referred to in A 1 need not be a phylogenetic classification, but the subsequent discussion will deal only with this alternative. It may be mentioned that premise (I) implies that the properties referred to have been acquired in the course of phylogenetic evolution.

(D 1) A taxon is defined by a set of properties distinguishing a particular class of animals. All individuals, past, present or future, possessing the whole set of properties are said to be members of the taxon.

(D 2) Taxonomic characters are properties which have been, or may be, used to distinguish a taxon.

In principle one may maintain that all properties possessed by an animal are taxonomic characters, but from D 1 it follows the latter must be exhibited not only by all extant members of a given taxon, but also by all members of succeeding generations. Hence it follows that the features which are the subject of genetical studies cannot be used as taxonomic characters.

I shall put down the following axiom:

(A 2) All properties possessed by an animal, and which are transferred unchanged from generation to generation, are either actual, or potential, taxonomic characters.

The eventuality that new taxonomic characters arise, through losses or gains, is dealt with later. One logical difficulty is encountered with respect to sexual characters, either the latter must be excluded from the characters referred to in A 2, or else sexual subtaxa must be erected for all bisexual animals. The former alternative obviously is not acceptable to practically working systematists, because sexual characters often are very valuable for taxonomic distinctions. It must be emphasized that this is a matter of expediency, I venture to postulate that it may be possible, in each and every instance, to find some characters, maybe chemical properties, which are shared by both males and females of a given taxon.

It needs be emphasized that A 2 should not be interpreted to mean that all the taxonomic characters known to distinguish a certain taxon must be used as diagnostic characters.

(A 3) All actual and potential taxonomic characters possessed by an animal can be known only for extant ones.

From A 1, A 2 and A 3 we may derive the following theorem:

(T 1) Only extant animals can be classified.

In order to appreciate the intended implication of this theorem, which possibly may be regarded as a provocation by some palaeozoologists, it should be noted that a phylogenetic classification is an empirical theory which must be exposed to continuous Popperian attempts of falsification. If we happen to have classified together some living and extinct animals on the basis of osteological

* In the present paper 'A' stands for 'axiom', 'D' for 'definition' and 'T' for 'theorem.'

characters, and subsequently discover that other properties, say, chemical parameters, dictate that changes are made in the classification of the living ones then, evidently, we shall not be able to decide whether or not corresponding modifications are required in the extinct ones. The fact that, in contrast to what holds for living animals, the classification of fossil ones is testable only within narrowly circumscribed limits, is the purported meaning of T 1. Whether or not the chosen phrasing appropriately covers this notion is, of course, a point that may be argued.

In any case I believe that the recently acquired insight in the soft anatomy of *Latimeria* may serve to corroborate the theorem, for this animal has turned out to be so 'primitive' in this respect that it must be much more distantly, related to the extinct Coelacanthidae than was heretofore supposed (cf. JARVIK 1968). From T 1 follows:

(T 2) The discovery of a new fossil has no impact on classification.

One encounters repeatedly in the literature statements to the effect that the solution of some phylogenetic problem must await the emergence of new fossil data. T 2 stresses the point that if, with the wealth of information which it is possible to extract from living animals, we cannot arrange the latter in a correct phylogenetic system, then no amount of fossil data will ever help us to approach this goal.

(A 4) Taxonomic characters differ with respect to the number of individuals in which they are found. Some prevail in all animals, some only in subsets among the latter, some only in subsets within the subsets, etc.

This axiom, stating an empirical observation, warrants the conclusion:

(T 3) Taxa can be arranged hierarchically.

The principles on which the hierarchy is constructed need no further explanation. The establishment of such a system allows for the ranking of the various levels. The rank of a taxon may be defined in the following way:

(D 3) A taxon T_j , of rank j , is a set of n_{j+1} taxa T_{j+1} , of rank $j+1$ ($j \geq 1$).

From D 3 it follows that, in contrast to the custom adopted in Linnean classification, the numbering begins at the apex of the hierarchy. To designate the relative location of a taxon in the hierarchy, I shall introduce the epithets 'superior' and 'inferior', defined in the following way:

(D 4) For $i < j$, the taxon T_i is superior to T_j , and T_j inferior to T_i .

At this stage we must introduce premises ensuring that our classification becomes phylogenetic. We may first observe that from (II) and A 1 it follows:

(T 4) Classification of animals will bear relation to their phylogenetic kinship.

Apparently, no matter how we classify, some phylogenetic affinities will be reflected. We shall, however, specify the demands to be made on a phylogenetic classification:

(D 5) A phylogenetic classification of kingdom Animalia is a classification which correctly discloses the phylogenetic kinship between the various animal taxa.

From (I) it follows that all animals have arisen through a unique process of evolution. and hence:

(T 5) The phylogenetic classification of Animalia is a unique hierarchy.

If we assume that similarities may obtain which do not reflect a phylogenetic relationship, as implied by the reservation with respect to convergence made in (II), then it follows that the properties which can be used as taxonomic characters must represent a genetic relationship, thus:

(T 6) In phylogenetic classification a property can be used as a taxonomic character for a taxon T_j only if it is non-convergent, i. e. if its presence in all members of the purported taxon can be referred to its acquisition at a unique occasion in the course of evolution.

A taxon which obeys the criterion stated in T 6 is called a monophyletic taxon, defined as follows:

(D 6) A monophyletic taxon T_j is a concept, defining a class of animals, comprising all those individuals which are descendants of the first individuals endowed with all the taxonomic characters of T_j .

Thus:

(T 7) The hierarchy of phylogenetic classification comprises only monophyletic taxa.

In order to establish the correspondence between phylogenetic classification and the process of evolution it is necessary to introduce a postulate concerning the mechanism through which members of new taxa arise. Here we encounter the first important contribution of HENNIG, who introduced the concept of 'sister group', defined as follows (1966, p. 139): 'Species groups that arose from stem species of a monophyletic group by one and the same splitting process may be called "sister groups"... and 'every monophyletic group, together with its sister group (or groups), forms — and forms only with them — a monophyletic group of higher rank'.

From these statements it appears that HENNIG allows for the possibility that a 'species group' may have two or more sisters. However, from HENNIG's book (1966) and elsewhere in the literature, it appears that sister groups usually are twins, and the process through which they arise accordingly is a dichotomy. I shall adopt this notion in the following axiom:

(A 5) Members of the taxa T_{j+1} have arisen through a process of dichotomy involving members of the taxon T_j in which they are included.

It appears that this axiom is regarded with considerable aversion by systematists. I acknowledge that the existence of trichotomies, tetrachotomies, etc., cannot be excluded, but I submit that their occurrence is inversely proportional to the purported number of branches and, furthermore, that among the superior taxa they probably are non-existent. On the genus-species level this phenomenon possibly is more common, maybe primarily because we do not possess the knowledge required to accomplish further subdivision. But this admission does not imply that a genus with hundreds of species correctly reflects a phylogenetic reality, rather, this marvel is a consequence of the strait-jacket which the Linnean categories impose upon classification, as evidenced by the fact that various auxiliary categories often are invoked to subdivide such genera.

Thus, although bifurcation must be the most usual type of branching, the categorical formulation of A5 is not theoretically justified. But this expedient, adopted for the sake of simplicity, ought to be acceptable when it is realized that, after proper modifications, most, maybe all, of the various theorems will be valid for trichotomous, tetrachotomous, etc., dendrograms.

From A 5 we may conclude:

(T 8) In phylogenetic classification there are two, and only two, taxa T_{j+1} included in any taxon T_j .

I further propose to replace 'sister groups' by 'twin taxa', defined as follows:

(D 7) The taxa T_{j+1} included in the taxon T_j are twin taxa.

As a token of conciliation I shall add that 'triplet taxa', 'quadruplet taxa', etc. may also occur.

From the principle used in the construction of phylogenetic hierarchies we may now derive the following theorem:

(T 9) If x is a taxonomic character in the taxon T_j , then either \bar{x} , i. e. not— x or absence of \bar{x} , must be a taxonomic character in its twin taxon or x will distinguish a superior taxon.

It is easily seen that if the phenomenon dealt with in T 9 is extended to comprise all T_j characters, then the taxon is undefinable. Hence the definition:

(D 8) The taxon T_j , purportedly distinguished by the characters x, y, z , etc., is undefinable if not at least one member of T_j possesses the characters $\bar{x}, \bar{y}, \bar{z}$, etc.

From T 8 also follows:

(T 10) The hierarchy of phylogenetic classification can be represented by a dichotomous dendrogram.

Evidently, a dendrogram need not be comprehensive in the sense that it represents the whole of the animal kingdom, it is possible to select a part of the hierarchy for special attention, and this will itself constitute a hierarchy about which we may conclude:

(T 11) Any part of the phylogenetic hierarchy of the animal kingdom comprising more than one taxon is a dichotomous dendrogram.

From T 7 and T 11:

(T 12) A phylogenetic dendrogram always represents the classification of a monophyletic taxon.

The truth of this theorem requires that the classification is inclusive in the sense that it represents all the members of the taxon.

From A 5 further follows:

(T 13) The taxon T_j is older than the taxa T_{j+1} which it includes.

A property that has originated at a unique occasion must have been present before the taxon defined by it gave rise to two new taxa through dichotomy, hence from T 6 and A 5:

(T 14) No taxonomic character defining the taxon T_j can have originated later than any of those defining the included taxa T_{j+1} .

And conversely:

(T 15) No taxonomic character defining the taxa T_{j+1} included in T_j can have originated earlier than any of those defining T_j .

We may also deduce:

(T 16) The initial step in the dichotomy leading from the taxon T_j to the taxa T_{j+1} must have involved that the at least one member of the taxon T_j acquired a T_{j+1} character \bar{x} , entailing that the remaining members of T_j came to belong to the T_{j+1} twin taxon distinguished by \bar{x} .

From the statements T 14 and T 15 it is possible to delimit the period during which a taxon T_{j+1} comes into existence, namely:

(T 17) The creation of the taxon T_{j+1} , i. e. the origination of all its taxonomic characters, has occurred during a period of time lasting from the subdivision of the taxon T_j , in which it is included, and until it itself became subdivided into two taxa T_{j+2} .

Evidently, the decisive event in the creation of a pair of twin taxa is that some members of the ancestral taxon, distinguished by a particular taxonomic character, become isolated. Since the process of isolation and/or the origination of a new taxonomic character may be fortuitous, we may state as an axiom which is empirically supported:

(A 6) The origination of a pair of twin taxa T_{j+1} from the taxon T_j , in which they are included, is a chance event.

From this it follows that it is impossible to predict when each of a pair of twin taxa undergoes dichotomy, and hence one cannot make any predictions about their relative age, since this parameter refers to the time when each of them gave rise to a new pair of twins. What happened when the taxon T_j , from which they arose, was bifurcated, was not that the taxa T_{j+1} became defined, but only the taxonomic level $j+1$. Therefore it would be more correct in T 17 to write 'two incipient taxa T_{j+2} '. It thus follows:

(T 18) Nothing can be predicted about the relative age of a pair of twin taxa.

This theorem stands in apparent contradiction to the assertion made by HENNIG (1966) that 'sister groups' are of equal age, the reason being that HENNIG measures the age of a taxon from the first, and I from the last, bifurcation involved in the history of a taxon.

From A 5, T 10 and T 17:

(T 19) The horizontal lines in a phylogenetic dendrogram represent the process of dichotomy through which new taxa arise, while the vertical lines represent the periods of time through which taxonomic characters have been acquired.

Since, in T 13, the taxon symbolized by T_j is nearer the apex than are the taxa T_{j+1} , it follows:

(T 20) The direction of the course of phylogenetic evolution corresponds to a movement from the apex to the base in the phylogenetic hierarchy, or from taxa of low, to taxa of high, numerical rank.

From this theorem, together with D 5, we derive:

(T 21) Phylogenetic classification must begin at the apex of the hierarchy.

From A 6 we may also conclude:

(T 22) Nothing can be predicted about the frequency of dichotomy in the various regions of a phylogenetic hierarchy.

The implication of T 22 is, of course, that the frequency may be expected to vary from one region to the other. In order to elucidate the consequences of this axiom, we shall introduce a concept called 'terminal taxon':

(D 9) A terminal taxon is a taxon located at the base of the hierarchy.

It is seen that if, in two twin taxa near the base of the hierarchy, one or more branchings have occurred in one of them subsequent to their separation, but none in the other taxon, then the terminal taxa cannot be of equal rank. Hence, we may conclude:

(T 23) The terminal taxa in the hierarchy need not all have the same rank.

From T 23:

(T 24) The numbering of the taxonomic levels in the phylogenetic hierarchy is consistent only when it begins at the apex.

This conclusion justifies the decision made above concerning the numbering of the taxonomic levels.

We shall now introduce the concept 'resolution':

(D 10) A phylogenetic classification has been brought to the point of complete resolution when it is impossible to subdivide the terminal taxa any further.

Complete resolution is the goal that is but seldom reached; most classifications must be considered to represent 'incomplete' or 'partial' resolutions. Depending upon the degree of resolution, the terminal taxa may vary considerably with respect to their rank in the Linnean classification, if they happen to occur in the latter. They may represent phyla, classes and orders, but also genera, species and subspecies, and nothing prevents the degree of resolution from varying in different parts of the dendrogram. In this connection it must also be stressed that in a completely resolved classification, the terminal taxa must by no means coincide with the lowest recognized Linnean taxa — species or subspecies. Rather, if it is possible, on the basis of variations obtaining within a taxon of this kind, to establish subgroups that have arisen through dichotomy as envisaged in A 5, then it is clearly not only permissible, but mandatory, to introduce these as terminal taxa in the system.

Since it is possible to assign a number to the rank of a taxon it follows:

(T 25) Within any monophyletic taxon the absolute rank of the included taxa may be objectively evaluated, irrespective of the degree of resolution.

It is evident that the 'absolute' rank thus determined will be relative if the classified taxon comprises only part of the living world. It is easily visualized that the taxonal ranks established in an incompletely resolved dendrogram are immutable for, if classification must begin at the apex, it follows that further resolution can concern only taxa inferior to those already prevailing. However, this theorem is valid only if the classification is inclusive, as defined above (p. 504).

It was observed in T 17 that a taxon comes into existence, in the sense of

being immutably defined, only at the moment it becomes subdivided into two taxa of higher rank. From this we may conclude:

(T 26) The terminal taxa in a completely resolved classification are taxa under creation and, as such, are not immutably defined.

We shall need the following concept:

(D 11) A phylogenetic line is a sequence of taxa in the hierarchy, $T_1, T_2 \dots T_n$, each of which is included in the preceding one.

It is readily grasped that a phylogenetic line will be step-like, the horizontal and the vertical parts having the implications stated in T 19.

In T 13 and T 18 we have deduced relations between taxonomic rank and age. These theorems may be generalized as follows:

(T 27) In a phylogenetic line T_j is older than T_{j+1} , which in turn is older than T_{j+2} , etc. Nothing can be predicted about the relation between age and rank in taxa in disparate phylogenetic lines.

It is a well-known fact that many taxa, particularly those of superior rank, differ from their twin taxon in a number of taxonomic characters. It is obvious that these characters must have been acquired at more than one occasion, and I shall even venture to submit the following postulate:

(A 7) The several independent taxonomic characters defining certain taxa have been acquired at separate occasions.

From T 16, T 17 and A 7:

(T 28) If the taxon T_j is distinguished by n taxonomic characters, then the creation of the taxon has involved n steps of dichotomy.

It is to be understood that if a set of properties are mutually dependent, then they are counted only as one character. Since, clearly, only one of the branches which arose through each of the repeated dichotomies implied by T 28 exists today, we may conclude:

(T 29) In the steps of dichotomy involved in the creation of the taxon T_j , all the branches that did not acquire T_j characters became extinct.

These extinct groups may be represented in the dendrogram by side branches to the vertical line which represent the phase of evolution during which they arose. To the extent they are known as fossils we may therefore conclude:

(T 30) All fossil groups represent extinct side branches to existing taxa, and more than one fossil group may be thus affiliated with the same taxon T_j .

We shall further state the consequences of two very likely events, namely, that a contemporaneous taxon becomes extinct or that a new taxon is discovered. From the rules involved in the construction of dendrograms it follows:

(T 31) The extinction of the members of a taxon T_{j+1} requires that its twin taxon is raised to the level j , its $j+1$ characters becoming j characters, and that the numerical value of the ranks of the taxa it includes is lowered by one.

(T 32) The discovery of the members of a new taxon T_{j+1} requires that, from the taxon T_j which includes the new taxon, a twin taxon to the latter is erec-

ted, defined by some of the previous T_j characters, and that the numerical value of the ranks of the taxa included in the twin taxon is raised by one.

The consequence of HENNIG's theory (1966), as interpreted by me, is that the phylogenetic 'tree' is a dichotomous dendrogram, with the reservation that in some cases it may be trichotomous, etc. If this is true, we may conclude that: (T 33) The origination of new taxa has occurred at all taxonomic levels.

This theorem is clearly at variance with the rather common notion that new forms arise from 'generalized types'.

The simplest dichotomous dendrogram which allows for alternative classifications is the one comprising three terminal taxa (Figure 1). It is seen that,

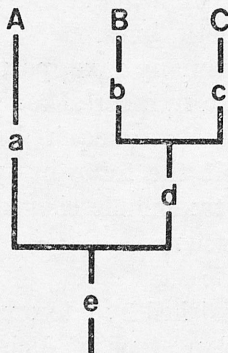


Fig. 1. Phylogenetic classification of the three terminal taxa, A, B and C, in a dichotomous classification, in the present context called a 'basic classification'. The vertical lines (a) — (e) represent the five separate taxa comprised by the dendrogram

by replacing A by either B or C, three different classifications will obtain. I have turned the hierarchy upside down in the figure, a measure implying that the time scale is represented by the ordinate. This way of illustration is a convention in phylogenetic literature which unquestionably facilitates the visualization of the course of evolution. I have not, however, changed the terminology correspondingly, hence, the base of the hierarchy and the terminal taxa are to be found at the upper side of the diagram.

Figure 1 is seen to embody five vertical lines, each of which represents a separate taxon. If we have to incorporate a new taxon, D, in this dendrogram, it may be a twin taxon to either one of these five taxa (Figure 2). As three classifications are possible for $n = 3$, it follows that for $n = 4$ the number of different classifications, C_4 , is $3 \times 5 = 15$. This is a special application of the general equation for the number of different dichotomous dendrograms, $C_n = \prod_{i=1}^{n-1} (2i+1)$, which can be constructed with n separate taxa (FITCH and MARGOLIASH, 1969).

It is possible to estimate the minimum number of taxonomic levels which are required to accommodate n terminal taxa in a dichotomous dendrogram. Thus, if n is a power of 2, and the frequency of dichotomy uniform, then the number of taxonomic levels, j , will be $j = 1 + \log n / \log 2$. The extra taxon added represents the monophyletic taxon in which all the terminal taxa are included.

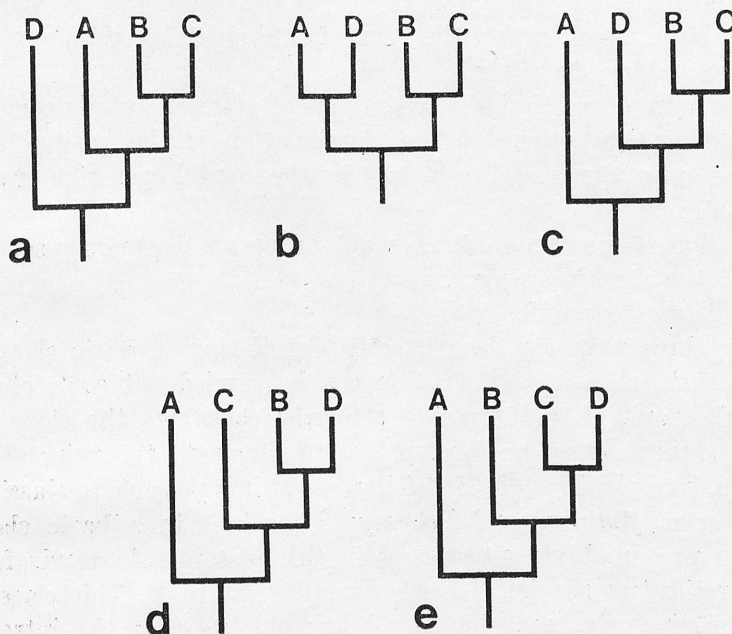


Fig. 2. The five possible alternatives for the classification of a fourth taxon, D, relative to the basic classification represented by Figure 1

Since n may not be a power of 2, and since, according to T 22, the frequency of dichotomy may be expected to vary, the calculated number represents a minimum value. Hence:

(T 34) The phylogenetic classification of n terminal taxa requires a number of taxonomic levels $j \geq 1 + \log n / \log 2$.

Therefore, although the twenty-one Linnean categories available for animal classification may suffice in some cases, their number is surely too small for the classification of the most populous taxa. There are, however, more weighty reasons why the Linnean categories cannot be accommodated in phylogenetic classification (cf. LØVTRUP, 1973; 1974).

With C_n growing so fast as shown by the above equation it is obvious that, unless special methods obtain for systematizing phylogenetic classification, the latter task must be insuperable. Fortunately, it seems possible to employ a stratagem called 'basic classification', defined as follows:

(D 12) A basic classification is a classification comprising three terminal taxa.

We may conclude:

(T 35) A basic classification contains five taxa, representing the levels j , $j+1$ and $j+2$.

The latter theorem is easily confirmed through reference to Figure 1, in which the vertical line (e) represents the level j , the lines (a) and (d) the level $j+1$, and the lines (b) and (c) the level $j+2$. For convenience we shall here introduce the following concepts:

(D 13) In a basic classification the taxa of rank $j+1$ are primary, the taxa of rank $j+2$ secondary, twin taxa.

We have seen above that the extinction of a taxon entails certain changes in rank number, but otherwise the classification of the various taxa is not upset. Since extinction may be replaced by the mental operation of omission we may conclude:

(T 36) Omission of one or more taxa in a dendrogram does not upset the relative positions of the remaining taxa.

From this we may infer:

(T 37) Any three taxa can be correctly classified in a basic classification.

Clearly, then, a basic classification can be carried out completely without regard to the rank of, or degree of affiliation between, the three taxa.

At this stage it may be appropriate to illustrate the principles outlined here with an example. From T 37 it follows that it is possible to classify the taxa *Insecta*, *Myxine glutinosa* and *Petromyzon marinus* in a basic classification. Nobody will presumably contest that in this instance A stands for *Insecta*, B and C for the two species of *Cyclostomata* (Figure 1). This classification is not, however, inclusive and the possibility obtains that the introduction of further taxa may alter the twin relationship between the latter taxa. If the taxon D in Figure 2 stands for *Gnathostomata* or any taxon included in the latter, e. g. *Dipnoi*, *Muridae* or *Homo sapiens*, then only three classifications are possible, viz., those represented by Figure 2c, 2d and 2e. Evidently, if 2c represents the correct classification, then *Cyclostomata* is a monophyletic taxon, otherwise not.

It is manifest that the successful ordering of three taxa in a basic classification will permit proclaiming a very important assertion concerning the phylogenetic kinship between the three taxa, namely:

(T 38) The members of the secondary twin taxa in a basic classification have ancestors in common that were not ancestors to the members of the other primary twin taxon.

This statement I propose to call HENNIG'S first theorem. It may be noticed that omitting the word 'other' in T 38 does not give rise to mistakes, and I shall therefore adopt this simplification in the sequel. Clearly, according to the notions developed here, the task of the phylogeneticist primarily amounts to determining which two out of three arbitrary taxa are secondary twins or, as HENNIG would phrase it, to searching for the sister group.

This undertaking must be based, directly or indirectly, on the taxonomic

characters displayed by the animals, and in order to distinguish between those characters which can be used for determining sister groups, and those which cannot, HENNIG (1966) introduced the concepts of 'symplesiomorphy' and 'synapomorphy'. One may suspect that a traditional systematist's outlook has influenced HENNIG'S choice of suffix, since the latter refers to morphological properties. Since it has become more and more usual to employ non-morphological characters, this terminology seems rather inappropriate. I therefore suggest to adopt TUOMIKOSKI'S terminology (1967), according to which 'morphy' is replaced by 'typy'. Furthermore, since the prefixes in HENNIG'S names do not seem to be of great importance, I shall take the liberty of introducing the concepts 'plesiotypy' and 'apotypy', the implications of which only in part coincide with the corresponding ones of HENNIG. Finally, as will appear from the following discussion, one additional concept, 'teleotypy', is required. The three notions may be defined as follows:

(D 14) In a basic classification the taxonomic characters distinguishing the taxon T_j and those superior taxa, in which the latter is included, are plesiotypic, those of the non-terminal taxon T_{j+1} are apotypic, and those of the three terminal taxa are teleotypic, taxonomic characters*.

On the basis of these concepts we can now derive another important rule of phylogenetic, HENNIG'S second theorem:

(T 39) Barring non-apotypy, the only taxonomic characters that are common to two out of three taxa in a basic classification are apotypic ones.

In this theorem I have introduced a new concept, 'non-apotypy', which only later will be defined. Yet, it is clearly necessary to make this reservation, for if this were not the case, then phylogenetic classification would be the simplest matter in the world. Rather, the problem facing the phylogeneticist is that in a basic classification each of the three pairs of taxa may be united by having some characters in common, and yet only one of the pairs represents the secondary twins. The ways and means to circumvent this dilemma will be discussed in the sequel. Before this is done we shall generalize the implications of D 14 and T 39.

(T 40) Barring non-apotypy, a taxonomic character x is, in an inclusive classification, apotypic for only one taxon, T_j . For all taxa of rank $r \geq j+1$, belonging to the phylogenetic lines including T_j , x is a plesiotypic, and to the taxa of rank $r \leq j-1$, belonging to the one phylogenetic line including T_j , x is a teleotypic, taxonomic character. When, in a classification new taxa are introduced, the status of a taxonomic character may change according to rules which can be derived from the preceding paragraph.

As concerns the practical approach to the collocation of a fourth taxon D

* To people unacquainted with HENNIG'S work, this terminology may be troublesome, at least in the beginning. But since these terms signify well-defined concepts for which no other names exist, it seems impossible to avoid their adoption. The implication of these words may possibly become more evident if it is mentioned that generally 'plesiotypic' may be equated with 'primitive' and often, but not always, 'teleotypic' with 'advanced'. However, for the most important notion, 'apotypy', no such transcription is possible.

in an already established classification, it appears that, as the outcome of the latter, a number of apotypic characters have been recorded, possessed in common by the taxa B and C in Figure 1. The first point to decide will be whether D possesses none, some or all of these properties. In the first case is either the primary twin to A and B+C (Figure 2a) or the secondary twin to A (Figure 2b). The choice between these classifications depends on the possibility of establishing apotypic characters for A and D. The second alternative implies that D is the secondary twin taxon to B+C (Figure 2c). If all of the apotypic characters for B+C are found in D, the classification will be a matter of determining which out of B and C is the secondary twin to D, the result being represented by Figure 2d and 2e. This working program can be continued *ad infinitum* and it is therefore possible to state this procedure as a theorem:

(T 41) Phylogenetic classification can be carried out through a succession of basic classifications.

It seems that there are two different approaches which can be used to establish the relationship between the three taxa in a basic classification.

With respect to these methods, we must begin by dealing with the fact that characters may be common to two taxa which are not secondary twins, a circumstance that serves to make the life of the phylogeneticist burdensome at times. This phenomenon, non-apotypy, may be defined as follows: (D 15) Non-apotypy is said to obtain when, in a basic classification, a property is found to be common to the primary and to one secondary twin taxon.

It is seen that a non-apotypic character will be apotypic to the twin taxa into which the primary, and the one secondary, twin taxon anticipatedly may be resolved. Hence:

(T 42) A non-apotypic taxonomic character is an apotypic character in two basic classifications.

Further, if we cannot distinguish between apotypic and non-apotypic taxonomic characters, then the discovery of a character which does not conform to a certain classification cannot *a priori* be regarded as falsifying evidence, it may be a non-apotypic character. Therefore:

(T 43) Allowing for non-apotypy, no classification can be falsified by the discovery of a character, the distribution of which runs counter to prediction.

Before we investigate the possibilities for circumventing the impediment to phylogenetic classification constituted by non-apotypy, we shall define one more concept, 'convergence':

(D 16) Convergence consists of the independent gain or loss of the same taxonomic character in two separate taxa in a basic classification.

A certain ambiguity resides in the word 'same'; the essential implication is, of course, that the character in question is regarded as the same by phylogeneticists or taxonomists. As defined here, 'convergence' covers the phenomena of convergence and parallelism encountered in the phylogenetic literature. It may be noted that the above definition does not exclude that a certain character has been acquired independently in three or more taxa. The implication of this

situation is only that the character in question will be convergent in more than one basic classification.

The easiest way to appreciate the implications of non-apotypy is to survey

Table I

Survey of the different ways in which a taxonomic character may end up being common to two out of three taxa in a basic classification

	A	B	C	Number of characters in common	
				AB AC	BC
(1) Plesio-apotypy	\overline{p}	$p \longleftrightarrow p$			Ft_1
(2) Plesio-non-apotypy	$p \longleftrightarrow p$		\overline{p}	Ft_2	
(3) Convergent plesio-apotypy	p	\overline{p}	\overline{p}		F_2t_2
(4) Convergent plesio-non-apotypy	\overline{p}	\overline{p}	\overline{p}		
(5) Apotypy	p	$\overline{p} \longleftrightarrow \overline{p}$			$F(t_1-t_2)$
(6) Apotypy	\bar{a}	$a \longleftrightarrow a$			$F(t_1-t_2)$
(7) Teleo-apotypy	t	$\bar{t} \longleftrightarrow \bar{t}$			Ft_1
(8) Teleo-non-apotypy	$\bar{t} \longleftrightarrow \bar{t}$		t	Fxt_2	
(9) Convergent teleo-apotypy	t	t	t		F_2t_2
(10) Convergent teleo-non-apotypy	t	t	\bar{t}		

A is the primary twin taxon, B and C the secondary, twin taxa. An arrow between two characters indicates non-convergence, a bar above a letter means absence of the character in question. Unencircled, this absence means 'nongain', encircled, 'loss'. The small letters refer to the rating of the characters; a, apotypic; p, plesiotypic; t, teleotypic. F stands for the frequency with which a taxonomic character originates. This value is assumed to be the same in both of the primary and the secondary twin taxa.

To designate the various phenomena some names have been proposed, the derivation of which appears to be straightforward.

the various manners in which two characters may end up to be common to two out of three taxa. This has been done in Table 1, from which it appears that altogether ten different ways are imaginable. The five first concern plesiotypic, the fifth apotypic, and the last four teleotypic characters. Furthermore, it is seen that although only two represent true apotypy, six of ten alternatives may be rated as apotypic, insofar as they unite the secondary twins, while the remaining four are cases of non-apotypy.

Convergence is habitually invoked to account for situations where characters are found to be common between two taxa which, for other reasons, are supposed to be only distantly related. This approach seems to imply that the possession of characters in common is explained either as due to apotypy or to convergence. As appears from Table 1, the situation is more complex than that, among other things because apotypy also can be convergent.

From the list in Table 1 it appears that we must expect that, whenever we endeavour to establish a basic classification, each of the three pairs of taxa will be united by a number of characters. I shall submit that there are two ways in which to deal with such lists of characters, the quantitative or numerical method, in which we do not pretend to possess means to decide which characters are apotypic, and which are not, and the qualitative or evaluative method in which we have, or believe to have, this advantage.

The first method means that a choice is made between the three alternatives in a basic classification on the basis of their respective probabilities. As a guiding principle which, of course, must be generally valid we may put down the following methodological axiom or postulate:

(A 8) Among the possible alternatives in a basic classification the one with the highest probability should be preferred.

In the quantitative method this probability is estimated on the basis of the frequency of the origination of taxonomic characters. With respect to this point we shall introduce the following axiom:

(A 9) The frequency with which taxonomic characters originate is distinguished by a certain mean value F .

This axiom is, evidently, a very crude approximation, because a great number of factors must affect the rate at which taxonomic characters appear.

The frequency involved in the occurrence of convergence may be stated in a theorem, derived from A 9:

(T 44) The frequency of the independent origination of the same taxonomic character in two separate taxa is given by F^2 .

Since this value is much smaller than the one representing the non-convergent origination of taxonomic characters, we may infer:

(T 45) The probability of a phylogenetic classification is inversely proportional to the number of cases of convergence it implies.

With reference to A 8 it is possible from this theorem to derive the following rule:

(T 46) In phylogenetic classification the number of cases of convergence should be minimized.

In view of this theorem it is rather disquieting to register the excessive use which has been made of convergence as an explanatory expedient in traditional phylogenetics. Unfortunately, it does not seem possible in classifications based on ordinary taxonomic characters to devise procedures specifically directed towards minimizing the number of cases of convergence, for the simple reason

that any distribution of taxonomic characters may always be explained either through convergence or non-convergence.

The implication of T 46 is in conformance with the requirement of POPPER (1972) that, among two scientific theories, the one should be preferred which has the highest degree of falsifiability. Thus, if in a basic classification, two pairs of taxa are united through the possession of characters in common, then the one set of characters is potentially falsifying evidence against the classification indicated by the other set. By introducing convergence as an explanatory expedient, this possibility of falsification is suppressed, and the accepted classification has a lower degree of falsifiability than it would otherwise have had.

The number of taxonomic characters defining a certain taxon must be Ft , where t is the time during which the taxon has been under creation. Since this period of time is generally unknown, the following argument must be based on the age of the various taxa. These two temporal parameters will coincide only for terminal taxa which are still under creation, and I shall therefore deal with only this kind of taxa in the present context. As a consequence it follows that unless the basic classification is completely resolved, the taxonomic characters do not represent those defining the terminal taxa in question but, rather, the taxonomic characters distinguishing the phylogenetic lines leading to the mentioned taxa from the bifurcations in the dendrogram.

If these stipulations are accepted, and the ages of the various taxa in the basic classification in Figure 1 are assumed to be t_1 for the terminal primary twin taxon, t_2 for the secondary twin taxa, and thus $t_1 - t_2$ for the nonterminal primary twin taxon, then the characters in common for eight of the cases in Table 1 can be calculated, as shown in the last column of the table.

In agreement with T 44 it appears from Table 1 that convergent apotypy is much less frequent than non-convergent apotypy. I shall, however, postulate that convergence may be more common among the apotypic characters than indicated by the table, for the simple reason that the other properties uniting the secondary twins may enhance the probability of the acquisition of a certain character through convergence. This does not change the fact that when convergence occurs in a pair of secondary twins, it may be indistinguishable from true apotypy, while it may be glaringly conspicuous under other circumstances.

Yet, although convergence must be accepted as a biological reality, and an impediment in phylogenetic classification, it will be neglected in the following semi-quantitative considerations.

From the values listed in Table 1 it can be calculated that the difference between the number of non-convergent characters uniting the secondary twins and any of the other two pairs is

$$D = 2(Ft_1 + F(t_1 - t_2) - Ft_2) = 4F(t_1 - t_2).$$

The requirement for the dendrogram being a basic classification rather than a trichotomy is that $t_1 - t_2 > 1/4F$, the time required for a character to

arise, through gain or loss, in either of the pair of primary twin taxa. For $t_1 - t_2 \rightarrow 1/4F$, we have $D \rightarrow 1$. The requirement for the dendrogram being a basic classification rather than a dichotomy is that $t_2 > 1/4F$, the time required for a character to arise, through gain or loss, in either of the pair of secondary twin taxa. For $t_2 \rightarrow 1/4F$, we have $D \rightarrow 4Ft_1 - 1$.

The quotient between the two sets of characters is

$$Q = \frac{2Ft_1 + 2F(t_1 - t_2)}{2Ft_2} = \frac{2t_1 - t_2}{t_2} = 2t_1/t_2 - 1.$$

For $t_2 \rightarrow t_1$, we have $Q \rightarrow 1$, involving that the numbers of non-apotypic and apotypic characters are of the same order for $t_2 \rightarrow 1/4F$ we have $Q \rightarrow 8Ft_1 - 1$, which represents the maximum possible.

On the assumptions made above*, we may therefore infer:

(T 47) In a basic classification the number of apotypic characters exceeds that of the non-apotypic ones.

This theorem formulates the rule of the quantitative approach to phylogenetic classification, according to which the relative number of characters in common decides the relationships between the taxa. This is evidently a rephrasing of the basic premise in numerical taxonomy, and I therefore propose to call it SNEATH and SOKAL's theorem. It is an endorsement of the view 'that numerical phenetics will in general give monophyletic taxa, because we believe that phenetic groups are usually monophyletic' (SNEATH and SOKAL, 1973, pp. 46—47).

It is possible to calculate the total number of characters, apotypic as well as non-apotypic ones, which must be sampled to make a correct classification. This value is a function of Q , and hence of t_1/t_2 . A few examplets are shown in Table 2** from which it appears that even when the secondary twins have been united into one taxon for 15/17 of the time since the separation of the primary taxa, one character is not enough to establish a correct classification; chances are still one to two that it is non-apotypic. It is further seen that if the separation of the secondary twin taxa is of old date, a large number of characters is required to ensure a reliable result.

* The present calculations are based on various simplifying assumptions, among which the one that the rate of change of taxonomic characters is constant. If only morphological features are considered, this proposition is manifestly not true, and even if all kinds of characters are included it may still, in many cases, be an unwarranted premise.

Therefore, although the result arrived at, viz., that the two taxa which have the longest history in common also have the largest number of taxonomic characters in common, conforms with anticipation, it is still necessary to allow for the possibility that in some cases it may not hold. This situation is most likely to occur if $t_1 - t_2$ is a relatively short period of time, and if one of the secondary twin taxa has been subjected to extensive changes. Although it is my firm conviction that such cases are exceptions, it nevertheless must be admitted that the theorems based on the above calculations may not be generally valid.

** The values for n and P in table 2 have kindly been calculated by Dr Göran BROSTRÖM, to whom I express my sincere gratitude.

T 47 suggests as an approach to the establishment of a basic classification that a search is made for taxonomic characters which unite two out of the three taxa, and the acceptance of those two taxa that have most characters in common as the pair of secondary twins.

Because apotypy implies that a character present in two taxa has originated at one occasion, the implication of T 47 is that the number of evolutionary modifications necessary to explain a certain classification is minimized. Since evolutionary modifications, i. e. the origination of taxonomic characters, is

Table 2

The minimum number of randomly sampled taxonomic characters required for the correct establishment of a basic classification

t_1/t_2	Q	n	P
1,5	2	43	0,95
2,5	4	10	0,95
4,5	8	5	0,96
8,5	16	3	0,97

These calculations are based on the procedure published by BECKHOFFER, ELMAGHRABY and MORSE (1959). n stands for the number of samples and P for the probability of a correct choice.

the outcome of mutations, not necessarily one for each taxonomic character, it appears that the expedient recommended in T 47 may be stated as a general rule of phylogenetic classification:

(T 48) The number of mutations required to account for a given phylogenetic classification should be minimized.

This theorem is a statement of the principle of parsimony as adopted by HENNIG and the molecular-biological phylogeneticists (cf. DAYHOFF and PARK, 1969).

Yet, one cannot relieve oneself of the nagging doubt that this quantitative approach, although being the only objective method, does not always deliver the correct answer. This situation may arise if the characters employed fail to comply with the specification stipulated above, namely, (1) that they should represent not individual taxa, but the phylogenetic lines leading from the bifurcations in the dendrogram, (2) that new characters should arise with a reasonably constant frequency and (3) that they should be independent.

The very fact that HENNIG (1966) has been able to state his rule of deviation shows that the second requirement is not fulfilled by the morphological

characters usually used in classification. This circumstance appears to represent the most serious source of error. There is further reason to suspect that morphological characters very often are interdependent, partly because their appearance during the course of embryogenesis is a series of causally connected epigenetic events, and partly because the acquisition of one property may pave the way for other ones arising through separate mutations. However, these phenomena should rather increase the likelihood that a phenetic classification is phylogenetically correct.

There can be no doubt that the quantitative approach is the most foolproof method in phylogenetics. Surely, whenever the affiliation between distant taxa, e. g. separate phyla, has to be determined, this method should be employed. However, since HENNIG (1966), the father of cladism, operates without taking recourse to it, the question evidently arises whether there are other expedients through which apotypy can be revealed, or whether he relies on a cladistic intuition, similar to the Linnean one invoked in traditional classification.

Before this question is answered it may be pointed out that it is easy enough to quote examples where no intuition is required, thus nobody would question which are the secondary twins among *Ambystoma mexicanum*, *Rana pipiens* and *Rana temporaria*, because the body shape of Salientia is a very obvious apotypic character, and the same holds for the chondrichthyan claspers, avian feathers, etc.

However, all classifications of this kind are trivial, so the validity of the method must be tested on more difficult problems. I believe that, using my own terminology, I can explain HENNIG's view by reference to the two cases of non-convergent non-apotypy in Table 1. In the first instance, (2), the primary, and one secondary, twin taxon have one, or more, plesiotypic characters in common which have been lost in the second secondary twin taxon, and in the second instance, (8), the latter has gained some character through teleotypy, and the other taxa are therefore united through the absence of this character. In these two cases, the properties in common evidently are not apotypic characters and should therefore, according to HENNIG (1966), be neglected when the phylogenetic relationship between groups is established. It is possible to state these ideas in a theorem:

(T 49) If, in a basic classification, one taxon, which must be a secondary twin, has many characters in common with both of the other taxa, then one of the two sets of characters will represent the presence of plesiotypic characters absent, and/or the absence of teleotypic characters present, in the third taxon. The latter is the second secondary twin taxon.

If we know which are plesiotypic, and which teleotypic, characters, then the application of this theorem as the rule of the qualitative approach to phylogenetic classification meets with no difficulties. Evidently, this method is much less toilsome than the numerical approach but, although it certainly is an advance compared to the classical Linnean approach, it is less objective, and the risk of mistakes cannot be excluded.

THE SPECIES CONCEPT

It seems that the primary concern of the critics of HENNIG'S theory is the status of the present Linnean classification. I have already discussed this question (1973; 1974) and pointed out that, to the extent the taxa in the latter system are monophyletic, they can be adopted unchanged in a phylogenetic classification, but that the Linnean categories cannot be accommodated. Furthermore, I dealt with various points concerning the species concept, and since my ideas on the subject have developed in the intervening time I shall conclude by a brief discussion of this topic.

On the basis of the preceding discussion it follows:

(T 50) The Linnean species is a set of one to several terminal, and subterminal, phylogenetic taxa.

It was inferred above (T 26) that, in a completely resolved classification, the terminal taxa are still under creation and, consequently, not immutably defined. Hence we may, with reference to T 50 conclude:

(T 51) When a species is subdivided into inferior phylogenetic taxa, it is, barring crossings between the subspecific taxa, as immutably defined as the other taxa of superior rank to which the members of the species belong.

From this theorem it follows that the taxa which are distinguished by representing 'evolution in the making' generally are not the Linnean species, but rather the terminal taxa in the phylogenetic classification which may, or may not, coincide with the species. Yet, it was necessary to make a reservation in T 51 with respect to crossings between members of the subspecific taxa within a species and this circumstance shows that in a certain respect the species is different from more superior taxa. In order to elucidate this question we must discuss the properties of genetic compatibility and genetic incompatibility which usually are regarded as important species criteria. We shall begin with the following axiom:

(A 10) In a completely resolved classification of a monophyletic taxon, the members of which reproduce bisexually, it is possible, close to the base of the hierarchy, to draw a wavering line representing the limit of interfertility. This line, which separates all terminal, and some subterminal, taxa from the rest of the hierarchy, will never pass below the level represented by the Linnean species.

This axiom implies that when two populations of animals are genetically incompatible, then they must be classed as different species, irrespective of whether or not it is possible to detect any other properties allowing for their distinction. This thus amounts to introducing genetic incompatibility as a taxonomic character, an expedient which must be adopted also in phylogenetic classification. In conformance with empirical observation it is not asserted that interfertility cannot obtain at levels superior to the Linnean species.

According to A 10 there must exist a considerable number of taxa, ranging maybe from genera to subspecies, races, etc., the members of which are geneti-

cally compatible. If they do not interbreed, then it may be inferred that they are wholly, or partially, isolated from each other. This point relates to the assertion made above that the first stage in the subdivision of a taxon into two twin taxa of higher rank must involve a step of isolation. This event may be active or passive (fortuitous) and it may, or may not, lead to immediate changes in the gene-pool of the, purportedly, small population of individuals which have become isolated from the main stock of the taxon to which they belong. Yet, if, and when, the members of either one of the two separate populations acquire properties which correspond to the definition of 'taxonomic characters', the original taxon T_j has become separated into two taxa T_{j+1} . If T_j was classed as a species, the latter has now become immutably defined, and we have two new subspecies, distinguished by the absence and the presence, respectively, of the mentioned taxonomic characters.

However, if the barrier of isolation between the two new taxa is not insuperable, the possibility still obtains that the two taxa may interbreed and, ultimately, form a single taxon again. This is stated in the following axiom: (A 11) As long as genetic compatibility obtains between members of different taxa, the course of evolution is potentially reversible.

From A 10 and A 11 we may conclude:

(T 52) The limit of interfertility represents the limit of reversibility of evolution.

And this limit coincides, as is well known, approximately with the one separating the species from the superior taxa in which they are included. I believe that the importance of genetic compatibility, stressed so much in the 'new systematics', may be the one stated in T 52. It must be pointed out, though, that whether reversion occurs, and at which level, is a matter of chance and that, for a number of reasons, this course of events appears to be unusual. And if reversion does not occur we may anticipate that, sooner or later, genetic incompatibility will ensue as the outcome of a chance event.

Another point which has caused much controversy in the discourse on phylogenetic evolution is the direction of the latter with respect to the classificatory hierarchy. According to the notions advanced by DARWIN (1859) a species in the past would, in the course of time, give rise to so many new species that it, on the basis of the actual course of this event, would be possible to establish a hierarchy outlining the phylogenetic kinship between these species. But to DARWIN all the taxa in the hierarchy are species, and the superior taxa are simply sets and subsets of the species located at the base of the hierarchy.

According to the cladistic theory a genus, a family, etc., is a taxon which, if it is monophyletic, is defined by a certain number of taxonomic characters, possessed by living animals. These properties were acquired when the taxon was created during a specific period of time in the past. The superior taxa therefore are not to be found at the base of the hierarchy, but higher up where, in contrast, no species are to be found. Thus, as has already been concluded above, evolution has progressed from the apex to the base of the phylogenetic hierarchy and since the species, through a Linnean convention, are located at

the latter station, they represent, approximately, the level of evolution which has been reached at the present moment.

But this means that if we go to the past, then the part of the hierarchy represented by the species did not exist and yet, interfertility clearly obtained between the animals living at that time. From A 10 and our knowledge about the way the phylogenetic hierarchy grows with time, we may therefore conclude: (T 53) With the passage of time the limit of interfertility gradually has moved downwards in the phylogenetic hierarchy.

From this it follows:

(T 54) In the course of evolution genetic compatibility has existed between members of taxa of any rank in the phylogenetic hierarchy.

From the present discussion I shall conclude:

(T 55) The species usually, but not always, represent the terminal, not immutably defined, taxa in the phylogenetic hierarchy.

(T 56) The species usually, but not always, represent the potentially reversible level of evolution.

Apart from the implications of these statements, which refer essentially to the temporal or 'historical' situation of the species, there is no justification for regarding the latter as being more 'real', and less 'abstract', than any other phylogenetic taxon. Rather, each animal is the bearer of the taxonomic characters defining all the taxa to which it belongs, from kingdom *Animalia* over the species and down to the terminal, not yet immutably defined, phylogenetic taxon.

CONCLUSION

In spite of more than one hundred years of phylogenetic classification, the perpetrators of this branch of biology have not succeeded in establishing a theoretical basis for their work. This, I submit, is clearly evidenced by the heated discussion going on around HENNIG'S theory of cladism.

After having learned what various anonymous persons think about my attempt to establish such a theory, I have come to realize that my power of logical reasoning is narrowly circumscribed, but also that there are thinkers within the trade whose acuity will ensure that all my errors and mistakes are revealed. If, after such attempts of falsification, only a few of my axioms, definitions and theorems should remain, but a better theory be created, then my endeavours, and even the risk of exposing myself to ridicule, would not be in vain, for I believe that phylogenetic classification can only benefit from the existence of such a theory.

There is, however, one point I want to make to my presumptive critics: Do not suppress the rule of the minimum number of mutations, in particular of the minimum number of convergences. If convergence is allowed to account for 'unacceptable' similarities, it may do so as well for the 'acceptable' ones. All similarities may be the outcome of convergence, and if that is true, phylo-

genetic classification is not a falsifiable empirical, but an unfalsifiable metaphysical, science. If the morphological systematists are not willing to adopt this principle, and accept the several changes in the present classification which will consequently entail then, I believe, their work will in the future be taken over by the molecular phylogeneticists who, by adhering to this rule, have established an empirically falsifiable approach.

In conclusion I wish to emphasize that although HENNIG's theory of cladism forms the basis of my axiomatization, I realize that I have arrived at several conclusions which HENNIG may not be willing to endorse.

I want to state my gratitude to Professor Henryk SZARSKI and the anonymous critics mentioned above for the time they have expended on scrutinizing my paper. Owing to their efforts I have been able to correct several errors.

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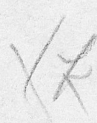
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Autor przedstawia ulepszoną wersję opublikowanej przez niego poprzednio próby aksjomatyzacji teorii klasyfikacji filogenetycznej. Większość klasyfikacji zawiera w sobie konstrukcję dichotomicznych dendrogramów. Praca omawia niektóre ich własności. Autor postuluje, że większość klasyfikacji filogenetycznych może być przeprowadzona przez kolejną klasyfikację trzech taksonów, co można nazwać "klasyfikacją podstawową". Praca wyjaśnia pojęcia plesiotypii, apotypii, teletypii i anapotypii, oparte na ideach rozwiniętych przez HENNIGA, ilustruje je przykładami i wyjaśnia. Omówiono różne możliwości klasyfikacji filogenetycznej, a także stan pojęcia gatunku na podstawie zaproponowanej w pracy teorii.

РЕЗЮМЕ

Автор даёт улучшенный вариант опубликованной им раньше попытки аксиоматизации теории филогенетической классификации. Большинство классификаций содержит в себе дихотомическую конструкцию дендрограмм. Работа посвящена некоторым их особенностям. Автор высказывает пожелание, что большинство филогенетических классификаций может быть проведено через очередную классификацию трёх таксонов, что можно назвать „основной классификацией“. Работа разъясняет понятия плезиотипии, апотипии, телетипии и анапотипии, исходящие из идей развитых Хеннигом, иллюстрирует их примерами и выясняет. Рассмотрено различные возможности трактовки филогенетической классификации. Вконец обсуждено состояние понятия вида на основании предложенной в работе теории.

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