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Classifications and other ordering systems

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Abstract

The enormous variety of things in nature must be ordered before it can be studied and understood. Unfortunately in spite of their great importance, the methods of ordering have been greatly neglected by the philosophers. In this article, we distinguish six systems of ordering. Classification, in which similar entities are grouped in classes (taxa), is one such ordering system, but not all ordering systems are classifications. The Hennigian system of cladification consists of the ordering of branches of the phylogenetic tree, strictly on the basis of a single criterion, the branching points of the phylogeny (holophyly) (Hennigian phylogeny). It is not a system of classification, as it does not lead to classes of entities possessing similar phenotypic attributes. A Darwinian classification, by using two criteria, similarity and common descent, leads to the recognition of classes (taxa) of similar entities consistent with common descent (monophyly) (Haeckelian phylogeny).

Key words: Classification – Hennig – Haeckelian Phylogeny – Cladification – Ordering systems

1. Introduction

Our world is characterized by an almost chaotic diversity of things and processes. The basic task of scientists is to provide explanations for all aspects of this diversity, while that of philosophers of science is to overview the approaches and methods used by the scientists in reaching these explanations. Ordering systems, including classifications, are needed to reduce this chaotic diversity into understandable, manageable arrangements before scientific explanations are possible. At the onset, we must emphasize that not all ordering systems are classifications, as is all too frequently assumed by both scientists and philosophers. Ordering systems is an overall term and includes all schemes that attempt to arrange a diversity of objects into particular categorizations. Classifications are a subset of ordering systems that attempt to arrange a diversity of entities into sets of classes based on similarities possessed by the included individual entities. In biology, classifications exist of living organisms, but also of organ, cell and tissue types of diverse organisms, of ecological communities, etc. These classifications are not all of the same type; hence, ‘biological classification’ is not a single concept. Not all biological classifications are evolutionary classifications of organisms, as is all too often erroneously assumed by biologists and philosophers alike. Yet other ordering systems exist in biology, such as phylogenetic trees or dendrograms, which are equally useful, but are not classifications. Haeckelian phylogenies and Hennigian cladifications (= cladograms; see Glossary and Mayr 1965) are quite different types of ordering systems from Darwinian classifications, as different as clades are from taxa which are respectively units of different types of ordering systems. Biologists have been so accustomed to thinking about all ordering systems as classifications that many statements in the literature about classifications are actually statements about ordering systems in general. Moreover, it is difficult to analyse earlier discussions of biological ordering systems because they may refer to evolutionary classifications of organisms, to phylogenies (both Haeckelian and Hennigian), to ‘essentialistic’ classifications of tissue, cell and other types, and to other types of ordering systems, the result being a confused morass.

Ordering systems are important not only for scientists and philosophers, but for all humans in most or all activities of their daily life. Most essential is that ordering systems, including classifications, are above all heuristic schemes and must be judged primarily on criteria of convenience, whatever these criteria might be for the particular system. We would never be able to find anything in the overwhelming diversity of nature (or of human activity) or be able to make any statements about it, if we did not have methods for bringing order into this diversity. Before they can be dealt with, the diverse items must be placed either into some groups or serial

sequences based on appropriate criteria. Placing entities into some chosen order is one of the most important methods of science and an indispensable activity of daily life. How could we find an item in a large market or a book in a library, if these items were not placed in an order according to some principles?

But what are these principles and how are they chosen? Ordering systems to deal with human artefacts may be constructed strictly artificially and for convenience only. But when developing ordering systems for scientific purposes for existing objects in nature, from biological cell types and species to chemical elements, minerals and astronomical bodies, one must remember that the ordering must be founded on the fundamental theories in the particular field of inquiry. One should be immediately wary of any claim about the existence of theory-free order in nature. There is simply no foundation for the belief that a natural order exists in nature independently of any theory and that it is ‘out there’ waiting to be discovered in the absence of any theory. Because biological classifications and phylogenies of organisms are historical-narrative explanations, they are dependent on the nomological-deductive theory of evolution if they are to be scientific (Bock 2000b). We disagree strongly with claims, such as are made by Brower (2000, p. 143) and many other cladists, ‘... Whether a theory of evolution is philosophically antecedent to systematics or systematics provides evidence that allows inference of a scientific theory of evolution. In this paper, I will advocate the latter point of view and highlight its utility in the current debate surrounding alternate methods of phylogenetic inference.’ Osche (2002, pp. 18–20) has discussed in some detail Hennig’s aversion to base systematic theory and methods on evolutionary theory.

Considering the enormous importance of this process of ordering in the diverse fields of science, it is quite astonishing to what extent its analysis has been neglected by philosophers. In fact, we have been unable to find a treatment of classification (and of ordering systems in general) in any philosophical publication between the 1840s (Whewell 1840; Mill 1843) and 1997 as comprehensive and aware of ambiguities as that of Whewell in his *Philosophy of the Inductive Sciences* (1840). Whewell very perceptively realized that ordering by the methods of logical division was something quite different from classifying by grouping (clustering), even though he did not always clearly separate the two methods. His treatment also suffered from his pre-evolutionary attempt to apply the same methods of classification to living organisms and to inanimate objects such as rocks and minerals.

In the 20th century literature of the philosophy of science, classification usually receives only the merest mention (Cohen and Nagel 1934; Hempel 1952, 1962, 1965) or none at all (Nagel 1961). These authors treat classification only in the

context of logic and consider logical division as the preferred or only method of classifying. Most recent authors (Beatty, Brandon, Hull and Sober) deal with specific modern controversies relating to Darwinian classification of living organisms, but none of them present a comprehensive treatment. Mahner and Bunge (1997) is the only recent book in which a whole chapter (Chapter 7, 38 pp.) is devoted to the philosophy of systematics. Unfortunately, its neglect of historical narratives, biopopulations, and other basic biological concepts, and its foundation on a rather typological logic make it unsuitable to deal with the modern problems of biological classification.

In this paper, we deal primarily with the ordering of organisms, but we realize fully that there are other systems of classification of importance to biologists. These include classifications of cell, tissue and organ types of different groups of organisms, of ecological communities, of behavioural activities and so forth. Most of these other systems of classifications are based on typological or near typological thinking (see Bock 2000a) and their construction is quite different from that of evolutionary classifications of organisms. Consult the Glossary for the meaning of technical terms (e.g. taxon) used in the text before they are rigorously defined.

2. Why ordering systems should be of interest to the philosopher?

The question might be asked whether the neglect of ordering systems by philosophers may not simply be because of an unsupported assumption by philosophers that the analysis of ordering systems has nothing to do with philosophy. Indeed, this seems to be the prevailing opinion of the philosophers of science. It is because we feel strongly that this is an unjustified viewpoint that we have undertaken this analytical survey.

Philosophy of science is definitely interested in scientific methodology, as documented for instance by the large philosophical literature on experimentation. But other scientific methodologies are also neglected by philosophers as, for instance, the comparative method (cf. Bock 1989a,b). Yet, there are sound reasons why ordering systems, including classifications, should be carefully analysed, and not so shamefully ignored by philosophers. Ordering and classifying pose numerous problems that challenge the philosopher. Most important is that the various types of ordering systems differ basically from one another and it is essential to identify and sort out these differences. Clarification of such terms as class, classification, similarity, relationship, convergence, phylogeny, and hierarchy, all of which are important in one or another ordering system, is of concern to the philosopher. Most of these terms have several meanings and the determination of which is the appropriate one for a particular ordering system, such as biological taxonomy, is still rather controversial.

3. The universality of diversity

There are endless kinds of diversity that call for ordering. Celestial bodies are placed into classes: stars (= suns), planets, moons, comets, asteroids, nebulae, galaxies, black holes, etc. Ordering is needed in most human activities: laws are ordered in codes of law according to subject matter, so are books in a library, and goods in a store. Subjects taught in college or technical schools are arranged in faculties and departments. Ordering and classifying is involved in almost all human

activities. One important question, raised by this situation, is whether the same principles apply to the ordering of living organisms and of inanimate objects. Whewell and other pre-1859 authorities focused initially on the inanimate world and proceeded as if all variation of animals and plants was the same sort of phenomenon as the diversity of minerals or stars. The discovery of biological evolution refuted this viewpoint and initiated the proposal of ordering systems applicable specifically to organisms, like Darwinian classification, Haeckelian phylogeny, and Hennigian cladification. However, some of the basic concepts of pre-evolutionary classification, such as how to define such terms as classification or hierarchy, were incorporated in Darwinian classification. One of the practical conclusions of recent studies is to show that the 'overall similarity approach' used for the ordering of inanimate objects is equally suited for a first ordering of organisms. But otherwise the principles by which animals and plants should be ordered have been controversial since the 17th century and still are.

The importance of and the need for a modern treatment of the principles of ordering systems is evident. The publication of numerous controversial papers in the taxonomic literature in recent years has made this need particularly obvious. The authors of many of these papers either had no personal experience as practicing taxonomists or were unaware of the history of the field and its literature. They thought that those approaches would be most successful that were based on some basic philosophical principles. We had adopted the same approach in our first endeavours. But none of our attempts was successful. Systems of ordering like Darwinian classification and Haeckelian phylogeny, which use simultaneously two different sets of criteria, similarity and genealogy, are particularly difficult to express in terms of traditional philosophical concepts. Frustrated by the failure of such an approach, we finally decided on a largely pragmatic approach. Being a pioneering effort, it is bound to be incomplete and, in part, one-sided or even wrong. What we hope is that it will stimulate criticism and thus lead to improvement. We wish once again to emphasize that when we speak of biological classification, we refer only to classifications of organisms.

4. Objectives of ordering systems

Ordering systems have a number of different objectives (Simpson 1945, 1961, Chapter 4; Hempel 1965, pp. 146–147; Warburton 1967; Bock 1974); we focus our attention on classifications. These objectives are:

4.1. Sorting

One of the foremost goals of most ordering methods is the recognition of groups (classes) of similar and/or related objects and their delimitation against other such groups (see section on 'Class and classification'), because 'a greater number of propositions can be made' about such groups, as Mill (1843) has said over 150 years ago.

4.2. Information storage and retrieval

Information storage and retrieval is a major objective of most ordering systems. In such systems, objects are grouped together (on the basis of various criteria) that permit storage

and retrieval of information about these objects. Classifications, therefore, can serve as summaries of a great deal of information (Warburton 1967). We must, nevertheless, emphasize that one cannot recover the same or all of the information from a classification that was used to create it, contrary to the claims of some systematists. As we shall see, stability is one of the most important prerequisites of such systems (Mayr and Bock 1994).

4.3. Identification of an unknown item

In the centuries when plants supplied nearly all medications for the cure of human diseases, the correct identification of the species of medicinal plants was of the utmost importance. The principal objective of any ordering system of plants used at that time was to lead as speedily as possible to the correct identification of an unknown plant. In present-day police forensic work, identification of human remains as compared with those of other vertebrates is of central importance. The procedure of identification (i.e. the use of dichotomous keys) is entirely different from that of classification.

4.4. Inferences about not yet studied properties

Most of the characters of a taxon will be the same or at least similar to those of other taxa located near it in a classification (Bock 1974). This conclusion permits predictions with a considerable degree of certainty concerning other not yet studied characters of a taxon.

4.5. To serve as baseline in comparative studies

Validity of the results of any comparative studies depends to a large extent on the goodness of the preceding research by which the studied items were grouped into classes (Bock 1974). In biology, this is strikingly evident in all comparative disciplines, such as comparative anatomy, comparative physiology, comparative behaviour studies, etc. Generalizations in almost all types of scholarly research are based on the comparison of classes of objects (Bock 1989a), although these classes do not have to be taxa of a Darwinian classification.

5. Kinds of ordering systems

5.1. General considerations

We use the term 'ordering system' for any arrangement that attempts to place diverse items into some type of order. As indicated by its name, the objective of an ordering system is to arrange a set of diverse entities into a heuristic scheme permitting further and faster comprehension of the diversity. Ordering systems play an important role in daily life (in libraries, telephone directories, etc.).

Early in the history of taxonomy, a distinction between natural and artificial classifications was suggested. Natural classifications are those that correspond to the fundamental theory of the particular science. Artificial classifications are those developed with particular ideas in mind, such as eatable versus poisonous organisms. There may be some purely natural classifications like the periodic table of the chemical elements, but all endeavours of a classification of organisms are at least somewhat artificial. This is because biological

classifications are based on subjective observations, on numerous inferences, and on the rather arbitrary evaluation of the weight of characters. In biology, an adoption of an absolute distinction of natural versus artificial would only lead to difficulties.

Ordering is guided by definite criteria or principles. Many of these principles apply equally to inanimate objects and to organisms. Others are used only in the ordering of living organisms (animals, plants, etc.). Information storage and retrieval are major objectives of most ordering systems. Until the 19th century and even later, taxonomy was dominated by essentialistic thinking. A species or higher taxon could be recognized by its essence ('definition'). Preferably, this essence was represented by a single characteristic.

Stress placed on single characters reflected the essentialistic thinking of the period. One feature should be sufficient to characterize the essence of a taxon. This way of thinking was often highly deleterious after the rise of evolutionary thinking and Darwinian classification, when some authors continued to distinguish taxa on the basis of single characters. Indeed, there was a widespread but erroneous assumption that 'a single feature was both necessary and sufficient for the inclusion of a species in a given taxon'. This was referred to as monothetic diagnosis. Eventually, it was realized that many taxa are polythetic, based on a considerable number of shared characters, no single one being either essential or sufficient to make an organism a member of the taxon, and with no individual or species necessarily having all the attributes that jointly characterize the taxon. This realization was strengthened during the replacement of essentialism by population thinking. Most unsuccessful classifications of the last 200 years were the result of too great a reliance on single characters.

After 1859, biologists began to realize that the classification of organisms, a product of their evolutionary history, was not the same as the classification of inanimate objects or even of biological entities such as cell and tissue types and ecological units, where methods based on essentialistic thinking are usually appropriate. By contrast, it is now understood that no adequate classification of kinds of organisms can be achieved that does not reflect the evolutionary theory of common descent.

For several centuries all ordering systems were thought to be classifications and the two terms were treated virtually as synonyms. Eventually, however, it was realized that classification means making classes and that ordering systems that are not based on classes, such as sequential listing or cladifications (Mayr 1995), are not classifications. Hence, ordering systems denotes the general concept that includes classification as one of its subdivisions.

In a Darwinian classification, what is ordered are populations, taxa, or classes – that is, groups of organisms, never single specimens as such. This was quite rightly emphasized by Simpson (1945, 1961), but was not understood by Jevons (1874, p. 719) or by Hempel (1965, p. 138). When an entirely new taxon is discovered, it is, of course, classified even if represented only by a single specimen.

The use of ordering systems in human activities, including science, has a long history. Different ordering systems may be based on entirely different principles and criteria. We list here six different kinds of ordering systems, but would not be surprised if still others would have to be recognized in the

future. What we are here presenting is only a first attempt (Table 1).

These six major ordering systems differ from each other not only in their methods but also in the objectives that they pursue. In addition, mixed systems are sometimes adopted. For instance, in a library arranged by subject matter, the books in a special field, such as philosophy, may be listed in the alphabetical sequence of the names of the authors. Even though the sequence of the main chapters in a book on clinical medicine may be arbitrary, the arrangement of the material in each chapter (for instance, infectious diseases) will be carefully determined by similarity in aetiology or the relationship of the pathogens. Such mixed ordering systems are frequently adopted in daily life.

Our primary interest is the classification of organisms. The principles that govern the methodology of such classification are well defined but often confused with those of other ordering systems. For this reason, it is advisable to present a concise treatment of all currently used ordering systems in order to characterize the specific properties of the ordering systems of taxonomy.

5.2. Ordering of single entities

There is a profound difference between the ordering of single objects and the grouping (clustering) of entities. The objective in the case of single objects is usually the correct identification. This is particularly true for inanimate objects considered to belong to natural kinds (Hacking 1991) as well as for animate objects such as cell and tissue types and ecological forms. But identification is also the objective when a key is used for the identification of an individual specimen to the correct species of organisms.

5.2.1. Assigning singular entities to a linear sequence (sequential listing) – type 1

5.2.1.1. *Arbitrary sequence.* An example is the sequence in which the major types of human diseases are listed in a textbook of clinical medicine: infectious diseases (caused by pathogens), malignancies, genetic diseases, age induced diseases, etc. In a book on kinds of ball sports it is arbitrary whether basketball is listed before or after volleyball, and soccer before or after rugby. Even though arbitrary, some

sequences may be quite widely adopted, because they have become traditional.

5.2.1.2. *Alphabetical listing.* An example is the listing of names in a telephone directory. The telephone number of any included person can be found very quickly and even if there are several identical names, the address permits an unequivocal selection. The index to a book is another example. Alphabetical listing is a near perfect instrument for information retrieval if a particular item of information is needed.

5.2.1.3. *Chronological listing.* This is the preferred ordering system for most historical subjects. Whether it is the history of a country, the sequence of rulers in a dynasty, the sequence of geological strata, or the history of the gradual improvement of the motorcar, the chosen sequence of presentation is nearly always chronological.

5.2.1.4. *Listing by rank or achievement.* Examples are lists of those who have successfully passed an examination ranked by their score, of the names of those who completed a marathon run based on their arrival time, or of best-selling books ranked by the number of copies sold. There are numerous such lists, ranked by these or similar criteria. No doubt there are other kinds of sequential ordering systems for singular entities that should be added to this list.

5.2.2. Ordering the chemical elements according to numerical properties of their atoms – type 2

It is rather uncertain where to place the periodic table of the chemical elements. Every element is a unique singular entity but occurs as a large number of discrete samples. Classification of minerals might fall under the same heading as the classification of elements into the periodic table.

6. Ordering by the clustering of entities

Included here is the arrangement of groups comprised of similar items into an ordering system. For biological organisms, this would involve arrangement of individual organisms into species and these into higher-level groups such as in a Darwinian classification.

6.1. Ordering by a single criterion

The single criterion may be some type of similarity, either a single aspect of similarity or overall similarity, or a single aspect of phylogeny such as branching point (= Hennigian phylogeny).

6.2. Ordering by special similarity – type 3

6.2.1. Establishing groups by logical division (mostly dichotomy = 'downward classification')

Most philosophers have considered this the standard method of classification. In this method, a large initial sample (summa genus) is step-wise divided by logical division (dichotomy) into smaller and smaller groups until all items are placed in a class. This method is also referred to as 'downward classification' (Mayr 1982, pp. 158–162). The choice of the characters by which the divisions are made is more or less arbitrary. This was the standard method of Linnaeus (1758) in the *Systema Naturae* (even though apparently he pre-sorted his material in order to find the most diagnostic key characters). For instance,

Table 1. Kinds of ordering

A: Ordering of single entities
1: Ordering them into a linear sequence (type 1)
2: Ordering the chemical elements, into rows and columns (type 2)
B: Ordering by the clustering of entities
1: Ordering by a single criterion
1a: Ordering by special similarity (type 3)
1aa: By logical division (downward classification)
1ab: By special purpose ordering
1b: Ordering by overall similarity (type 4)
1c: Ordering by the single criterion of Hennigian phylogeny (Hennigian cladification) (type 5)
2: Ordering by two criteria, similarity and Haeckelian phylogeny (Darwinian classification) (type 6)

The numbers (type 1–type 6) refer to the six ordering systems recognized by us.

vertebrates by the application of a single character (body temperature) are divided into those that are cold-blooded and those that are warm-blooded. The warm-blooded ones are again divided by dichotomy into those with a body covering of hair, the mammals, and those covered with feathers, the birds.

The so-called 'classes' of groups of organisms established by logical division do not qualify as classes according to the traditional definition in taxonomy (see below), because these 'classes' do not consist of overall similar items. Warm-blooded vertebrates include not only the mammals, but also the only distantly related birds that evolved this characteristic independently from mammals. The cold-blooded vertebrates include reptiles, amphibians and a vast diversity of kinds of fishes. Indeed, most subdivisions of plants and invertebrate animals obtained by logical division are highly heterogeneous. In other words, the divisional method does not produce classes of entities of overall similarity, as traditionally defined in taxonomy. Therefore, rigorously defined, ordering systems produced by logical division are not classifications, they are groupings by singular similarity. In many treatments of classification by philosophers, the method of 'downward classification' by logical division is mentioned as the only method of classification in taxonomy. Most taxonomists largely abandoned it as a method of classification around 1800 (Mayr 1982; Stevens 1994).

Downward classification survived longest in the classification of the taxa of the higher categories. Cuvier, in the early 19th century, still used downward classification when he divided animals into four phyla or embranchments and this arrangement, or improved versions of it, were in use far into the 19th century. Indeed, some zoologists divided animals into vertebrates and invertebrates still as recently as in the early 20th century, and such groupings as coelomates and acoelomates survived even longer.

Cladistic methodology became compatible with downward classification with the abandonment of comprehensive similarity as a criterion of classification, and the acceptance of key synapomorphies as crucial in cladistic ordering. For instance, Eldredge and Cracraft (1980, p. 147) state: 'alternatively, classification can be viewed as the subdivision of a larger set into smaller sets.' The nature of cladograms and of the nested set of clades advocated by cladists are clearly reminiscent of downward classification. Indeed, cladistic classifications have all the basic characteristics of identification keys that are downward classifications.

Traditionally, almost all theoreticians believed that the best classifications are those that are based on the greatest possible number of characters. This is one of the main reasons why the method of so-called downward classification was abandoned around 1800. Darwinians retained the downward approach only as a method of identification. If one had an unidentified specimen, one ran it through a 'key', that is, a sequence of dichotomous divisions, until one had achieved the final identification at the last division. The sequence in which the different characters in a key are selected is essentially arbitrary, with convenience being the foremost consideration. Hence clear-cut conspicuous characters are used first. This often leads to very artificial groupings, not suitable for a classification, as demonstrated by the not infrequent correct identification of a member of the same group at different terminations of such keys.

6.2.2. *Special purpose ordering*

For many practical purposes, the so-called 'special purpose classifications' are widely used. They are based on a single ordering criterion of special importance in the particular context. Some ecologists, for example, may divide plants in certain analyses into trees, shrubs, herbs, forbs and grasses, as was already done by the Greek botanist Theophrastus several thousand years ago. A limnologist may divide plankton organisms into autotrophs, herbivores, predators, and detritus feeders. In ecological research, one may recognize swamp plants, soil microorganisms, freshwater fishes, and cave animals, but the various species of such special purpose groupings are in most cases not each other's nearest relatives, and therefore have less in common with each other than groupings based on similarity and common descent. Classifications of organs, tissues and cell types clearly belong to this type.

An ordering system based on the single criterion of phylogeny would seem in some respect to answer the definition of special purpose ordering, while a Darwinian classification is multipurpose ordering because it attempts to use the totality of phenotypic and genotypic information in the construction of a classification.

6.3. Arrangement of entities into classes based on overall (comprehensive) similarity – type 4

Upward classification results from arranging these classes hierarchically. Practicing botanists, beginning with Ray and Magnol, discovered that by assembling similar species into a genus, similar genera into a family, and up through the hierarchy of categorical ranks, until all species were included in a single hierarchy, one could achieve a classification that was far superior to any ordering produced by downward division. As a result, towards the end of the 18th century, this new 'upward' procedure was ever more widely adopted, particularly at the levels of genus and family (Mayr 1982). One could call this the 'Jussieu Approach', because Jussieu was particularly effective in promoting this approach (Stevens 1994). In the Linnaean and post-Linnaean period, through the efforts of various taxonomists, most of them botanists, such upward classification based on the single criterion of general similarity was employed ever more frequently and by the beginning of the 19th century it had become the prevailing method for the classification of organisms and after 1859 for any Darwinian classification of organisms.

This procedure of constructing a classification of organisms consists of combining similar species into classes, called taxa. A taxon is defined as a monophyletic group of populations or taxa that can be recognized by a definite set of shared characters. Such a group must be sufficiently distinct to justify giving it a name and to rank it in a definite taxonomic category (Mayr 1969).

A higher taxon has certain ontological characteristics (e.g. restriction in time and space, etc.), which are associated by philosophers with the designation 'individual', but it lacks the internal cohesion of an individual. This is why various taxonomists do not adopt the designation 'individual' for higher taxa. But they are definitely not classes in the Platonic sense, but biopopulations (Wiley 1981; Mayr and Ashlock 1991; Bock 1989a, 2000a). Ignoring the different meanings of the word 'class' leads to equivocation.

6.4. Ordering by phylogeny or by similarity and phylogeny – types 5 and 6

The last two systems of ordering, by the single criterion of Hennigian phylogeny (Hennigian cladification – type 5) and by the two criteria of similarity and Haeckelian phylogeny (Darwinian classification – type 6) will be discussed below (see 10. and 11.). But before these last two types of ordering systems can be considered, it is necessary to examine several properties of ordering systems, mainly but not exclusively of biological classifications.

7. Evolution versus phylogeny

7.1. Darwinian evolution

As stated above, the major thrust of this paper is a consideration of natural ordering systems of organisms. Hence, it is necessary to enquire closely into the meanings of the terms ‘evolution’, as in evolutionary classification, and ‘phylogeny’, as in the phylogenetic history of organisms.

When Darwin introduced in 1859 his ideas about biological transformation (= evolution, a term he did not use in this book), he did so in the belief that this was a single theory. Darwin always referred to his ideas as ‘my theory’ – always in the singular. This caused much confusion because various workers rejected Darwin’s theory of evolution completely when they disagreed only with one or another component of his multipartite theory. Well over a century later, Mayr (1982, 1985) presented an analysis of Darwin’s ‘theory’ and demonstrated clearly that it consisted actually of a bundle of five independent, but associated theories – all of which fitted under the heading of evolution. Hence, in many cases, when a worker uses the term ‘evolution’, it is simply not clear which of these several meanings is meant.

7.2. Haeckelian phylogeny

One of these original five theories of Darwin, and indeed the most important one to biologists in the latter part of the 19th century was that of common descent. In 1866, Haeckel introduced the term ‘phylogeny’, which corresponded quite strictly to this theory of common descent of Darwin’s bundle of five theories. That is, Haeckelian phylogeny is equivalent to Darwinian common descent (genealogy: theory 2 of Darwin, Mayr 1985, p. 758) and not to the entire bundle of Darwin’s five theories of evolution as often assumed by biologists and philosophers. Haeckelian phylogeny clearly does not include Darwin’s mechanism for evolutionary change (= Darwinian natural selection). But Haeckelian phylogeny clearly does include both the amount of evolutionary change (anagenesis) and branching (cladogenesis).

The study of phylogeny was traditionally considered to be, so to speak, a backward looking endeavour, the search for and study of common ancestors. The starting point in such an analysis is a particular taxon and the student of phylogeny attempts to infer the properties of its ancestors. The species left in a tentatively delimited taxon, after the removal of all erroneously associated species, are the descendants of the nearest common ancestor. Such a taxon is called *monophyletic* (Simpson 1945, 1961; Mayr 1969, Mayr and Ashlock 1991, pp. 253–255). Arranging such taxa hierarchically makes a Darwinian classification automatically phylogenetic in the strict Haeckelian sense.

Genealogy for Darwin did not mean simply branching of evolutionary lineages although he stressed this point as it was the new idea he introduced for the history of organisms, but he clearly included evolutionary change between branching points. For cladists, however, genealogy acquired strictly the meaning of branching point phylogeny (= Hennigian phylogeny). Evolutionary dendrograms are based on Haeckelian phylogeny (= Darwinian common descent) and can be considered Haeckelian dendrograms or Darwinian dendrograms; these terms are strictly equivalent but differ from Hennigian phylogeny.

7.3. Hennigian phylogeny

When Hennig (1950, 1966) introduced his ideas about classification, he stated that they were based on phylogeny, implying Haeckelian phylogeny. However, Hennig’s phylogeny is not the same as Haeckel’s phylogeny. He introduced an entirely different concept. The study of phylogeny was for him a forward (to the future) looking process. Its starting point is a stem species. The Hennigian systematist distinguishes a phyletic branch (clade) containing the stem species and all its descendants, no matter how diverse such a clade may be. For instance, the particular species of vertebrates that gave rise to the branch that ultimately became the mammals was an early synapsid reptile of the order Pelycosauria. Hence, the mammalian clade includes not only the mammals but also such very different groups as primitive reptiles (Ax 1984). Although Haeckel included both the amount of change and branching in his notion of phylogeny, Hennig embraced only branching of phyletic lineages in his notion of phylogeny. Hennigian dendrograms are cladograms and are in no way equivalent to Haeckelian or Darwinian dendrograms.

Hennig (1950, 1966) also transferred the traditional term monophyly to the new concept of phylogeny that caused great confusion (see sections on ‘Phylogeny’ and ‘Shift to holophyly’). To end this chaos, Ashlock (1971) introduced the term *holophyly* for Hennig’s new concept. The Haeckelian monophyly concept and the Hennigian holophyly concept are fundamentally different and have drastically different consequences for taxonomy. A holophyletic clade encompasses a stem species and all of its descendants. A monophyletic taxon consists of descendants of the nearest ancestral taxon.

Although Hennig and most other workers state that Hennigian classification is based on Haeckelian phylogeny, this is really not so. Hennig’s approach is not based on the complete notion of Haeckelian phylogeny and consequently is not properly a phylogenetic classification. Rather, it is a cladistic (phylogenetic branching only) system. For this reason we prefer to consider the Hennigian ordering system as a cladification and the resulting dendrograms as cladograms. Furthermore, in no way is it valid to claim that Hennigian cladograms provide the foundation for understanding the evolution of biological organisms as these cladograms include only branching points (cladogenesis) and not the amount of evolutionary change (anagenesis).

8. Class and classification

8.1. Definition of class

Ten different meanings of the word ‘class’ are recorded in the Oxford English Dictionary, second edition (1989). The sixth

one is the one relating to taxonomic classification: 'Class. A number of individuals (persons or things) possessing common attributes, and grouped together under a general or "class" name, a kind, sort, division. (Now the leading name).' The American Heritage Dictionary, 3rd edition (1992) calls a class: 'A set, collection, group, or configuration containing members regarded as having certain attributes or traits in common'. Several other dictionaries consulted have definitions that are in principle the same – that a class is a collection of similar entities. All authors dealing with classification have emphasized that in the context of classification, classes are composed of similar items.

The concept class in the vocabulary of the taxonomist must never be confused with any of the other meanings of class listed in the Oxford English Dictionary. In particular, it should never be confused with the concept corresponding to Plato's *eidos* or to the natural kind of the philosopher.

8.2. Construction of classes (taxa)

The construction of classes in an upward classification involves a number of consecutive steps (Mayr and Ashlock 1991), as follows:

- Entities (for instance species) to be classified are assembled into classes of similar entities that are as homogenous as possible.
- A given entity is included in that class with the members of which it shares the greatest number of attributes.
- A separate class is established for any item that is too different to be included in one of the previously established classes.
- The degree of difference among the classes is expressed by arranging them in a hierarchy of nested sets. Each categorical level (rank) in the hierarchy expresses a certain degree of distinctness.

8.3. General definition of classification

The logical consequence of the definition of class is that classification must be defined as the ordering of diversity into classes of similar entities. And this has been traditionally the almost universally accepted concept of classification. The Dictionary of the History of Science (Bynum et al. 1981, p. 68) defines classification as: 'The arrangement of objects into groups or classes usually on the basis of perceived similarity or difference.' This definition is equally applicable to the ordering of organisms in taxonomy and to many ordering activities in daily life. A classification of organisms is based on the shared possession of their diverse attributes. The units of similarity in a Darwinian classification are called taxonomic characters that have the property of being homologous to one another in the several entities or groups. The claim of a few modern authors that there is no agreement on the definition of the word 'classification' is quite misleading. Actually, prior to 1950 there was virtually total unanimity on the usage (in classification) of the words classification and class, as referring to the grouping of similar items.

A classification is defined as 'The arrangement of entities in a hierarchical series of nested classes, in which similar or related classes at one hierarchical level are combined comprehensively into more inclusive classes at the next higher level.' This definition evidently requires an equally careful definition of the term class (described earlier). Any

ordering system that does not consist of hierarchically ordered classes as defined is not a classification. The correct definition of the word classification depends on the correct choice of the word class.

Upward classification, based exclusively on overall similarity, was obviously so superior to classification by logical division that by *ca.* 1800 it was virtually universally adopted for the classification of organisms. However, perceptive taxonomists were aware that by adopting a method that depended exclusively on a single criterion, similarity, they were somehow ignoring information that might lead to an improvement of the current classification.

8.4. Biological classifications as hierarchies

All classifications, but not all ordering systems, are constructed hierarchically (lower classes nested within higher classes). A hierarchical arrangement is characteristic of all genuine classifications, not only those of organisms. The classification of the human language families is hierarchical, and even artificial classifications, such as those of books in a library, are largely hierarchical. A hierarchical arrangement has many virtues, telling us for instance that a class (e.g. taxon) of lower rank also has the attributes of the higher classes under which it is ranked. Once we know that a given organism is a thrush, we also know that it has the attributes of songbirds, birds, vertebrates, chordates, and animals. A hierarchical arrangement is enormously important for easy information storage and retrieval.

To construct a hierarchy of relationship in a Darwinian classification, one combines related taxa at a given categorical level into a taxon of the next higher categorical level. Thus, similar species are combined in a genus, similar genera in a family, and this is continued up to the highest categorical ranks. The final result is the so-called Linnaean hierarchy. A Linnaean system consists of a nested set of taxa of different categorical ranks of seven basic levels. For instance, the genus *Canis*, composed of the species of dog-like animals, is grouped with other similar genera (e.g. *Vulpes*, foxes) in the family Canidae; the members of this family and those of other carnivorous families, such as the Felidae (cats) and Mustelidae (weasels), are grouped in the order Carnivora, and so on to larger and larger groups of ever higher categorical rank. This process is continued until all living organisms are grouped into a number of kingdoms, which in turn are assigned to two empires, the Prokaryota (bacteria) and the Eukaryota (all organisms with nucleated cells). Once a taxon has been properly delimited, it must be included in its proper place in the Linnaean hierarchy, it must be ranked (see below).

As common descent was accepted also by most Neo-Lamarckians in the second half of the 19th century, they usually also adopted a hierarchical Darwinian classification. Classifying organisms on the basis of Darwin's theory of common descent (monophyly) will result in a hierarchical arrangement. When the ordering of the so-called classes cannot be made hierarchical, this means that the groupings are not the kind of classes as defined above for classes in a classification. For instance, the stages in the development of an organism from egg to adult do not fit the above given definition for classes in a classification. Therefore, the ordering of these stages is not a classification in the proper sense of this word.

8.5. Ranking

After a taxon has been properly delimited in a Darwinian classification, it must be included in its proper place in the Linnaean hierarchy; it must be ranked, which is determined by the degree of difference among the taxa. Rank in this hierarchy, other things being equal, indicates degree of similarity and recency of common origin. The lower the rank of a taxon, the more similar the included species are, and usually the more recent was their nearest common ancestor. It must be remembered, however, that these two factors, similarity and recency, are not always closely correlated in the evolution of organisms.

The number of levels in this hierarchy is arbitrary. Some taxonomists recognize more levels than others do. 'Splitters' tend to recognize more levels because they want to express as many degrees of difference as possible. 'Lumpers' recognize fewer levels owing to their intent to demonstrate relationships. Ranks at the lower end of the hierarchy may have somewhat different functions. The species indicates distinction, the genus relationship. Too fine a splitting of genera destroys their value as indicators of relationship. For a detailed discussion of ranking see Mayr (1969, pp. 233–244).

When a phyletic lineage enters a new adaptive zone, such as a branch of the archosaurs becoming flying birds by entering the air space, it is exposed to very strong new selective demands and may undergo rather drastic reconstruction. Darwinian taxonomists recognize this macroevolutionary event in their classifications by raising the new taxon to a higher categorical rank (less similarity). On the other hand, cladists, when following Hennig's principle of holophyly, usually do not change the rank to indicate greater anagenetic change in one lineage, because for them ranking is determined strictly by the sequence of splitting events. This decision is responsible for the most drastic differences between Darwinian classifications and Hennigian classifications. The great difference between the slow gradual change of a phyletic lineage and the often drastic restructuring following either the budding off of an evolutionary innovation or the entrance into a new adaptive zone, is neglected by many taxonomists. This neglect often results in unbalanced classifications.

It is an obvious weakness of the traditional ranking system that it has not been able to find a suitable yardstick for making the ranking of the categories of all different groups of organisms more comparable. Degree of similarity, no matter how measured, in different groups of organisms is not absolutely correlated with the amount of evolutionary change in diverse groups. Orders of birds, for instance, are morphologically much more similar to each other than the orders of arthropods or of other phyla of invertebrates. What the students of fossil hominids call different genera, would certainly not receive generic rank if they were artiodactyls. But as there is usually a rather uniform standard within a given higher taxon (e.g. birds, butterflies, spiders) not much damage is done. Actually, little loss of understanding results from any inequality of standards of ranking as long as taxonomists realize that the ranking in different higher taxa is not necessarily based on the same yardstick. A wholesale changing of the ranking throughout the system, in order to make the standards of ranking more uniform, would lead to a great deal of instability of the system, and is therefore to be avoided.

A number of proposals have been made to find a strictly objective uniform criterion for ranking. Hennig (1950) at first

proposed that each higher taxon be ranked according to its geological age. This proposal found few followers, because the rates of change in different phyletic lineages are far too different. One only needs to compare genera of cichlid fishes that originated within thousands of years with living fossils that hardly changed in more than 100 million years. Another proposal was that of Sibley and Ahlquist (1990) to use a fixed amount of change of DNA as a yardstick. Again this was an unsuitable criterion because other evidence showed that rate of DNA change was highly variable, with some lineages changing at least twice as fast as others. Although fully aware of the enormous difference in rates of change of cichlid genera and species of *Drosophila*, Avise and Johns (1999) returned to Hennig's original proposal to adopt a ranking schedule strictly based on geological time. It would place diverse species of the genus *Drosophila* into different families and subfamilies. Rank in this scheme no longer expresses different levels of similarity and this scheme is therefore not likely to become popular among adherents of Darwinian classification.

9. Similarity

9.1. General concept and use in classification

Goods in a market are arranged by similarity: meats, vegetables, fruits, cereals, etc. Similarity must relate to fundamental properties of the objects to be classified. Books in a library are classified by their contents and not by the colour or the material used for the binding, their size or colour. Canned goods in a store also are classified by their contents (coffee, soups, fruits, oils, etc.) and not by the type of container. It would hardly be necessary to mention this, if this obvious criterion had not been violated by some recent authors, perhaps to ridicule the use of similarity in classification.

Philosophers have been remarkably unanimous in stating that classifications are based on similarity. Mill (1843, vol. 8, p. 714) stated: 'The ends of scientific classification are best answered, when its objects are formed into groups respecting which greater number of propositions can be made.' Or, to quote another philosopher, Jevons (1874, p. 677): 'By the classification of any series of objects is meant the actual or ideal arrangement together of those which are like and the separation of those which are unlike.' Whewell (1840, pp. 521, 523) says approximately the same in his famous statement: '*And the maxim by which all systems professing to be natural must be tested is this: that the arrangement obtained from one set of characters coincides with the arrangement from another set.*' (italics his) Essentially, the same thought was expressed quite recently by Hempel (1965, p. 146): 'In a [natural] classification those characteristics of the elements which serve as criteria of membership in a given class are associated, universally or with high probability, with more or less extensive clusters of other characteristics.' and (Hempel 1952, p. 53) '... of which they are logically independent.' A leading paleontologist (Bather 1927, p. 65) said it in these words: 'The philosophical purpose [of a classification] ... is best fulfilled by classing together the things that possess in common the greatest number of attributes.' Dictionaries and encyclopaedias almost unanimously have definitions of classification in which similarity is stressed as the ordering principle, as for example, the New Encyclopedia Britannica [15th edn (1993 printing), vol. 3, p. 356]: 'Classification theory, principles governing the organization of objects into groups according to their

similarities and differences or their relation to a set of criteria.' Not only the philosophers, but also the practitioners of classification have taken it for granted that similarity is the best classifying criterion. The librarian Broadfield (1946) stated: 'Classification is defined as the putting together according to likeness ... [or] likeness governs classification.'

9.2. Meaning of similarity in biological classification

What happened in 1859 was a drastic change in the explanation for the similarity shared by the members of a taxon. Prior to Darwin, this similarity was explained essentialistically. Members of the same taxon were similar as belonging to the same idealistic type. Their similarity was because of to the possession of the same essence (*eidos*). After 1859, their similarity was attributed to the fact that they are the descendants of the nearest common ancestor. Hence, the important similarity for biological classification is ancestral similarity that provides the definition for the concept of homology (see Bock 1989b). This truly drastic change in explanation curiously caused little change in the actual taxonomic practices. The classes of the taxonomist continued to be delimited by degrees of similarity, no matter how this similarity was to be explained.

For biological classification, the correct formal statement is that entities are grouped together as members of a taxon because they share a suite of homologous features (Bock 1989b; Hall 1994). Homologous features are those features in different organisms that are derived phylogenetically from the same feature in the immediate common ancestor, and are tested empirically by the shared possession of some attributes of similarity (Bock 1989b). Analogously, the other term introduced by Owen, has had a difficult history in biological comparisons, but can still be most useful in functional and other studies (Homberger 2000). Homology is a relative concept (Bock 1989b, p. 333) and all statements about homologous features must include a conditional phrase that describes the nature of the homology and as such, the characteristics of the feature in the immediate common ancestor. It is because homologous features are tested empirically by shared similarities that one can say in an abbreviated fashion that biological classification is based on similarities (Bock 1989b, p. 337). Because all approaches to classification must begin with the recognition of homologous features and because the testing of hypotheses about homologues can only be done on the basis of shared similarities, then all approaches to biological classification must be based (or if one prefers, must use) shared similarities in their analysis. When biologists state that different organisms are placed in the same taxon because they share certain similarities, they are not ignoring the intermediate steps of formulating and testing homologies, but simply assume tacitly the entire formal procedure.

9.3. How to determine similarity?

Similarity of two or more entities simply means that they resemble one another – that is the description of one entity agrees largely with the description of the other. Identity means that the entities agree in all aspects of their description. Similarity, as a determinant in classification, must be carefully evaluated to ascertain whether the features are truly homologues. Even the simple question 'What is similar?' is often

difficult to answer. Is an eel similar to a snake? Yes, as far as body form is concerned, but otherwise an eel has the characters (homologues) of a teleost fish and a snake those of a reptile. The same is true for bat and pterosaur. Both are flying vertebrates with a membranous wing, but otherwise one has the characters of a mammal, the other those of an archosaurian reptile. In both cases the correct classification is achieved 'by classing together the things that possess in common the greatest number of attributes.' Such similarity is usually referred to as 'overall similarity'.

9.4. Overall similarity

The criterion 'perceived overall similarity' or 'comprehensive similarity' would seem at first sight to be extremely vague and ambiguous. For biological ordering systems, overall similarity is a 'short-cut' term to denote organisms sharing a large number of homologous features. Actually, taxonomists rarely have doubts as to which are the nearest relatives of a given taxon once a sufficient number of homologous features have been well studied, including thorough functional/evolutionary analyses. Major exceptions are organisms with an insufficient number of taxonomic characters (e.g. amoebae, certain nematodes) or isolated old taxa without a fossil record (e.g. parrots). Indeed, overall similarity has long been used by philosophers, as illustrated by the cited statements of Mill, Whewell, and Jevons.

But there are a number of cases in the literature where 'overall similarity' has been actually deceiving. The New World Vultures (Cathartidae) were until recently classified with the Old World Vultures (Accipitridae) in the order Falconiformes owing to their convergent adaptations as carrion feeders. Actually, the Cathartidae are related to the storks (Ciconiiformes: Ciconiidae). The New World and Old World porcupines were until quite recently considered closely related which they are not. Their similarities are because of convergence. The golden moles (Chrysochloridae) of South Africa were always considered to be closely related to the Holarctic moles (Talpidae), until molecular analysis showed that they do not even belong to the same order (Insectivora).

This is the reason why the tentative recognition of taxa by overall similarity must always be reinforced by further testing of the homologous features or by a phylogenetic (genealogical) analysis to confirm or refute common descent. A properly conducted analysis of the homologous features, including a careful consideration of the hierarchy of conditional phrases is equivalent to a phylogenetic investigation (Bock 1989b). Yet, the history of taxonomy has shown that overall similarity by itself is remarkably often a reliable indication of close relationship. Perhaps this is not surprising, as one would expect organisms derived from the nearest common ancestor to be more similar to each other than members of arbitrary groupings.

A first approach is to say that two objects are the more similar to each other, the more properties they have in common. However, different sets of characteristics are sometimes in conflict with each other. Furthermore, there are a number of constraints on the use of similarity. For instance, only such characters can be used for the determination of overall similarity that are properly independent. If large size is one utilized character, it is not permissible to use separately other measures of size.

9.5. Sources of similarity in organisms

Two taxa may be overall similar (*homoplasy*) to each other for four different reasons:

9.5.1. Evidently descended from the same ancestor

This impression must be confirmed by additional testing of homologous features, especially a further detailed analysis of the nature of conditional phrases (Bock 1989b, pp. 333–335) and/or by the inclusion of additional attributes. The turtles, for instance, long believed to be a very isolated group of primitive reptiles, have recently been shown by molecular methods to apparently share numerous characteristics with diapsid reptiles, particularly with the crocodylians (Zardoya and Meyer 1998, 2001). If this is supported further, the turtles are not isolated within the Reptilia, but belong to the diapsid lineage. Likewise, it is indicated both by the study of morphological characters (setae) and by molecular evidence that the Pogonophora and Echiura are not isolated phyla, but are derived from certain families of polychaetes. Most relationships between two taxa of organisms are considered to be reasonably well established when it is found that they share more, indeed usually many more, characteristics with each other than with any other taxon. Highly isolated taxa often cause considerable difficulties.

9.5.2. Parallelophyly

The phenotypic similarities were independently acquired owing to an inherited ancestral propensity of their lineage to develop these characters. A classical case is the stalked eyes of acaelypteran flies. Other examples are the numerous independent developments of ‘flycatchers’, ‘warblers’, ‘finches’, ‘titmice’, ‘shrikes’, and ‘nectar feeders’ among songbirds (Passeriformes: Oscines) in different parts of the world. The great similarity of the pelvis and posterior extremities of certain bipedal dinosaurs to those structures of the (bipedal) birds may well be because of the fact that both are derived from thecodont ancestors and acquired the bipedal specialization controlled by the same ancestral genotype. Many cases of parallelophyly in the genus *Drosophila* have been analysed elegantly by Throckmorton (1963, 1969).

9.5.3. Reversal

Reversal occurs when further evolution of a feature results in a derived condition that is similar to the ancestral (earlier) condition. This often results from the independent loss of the same character in different lineages, such as the loss of wings in many taxa of insects, the condition found in primitive insects, and the loss of the paired limbs in the snakes and in several groups of limbless lizards, a return to the condition in the earliest group of fish. The evolution of avian cranial kinesis (see below) is another excellent example. Mayr and Ashlock (1991, pp. 216–218) give suggestions how to cope with difficulties associated with reversals.

9.5.4. Convergence

This is a similarity of characters of two only distantly related taxa. Such similar characters are not derived from the nearest common ancestor; they are not homologous. The wings of birds and bats are an instance. There are apparently only a limited number of possible functional or adaptive answers to certain challenges of the environment. Very similar responses to a particular challenge may evolve independently in totally

unrelated taxa. Photoreceptor organs (eyes) have apparently evolved independently in at least 40 different animal lineages (Salvini-Plawen and Mayr 1977), numerous flightless (wingless) taxa have evolved in winged orders of insects, bioluminescence at least 26 times independently. A failure to correctly identify such observations as cases of convergence would be a grave error. It is particularly important not to be deceived by ‘concerted homoplasy’, a particular form of convergence. This occurs when different lineages independently colonize the same adaptive zone and independently acquire the same set of adaptations. Haszprunar (1998) shows, for instance, that five to 10 groups of marine gastropods became terrestrial independently. A whole set of characters changed in parallel in all of these groups in response to the new environment. It would be completely misleading to count each of these characters as independent evidence for a close relationship among these terrestrial taxa. Australian shrike-tits (*Falcunculus*; ? Pachycephalidae) have a predatory hooked bill very similar to that found in the true shrikes (Laniidae); the bills in the two groups are morphologically convergent for functional reasons, but not adaptive ones (Bock 1977a, p. 75). Other such features in birds are the intramandibular hinge and enlarged mucous-secreting glands. Many examples of adaptive convergence in bill structure and feeding habits are known in the passerine birds as mentioned above. The last three kinds of similarity (9.5.2, 9.5.3) are usually combined under the term *homoplasy*.

9.6. Significance of characters (weighing)

The experienced taxonomist knows that there are several methods by which the validity of a seeming similarity can be tested. Weighing of the utilized characters is one of them. As was stated by Whewell (1840), a character has the more weight, the more often it is associated with other characters found in a provisional class (= taxon); and he emphasized the importance of weighing also elsewhere (pp. 468, 567). It is often stated that ‘the relationship of two species is the closer the more characters they share.’ Every experienced taxonomist knows that different characters have different weights. Brown fur in a mammal has low weight because of the high frequency with which it originated independently. The presence of a single character, the notochord, in tunicate larvae demonstrates their relationship to the chordates. Numerous empirical rules exist for the weighing of characters (Mayr 1964, pp. 26–29; Mayr and Ashlock 1991, pp. 183–192). However, there has been so much arbitrariness and bad judgment in the past in the evaluation of morphological characters that many taxonomists hesitate to use any method of weighing. Yet, experienced taxonomists who thoroughly know the taxon they work with, usually have a rather accurate idea of which characters have high weight and which others do not. But there are always exceptions, warning us to be very cautious when using any method of weighing. No system of weighing is perfect, but almost any method of weighing is preferable to using unweighed characters, that is, to give all characters the same weight. Actually, to give all characters the same weight is also a method of weighing. Weighing is particularly important when different methods produce different classifications and one wants to construct a consensus tree, also when one uses very different kinds of characters, such as morphological and molecular, as well as different kinds of molecules. The literature provides suggestions on how to proceed in such situations.

The most important method of weighing characters is an evolutionary analysis (Bock 1989b) based on an investigation of the functional-adaptive aspects of the homologous features and other attributes such as the complexity of the feature and its morphological-functional connections to other features. In this method, it is determined whether a character is 'derived' (newly acquired in a lineage) or ancestral, and the possibility that it could have evolved independently two or more times. This determination avoids the difficulties encountered by those who relied on unweighed phenetic and cladistic methods. Actually, however, the unreliability of similarity has been exaggerated by some authors recently. We know of relatively few cases in the last 100 years, where a spurious similarity had led to complete misclassification. Presumably, most authors had made use of carefully reasoned weighing. A few obvious generalizations can be made. Complex features usually have higher weight than simple ones, particularly if they consist of a number of different parts and are broadly connected with other features. Characters, lost during evolution, such as limbs in reptiles, have little or no weight.

What is meant by 'overall similarity' is similarity in the vast majority of available and independent characters. Most objections to the term overall similarity have come from philosophers while the practicing taxonomists only rarely have any doubts as to which two among a number of taxa show the greatest overall similarity. However, to eliminate any error in the Darwinian procedure, every tentative classification based on similarity must be confirmed by a phylogenetic analysis and preferably one based on a functional/adaptive evolutionary investigation (see below) that would reveal any misjudgements of similarity.

9.7. Numerical approaches

A school of numerical taxonomists, the pheneticists, grouped all organisms on the basis of 'overall similarity' (Sneath and Sokal 1973). This endeavour, for a number of reasons, was unsuccessful. An exclusive reliance on overall similarity encountered numerous difficulties owing to convergence (homoplasy – the individual characters assumed to be homologous were not carefully analysed), mosaic evolution of characters (different rates of evolution of different characters), and most importantly, a shortage of diagnostic characters. This is why an application of purely phenetic methods has largely been abandoned in modern taxonomy (Mayr and Ashlock 1991, pp. 195–205). However, after the rise of molecular systematics, the so-called distance methods have become popular and are basically phenetic methods. They are vulnerable to the same problems especially that of homoplasy, as the original numerical phenetics, as is the recent development of a 'numerical cladistics'.

The basic problem in all of these approaches is the reliance placed on using a large number of taxonomic characteristics about which the conclusion of their homology has a low to a very low degree of confidence. Unfortunately, the use of a large number of such homologous features does not provide strong support for a conclusion about the evolutionary relationships of organisms, be it classificatory or phylogenetic. That is (Bock 1989b, p. 341), '... a group hypothesis appears to be tested more convincingly with ten homologues, each of which has a degree of confidence of about 90.0%, than with 100 different homologues, each of which has a degree of confidence of only 9.0%.'

10. Ordering by using only the criterion of phylogeny – type 5

10.1. Hennigian cladification

In the first half of the 20th century, there was considerable disagreement among leading specialists on how to classify insects, particularly at the generic and family level. When the entomologist Willi Hennig encountered this situation and, in particular, discovered that several generally accepted higher taxa included unrelated species that had been placed there only owing to their superficial similarity, he decided that an entirely different approach to the ordering of species should be proposed. Claiming that any classification based on similarity was typological, he proposed that species should be ordered instead only by common descent (genealogy). His discussion implies that he thought this approach to be a novel idea; at least he does not specifically cite other authors who previously had employed an exclusively genealogical approach to classification.

Why did Hennig present his conclusions as if he had made a great discovery? Why did he fail to mention that using genealogy is precisely what Darwin had also done in 1859 in his theory of classification? At first this seems indeed a very strange omission, until one discerns that Hennig apparently had never read Darwin. The few times he refers to Darwin is by way of secondary sources. Obviously, one book more than any other, Darwin's *On the Origin of Species* (1859, chapter 13), is the logical starting point for Hennig's proposal. Yet, Darwin (1859) is conspicuously missing from Hennig's bibliography. That Hennig apparently never read Darwin's 1859 *On the Origin of Species* is not surprising because this book was little read in Germany up to the middle of the 20th century. And thus Hennig did not appreciate that Darwin had found the solution to the problem of combining complete adherence to genealogy (= phylogeny, or evolutionary history) with the traditional system of classification (classes of similar entities). Curiously, D. D. Davis and R. Zangerl, who were responsible for translating Hennig's manuscript (Hennig 1966), which popularized his ideas, were apparently equally ignorant of the importance of Darwin's chapter 13 to Hennig's approach (see also Osche 2002, pp. 18–20). Because Hennig apparently was not aware of Darwin's application of evolutionary ideas to classification and because Hennig's system of classification is now so widely adopted, we feel that it is necessary to analyse Hennig's cladistic system as a classification, although as we shall point out later that even though cladifications are ordering systems they are not classifications.

Unlike Darwin, Hennig decided not to make use of similarity at all, but to rely exclusively on the results of phylogenetic analysis. This would permit construction of a cladogram of the derived characters that would reveal the branching phylogeny of the studied species. In this ordering process, all species would be assigned to branches (clades) of the cladogram, rather than to classes of similar species (taxa) as in a traditional classification. Each branch would consist of the stem species of this branch (clade) and of all of its descendants. The result is a phylogenetic ordering of clades, a cladification, based on the principle of holophyly (Ashlock 1971). A clade is holophyletic when it includes the originating stem species and all of its descendants.

Hennig's methodology is actually in some conflict with his claim that similarity has no role in his system and methodology. He advocated analysis of the phylogeny of organisms by

the possession of synapomorphic features by members of each group (= clades or cladons), but synapomorphies are synonymous with derived homologous features. The first step in a Hennigian analysis must be the determination of homologous features possessed by these organisms, but this step is either dealt with in a most obscure way or ignored completely by Hennig and his followers. Moreover, many to most cladists believe that homologous features can be ascertained only after the cladogram has been established, which turns on its head the traditional procedure of first establishing homologues and testing them against empirical observations of similarities and secondly using these homologues to test group hypotheses of classification and phylogeny. It must be pointed out that many other non-cladistic systematists also share this misconception. If systematists claim that homologues can be determined only on the basis of a known phylogeny or cladogram, then it is essential for them to show how they established the features used in the analysis of the plesiomorphic–apomorphic axes. The only approach for testing the homology of features in diverse organisms is by similarities of all types. Hence, assessment of similarity is an integral part of the Hennigian system, contrary claims notwithstanding. Yet Hennig's insistence that the criterion of similarity should have no role in biological classification is completely at variance with the full methodology used in cladistic classification – an irresolvable conflict. Consequently, the cladistic method has much in common with that used in Darwinian classification that is the initial determination of homologous features followed by a phylogenetic analysis (see Bock 1989b, 1992). Although Hennig claimed that his phylogenetic classification is based only on the criterion of phylogeny, one can question whether it is possible in principle to disregard the use of similarity when testing homologous features – an essential step in the cladistic analysis. We think not.

10.2. Peculiarities of Hennigian terminology

A particularly unnecessary but highly injurious source of misunderstandings between cladists and non-cladists is the terminology that Hennig adopted when he introduced his new system. Evidently, he did not realize how drastically different his new methodology was from the traditional one. Unhesitatingly, he took over part of the terminology of the traditional method of classification and used it for very different components of his new ordering system. Terms that had been universally used for certain aspects of Darwinian classification for more than 100 years were transferred by Hennig to totally different concepts. This was in clear conflict with established scientific procedure. Equally unsettling was his introduction of the new concept of paraphyly. The new terminology is now an inseparable part of cladification. A thorough discussion of these terminological problems is therefore necessary.

10.2.1. Paraphyly

In a Darwinian classification, whenever a taxon gives rise (almost always by budding) to a derived new higher taxon, this taxon is given the rank appropriate to its degree of difference. Everybody agrees that birds and mammals were derived from reptiles, but having become adapted to new adaptive zones, these two warm-blooded classes of vertebrates are now so different from the ancestral cold-blooded scaly reptiles that traditionally they have been ranked as separate classes. More importantly, the fact that the reptilian Therapsida–Cynodontia

gave rise to the mammals and that the reptilian Archosauria gave rise to the birds, had no retroactive influence whatsoever on the nature of the parental taxa, the Therapsida and Archosauria. In other words, in a Darwinian classification the origin of mammals and birds had no effect whatsoever on the classification of the ancestral group – the reptiles. To combine the ancestral reptiles with the derived warm-blooded birds in a single taxon ('avian dinosaurs') would be in complete conflict with a basic principle of classification, the endeavour to make homogeneous classes of similar entities.

The situation is different for a cladist who sorts branches rather than classes. Cladists call a taxon paraphyletic if the basal clades of a derived taxon have been removed. Hence, in a cladification, the reptiles are called paraphyletic after the Therapsida and Archosauria had been transferred from the Reptilia to the Mammalia or Aves. The Therapsida (or even earlier fossil reptiles) contain the stem species of the branch that leads to the mammals. In the construction of a cladogram, this branch of synapsid reptiles is taken out of the Reptilia and attached to the mammals (Ax 1984). Likewise, the archosaurs, which are part of the diapsid branch that leads to the birds, are removed from the Reptilia and attached to the birds. What is left of the traditional reptiles is a paraphyletic wreck, even though the existence of the derived classes had no influence whatsoever on the taxonomic characterization of the Reptilia. Paraphyly does not exist in a Darwinian classification. In a cladification, however, it has devastating effects. Most fossil taxa (except terminal ones) are paraphyletic, and must be restructured and renamed. The chaos this would create for traditional classifications is unimaginable.

Is there any justification for the introduction of the concept of paraphyly? Birds branched off from the archosaurian stem, sometime in the Mesozoic, either from an older (thecodont) or a more recent (dinosaurian) ancestor. Did this origin of a derived lineage have any effect on the characteristics of the ancestral taxon from which the new lineage was derived? None whatsoever! Then why should the placement and ranking of a taxon be changed because it gave rise to a new taxon? The taxonomic characters of the ancestor, which alone (at least for a Darwinian) could determine its classification, had not changed in any way. The appearance of a new side branch has no retroactive influence on the classification of its ancestors. Hence, we cannot conceive of any valid reason why the ancestral part of the new lineage should be removed from its current taxonomic position in the Reptilia, merely because it gave rise to a new derived taxon. Even though mammals and birds budded off from the Reptilia, this ancestral group remains as untouched and sound a Darwinian taxon as ever. And the same is true for turbellarians and polychaetes, when giving rise to strikingly different derivative groups. Removal of the ancestral taxa of these derived groups from their traditional position would leave a paraphyletic mess in every case. For these reasons, cladistic classification is exceptionally unsuited when applied to fossil organisms for which a mixed practical system of horizontal and vertical classification appears to work best (Simpson 1945, 1961).

There is no paraphyly in a Darwinian classification because the ancestral group stays essentially unchanged, and likewise, because the newly evolved side-branch is considered to have no effect on the nature of the branch from which it arose. Paraphyly is a consequence of the cladistic method of making holophyletic branches the units of their ordering system rather

than taxa. We can see no reason why a Darwinian should adopt the concept of paraphyly.

10.2.2. Monophyly

The study of phylogeny has been traditionally considered to be, so to speak, a backward looking endeavour, the search for and study of common ancestors. The starting point in such an analysis is a particular taxon and the student of phylogeny attempts to infer the ancestors of this taxon. If all the species of a tentatively delimited taxon are the descendants of the nearest common ancestor, the taxon following Haeckel (1866) is called *monophyletic* (Mayr 1969, Mayr and Ashlock, 1991 pp. 253–255). Hennig (1950) introduced an entirely different concept. The study of phylogeny was for him a forward (to the future) looking process; its starting point was a stem (mother) species. The Hennigian distinguishes a phyletic branch containing the stem species and all its descendants as a taxonomic unit, as a *clade*, no matter how different the beginning and the ending of a clade may be. Hennig transferred the traditional term *monophyly* to his new concept of phylogeny, causing great confusion. To terminate it, Ashlock (1971) introduced the term *holophyly* for Hennig's new concept. The traditional monophyly concept and the Hennigian holophyly concept have drastically different consequences in taxonomy. A holophyletic clade encompasses a stem species and all of its descendants. A monophyletic taxon consists only of the descendants of the nearest ancestral taxon.

10.2.3. Relationship

In taxonomy, this term originally meant nothing but resemblance (Padian 1999, p. 353). But for Darwin and most of his followers, it also indicated genetic similarity. You are, on the average, twice as closely related to your children as to your grandchildren. What is of crucial importance is that relationship in a Darwinian classification includes not only nearness of branching points, but also the amount of change after each branching point. This part of the difference between two taxa is ignored in the cladistic methodology. Furthermore, relationship for a Darwinian also includes lateral relationships (like siblings and cousins) while in cladification genealogical relationship means only 'the relationship between parent and child or ancestral species and its descendant daughter species', as stated by Wiley (1981). In other words, the cladist is concerned only with straight-line vertical phyletic relationships. Relationship in cladification simply means belonging to the same clade, the clade that is derived from the same stem species. Sister taxa, although genetically and phenotypically very similar to the stem group of a clade, are considered less closely related than species at the far ends of the same clade. To express this in terms of present-day cladistic relationships, Charlemagne is considered more closely related to his present-day descendants than to his brothers and sisters. The replacement of monophyly by holophyly requires this peculiar concept of relationship.

10.2.4. Classification

Classifications are traditionally defined as *hierarchically ordered systems of classes of similar objects*. Hennig's cladification, however, is a cladistic ordering of branches (or parts of branches) of phylogenetic trees. These branches are often quite heterogeneous and do not satisfy the definition of classes. A Hennigian cladification therefore is not a classification, but it is still a proper ordering system – a cladification.

10.2.5. Taxon

Taxa are traditionally used in a Darwinian classification for a class of similar species but are misleadingly used by most cladists for a branch (clade) or part of a branch of a cladogram. The entities ordered in a cladification are not classes, but clades or cladons. The term taxon applies to taxonomic classes.

10.3. Cladistic analysis

No argument exists that hypotheses about branching (= Hennigian) phylogenies are tested by the possession of synapomorphic (= derived homologous) features in sister groups. Yet, major questions exist on the methods by which hypotheses about these synapomorphic features are tested. Most cladists have relied on methods such as the 'out-group comparison' (Hennig 1966). The problem with these methods, as with many other methods in the establishment of ordering systems of biological organisms, is that they are directly circular (Bock 1981, p. 15) because the test of the character hypotheses depends on the distribution of the character states in the taxonomic groups and these character states are subsequently used to test hypotheses about the same groups of organisms in the ordering system. The question is, of course, how were the groups discerned initially. Non-circular procedures to test taxonomic characters that are then used to test group hypotheses in ordering systems of biological organisms are difficult to formulate and apply. We would argue that the best such methods involve functional/adaptive evolutionary approaches (Bock 1977b, 1992).

For cladistic analysis, the procedure involves the following steps:

- (a) First is establishing homologous features among the organisms being ordered using the methods outlined in Bock (1989b), including an estimation of the degree of confidence about each hypothesis of homology. Herein, it is necessary to postulate whether similarly appearing features may be homoplastic.
- (b) Second is arranging these homologous features into a transformation series which reflect the most reasonable pattern of evolutionary change of these features according to our knowledge of the structure, function, adaptiveness, etc., of each type of feature. This arrangement of the homologous features into a transformation series depends on our knowledge of how the particular feature could change during evolution. Hierarchical series of ever more precise conditional phrases about homologues constitutes one such transformation series.
- (c) Next is determining the direction of change in the transformation series from the presumed primitive state to the derived condition. Together with (b), it is necessary to determine whether reversal has taken place resulting in 'secondary' primitive conditions.
- (d) Following is testing the hypothesis about the transformation series and the direction of change using knowledge about evolutionary change in general and about how the particular features change in particular. A second valid test of the polarity of transformation series in the stratigraphic position of fossils possessing the primitive or plesiomorphic condition; such fossils would be found earliest in the stratigraphic record.

- (e) Last is determining which apomorphic features in different organisms are synapomorphic (derived homologous features) and the final testing of these hypotheses about synapomorphs which involved considering of the homology of the features, the possibility of reversals, etc.

Impediments in cladistic analysis of features are well shown by the property of cranial kinesis in vertebrates in general and in birds in particular (Bock 1964, 1999a,b, 2002). It is possible to show with a high degree of confidence that the kinetic condition is primitive in vertebrate skulls, that the akinetic condition is derived, that evolution from the akinetic to the kinetic condition is not possible, and for birds, that the mesokinetic condition is primitive and both prokinesis and rhynokinesis are derived, yet cranial kinesis is exceedingly difficult to impossible to use for cladistic analysis (as well as for other ordering systems) because of the problems in separating true homology from homoplasy of particular conditions and in the possible numerous reversals in the evolution of different kinetic conditions in birds.

10.4. Recognition of clades

The basic units of a Hennigian cladification, corresponding to the taxa of a traditional Darwinian classification, are clades, that is, parts of a phylogenetic tree. A branching tree in a cladification, a cladogram, is a tree of taxonomic characters. As Hennig's system of holophyly, in contrast to Darwin's two-criteria system, is based on a single criterion – the branching pattern of descent – its units are not classes of organisms. Ordering kinds of organisms exclusively on the basis of their location on the cladogram is in conflict with the basic concepts of classification because degrees of similarity are not considered in the construction of a cladogram, only branching points. Degrees of similarity are specifically ignored in a Hennigian cladification. The basal and the crown parts of a clade may be as drastically different from each other as early archosaurians (or dinosaurs) and birds. By not being delimited on the basis of similarity, clades do not qualify as classes. Knox (1998) has therefore rightly said, the term 'cladistic classification' is an oxymoron because 'cladistics lacks the class concepts needed to construct a classification'. Hennig called his system of ordering a 'phylogenetic classification'. It is indeed phylogenetic, but so is also any properly constructed Darwinian classification, yet Hennig's system of ordering fails to meet the qualifications of a classification. This failure stems from the usual heterogeneity of clades because of the frequent highly unequal divergence of sister lineages after the branching point, as well as the frequently drastic change in rate of evolution whenever a phyletic lineage enters a new adaptive zone.

It was Hennig's (1950, 1966) great contribution to taxonomy to have introduced a concept that is most important in the search for branching points. He called attention to the fact that only derived (= apomorphic) characters give reliable information on the origin of new branches (branching points) in a phylogeny. Therefore, only 'derived' (newly acquired, apomorphic) characters possessed in common (synapomorphs or derived homologues) can be used in the construction of a phylogenetic diagram. This concept, as Hennig himself has stated, had apparently been used by some earlier authors to judge from their classifications and phylogenetic diagrams; but Hennig was the first taxonomist to have formally described it

in print. The branching pattern in such a phylogenetic analysis is constructed entirely on the basis of shared derived homologous characters (= synapomorphies); symplesiomorphic features (= shared ancestral homologous features) are strictly excluded. This concept permits the determination of the strict monophyly (traditionally defined) of the taxon under consideration. All species of a monophyletic taxon share the same derived characters, except when some species have secondarily lost an ancestral character (e.g. legs lost in diverse groups of legless lizards) or in some cases of parallelism, when not all related species have realized a particular potential (= the independent evolutionary origin of the phenotype) of the ancestral genotype (Throckmorton 1963, 1967). The branching pattern established by phylogenetic analysis generally permits the recognition of the descendants of a common ancestor. It not only helps to find the branching points in a dendrogram but also to discover polyphyletic taxa, that is, seemingly monophyletic taxa that include species not derived from the nearest common ancestor. Phylogenetic analysis, therefore, is as useful in Darwinian classification as in Hennigian cladification.

The arrival of the computer has revolutionized the methodology of cladistic analysis. There are now various computerized algorithmic methods available, and the software that goes with them permits the determination of the branching points in a cladogram with considerable certainty. These methods are quite elaborate and far too complex to be spelled out in this paper. Anyone wishing to become acquainted with the methods should consult one of the available textbooks, such as Kitching et al. (1998) or Hall (2001). The algorithms usually have several solutions and there are various methods available to determine which solutions include the most likely correct one. Parsimony methods are preferred, but they are criticized or even rejected by some authors. We should note that these methods of 'numerical cladistics' may well suffer from the same problems that affected phenetic methods of numerical taxonomy. These problems stem from the failure of distinguishing homologous from homoplastic similarities which are far more common than admitted by most cladists and are not solved with the use of a large number of taxonomic characters as had been advocated earlier by phenetists and in a tacit way also by numerical cladists.

Neither of the authors of this paper is a practitioner of these computer methods. We are therefore not competent to discuss them critically. Many of the recent attacks on cladistics were based on weaknesses in the cladistic analysis. These actually may not have anything to do with the principles of cladification. Cladistic analysis is based on holophyly and has the strength and weakness of this base line. What kinds of computer methods could be adapted for the Darwinian approach to classification? In other words, are there computer methods that would produce Darwinian classifications, based on degrees of similarity and at the same time being strictly genealogical? This now seems to be the challenge. We are not qualified to provide the answers.

11. Upward classification by two criteria, clustering by similarity and by common descent – type 6

11.1. Pre-Darwinian classification

Long before Darwin, leading systematists had been aware that more was involved in the ordering of animals and plants than mere similarity. There was a need to distinguish between true

similarity and false similarity, with true similarity being that associated with the essential characteristics of the class. Although they could not explain it, they gave this unknown factor a name, affinity (Strickland 1840a,b, 1846a) or homology (Owen 1843). The use of this pre-evolutionary concept of affinity/homology is difficult for present-day biologists to understand as it was part of the then widespread acceptance of essentialism. As Whewell (1840, p. 410) stated it: 'The assumption that there is a Natural System, an assumption made by all philosophical botanists, implies a belief in the existence of Natural Affinity, and is carried into effect by means of principles which are involved in that Idea.' Further, Whewell (1840, p. 517) said that this affinity cannot be determined '... by an arbitrary subordination of characters.' And Whewell (1840, p. 529) then indicated how affinity can be determined through '... the Idea of Natural Affinity; of which the fundamental maxim is that arrangements obtained from different sets of characters must coincide.' But prior to the acceptance of evolution no one could explain this natural affinity or knew how to determine it. Strickland (1840a,b, 1846a) discussed in full detail the concept of analogy and its use in establishing natural classifications and pointed out (Strickland 1846b) that the concept of affinity was the same as that of homology recently introduced by Owen (1843). Affinity as used by Strickland is a term applicable to features, not to organisms or to taxa. It designates a particular type of similarity of features, namely of correspondence to the feature in the ideal type of class (taxon).

Interestingly, Darwin (1859) used the term 'affinity' and not 'homology' for such similarity of features.

A new principle, adopted in the early 19th century by some practitioners of ordering systems, showed the way. It stated that when a grouping (clustering) of entities is because of a particular causal factor, a consideration of this factor must be included in the making of a classification. Applying this principle to the classification of human diseases, for instance, led to their complete reclassification. While formerly they were classified according to whether they were acute or chronic, curable or not, accompanied by fever or not, affecting the digestive or the respiratory system, etc., they were henceforth classified as to whether caused by pathogens (bacteria, viruses, fungi, protists), by malignancy, by deleterious mutations (genetic diseases), by old age (degenerative diseases), etc. This approach is still used today in such biological classifications for organ, tissue and cell types as well as ecological characteristics, etc. (Bock 2000a).

11.2. Post-Darwinian classification

By adding a second criterion, common descent (genealogy = Darwinian descent from a common ancestor = Haeckelian phylogeny), to the classifying criterion of similarity, Darwin produced a major revolution in the classification of organisms (Darwin 1859, chapter 13). He took it for granted that similarity was a basic classifying criterion, and in this he agreed with all of his contemporaries, but he also realized that there was a second classifying criterion. When classifying organisms, Darwin felt that the causation of their grouping also had to be considered, and he concluded that this was common descent. That is, the similarity important for grouping organisms into classes is ancestral similarity – similarity that was inherited from the common ancestor of the group. The foundation for homology is common ancestry, not

correspondence to an ideal type. Darwin therefore demanded that all members of a taxon must have the same genealogy; 'the species included in a taxon must be descendants of the nearest common ancestral taxon.' This is the principle of *monophyly*, so named by Haeckel (1866; see Simpson 1961, p. 124 for a discussion of practical application of monophyly).

The most important aspect of Darwin's innovation was that he did not propose to treat 'ordering by descent' (phylogenetic ordering) as an alternate method to ordering by similarity, but demanded that a classification guided by his principles had to satisfy the demands both of similarity and of descent. 'Genealogy alone does not give classification.' was his motto. By this two-criteria approach, Darwin avoided all the difficulties that Hennig later encountered when he proposed a cladistic ordering based on cladification. Darwin's approach required the backward looking definition of monophyly that from the time it was introduced by Haeckel in 1866 until mid-20th century had been unanimously adopted by systematists. Hennig, by going back to a single criterion approach, initiated the controversy 'similarity or "phylogeny"', which has been so deleterious for biosystematics in recent years. For Darwin, neither similarity nor genealogy is the 'primary' criterion for ordering, because the analysis of genealogy simply leads to a more reliable use of similarity in the establishment of classes (= taxa) of organisms.

The criterion of common descent was for Darwin not a replacement of the criterion of similarity, but rather a constraint on what kind of similarity could be accepted as evidence for relationship. That is, the definition of homology was changed to mean features in different organisms that stem phylogenetically from the same feature in the immediate common ancestor, and hence that similarity was parental (= ancestral) similarity (Bock 1989b). An evolutionary analysis would permit the discovery of those similarities of taxa that are not because of common descent and this would lead to the removal of such taxa from the provisional taxon. This would be accomplished largely, but not entirely, by more detailed analyses of homologous features (Bock 1989b, 1992). The theory of common descent also explained what was the mysterious 'affinity' (= homology) of which Whewell, Strickland, and other pre-evolutionary authors had spoken; it was common descent. An evolutionary definition of homology and an evolutionary concept of similarity (= ancestral similarity) replaced the essentialistic definition of homology (i.e. affinity) and the unknown causal basis for similarity (Bock 1989b).

The term Darwinian classification requires a very precise definition, which clearly states that a taxon is to be delimited by two criteria: similarity and common descent. Such a definition is: 'A Darwinian classification is the ordered grouping of organisms into classes according to their similarities and consistent with their inferred evolutionary descent.' Such a classification is an evolutionary classification (= Haeckelian phylogenetic classification). It is more inclusive than an ordering based on just the pattern of branching points, because it also considers the amount of evolutionary change after the branching points.

Some philosophers, after 1859, appreciated the importance of giving due consideration to genealogy in the classification of organisms. Jevons (1874, p. 680) agreed with Darwin that the ideal arrangement would be 'that arrangement which would display the genealogical descent of every form from the original life germ.' But only a few pages later (Jevons 1874, p. 694), he slid back into an endorsement of logical division:

'Every system of classification ought to be formed on the principles of the logical Alphabet. Each superior class should be divided into two inferior classes, distinguished by the possession or nonpossession of a single specified difference.' Basically, classification for Jevons was simply an exercise in logic. He apparently did not realize that logical division could never give him a genealogical system.

11.3. Genealogy alone does not give a classification

Genealogical branching alone is not sufficient for the construction of a sound classification of living organisms. Darwin (1859, p. 420) said rightly, '... but that the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor [at branching points], may differ greatly ... and this is expressed by the forms being ranked under different genera, families, sections, or orders.' A sound Darwinian classification, therefore, must be based on a balanced consideration of both genealogical branching (cladogenesis) and similarity (amount of phyletic evolutionary change = anagenesis). Darwin (1859) was the first author to promote clearly the use of both types of criteria in the classification of organisms, although some 'tree diagrams' showing relationships of organisms were published prior to 1859.

A classification adopting this principle, therefore, may be called a Darwinian classification. A Darwinian classification is as genealogical as a cladification, only it is a genealogy of groups (classes) and not of clades. A Darwinian classification is strictly evolutionary and hence (Haeckelian) phylogenetic. Each taxon consists by the principle of monophyly of the descendants of the nearest common ancestral taxon. Darwin, unfortunately, never published a detailed analysis of his basic principles of classification. They must be inferred from his general discussion. In his barnacle monograph (Darwin 1851–1853), his only major taxonomic work, Darwin does not present any general thoughts on taxonomic philosophy as pointed out by Padian (1999) and various earlier authors. It was standard at that period (1846–1854) to base taxa on similarity. This is well reflected in this statement by Darwin's friend and collaborator Huxley: 'By the classification of any series of objects is meant the actual, or ideal, arrangement together of those which are like and the separation of those which are unlike, the purpose of this arrangement being to facilitate the operation of the mind in clearly conceiving and retaining in the memory, the characters of the objects in question' (Huxley 1867). And similarity was evidently also Darwin's criterion. He made no conscious effort to base his delimitation and ranking of taxa of barnacles on genealogy. His theorizing on common descent probably had not yet matured to the level it reached in his *On the Origin of Species*. But the barnacle work does reflect the state of his thinking 5–10 years before the *Origin*. And it indicates the obviously high regard Darwin had for similarity at that time. This clearly carried over into his later thinking.

Padian (1999) has provided us with an exemplary analysis of Darwin's relevant writings. However, he is so intent on proving that Darwin was a Hennigian that he minimizes the opposing evidence that shows clearly that Darwin was not a Hennigian (= a cladist). Padian was not aware that Haeckelian phylogeny (= Darwinian genealogy) differs from Hennigian phylogeny. Further, Padian overlooked that in the first half of the 19th century classifying was unanimously considered as a

process ordering things by similarity. This was so much taken for granted by Darwin that it was not necessary for him to single it out specifically. Note, as mentioned above, that Darwin (1859) used the term 'affinity' and not 'homology' stressing that he thought classifications are based on similarities. Where Darwin differed from the prevailing consensus was in including a second factor, common descent. This is the factor he had to emphasize, and this is what he did. But he only stressed that genealogy had to be added to, but not replacing, similarity. In much of the later 19th century, it was heatedly argued whether phylogeny gives similarity or similarity gives phylogeny. As prior to 1859 no phylogeny had yet been reconstructed, it was at that time, of course, similarity that gave phylogeny.

These disputes did not clarify the important distinction between theoretical statements (about homologies) and their testing (use of similarities). What Darwin realized was, that a new phyletic lineage (clade) may have an entirely different rate of change from the parental one and from its sister lineages, a situation not considered in cladification. He concluded (Darwin 1859, p. 420) that the arrangement of taxa 'must be strictly genealogical, but that the amount of difference [degrees of similarity] in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly.' And this, says Darwin, must be carefully considered in the ranking of taxa. And it is precisely this different rate of evolutionary divergence, which makes an ordering system, based exclusively on branching points, unsatisfactory as a classification. It is this insight that led Darwin (1859, p. 422) to conclude that 'the degrees of modification which the different groups have undergone, have to be expressed by ranking them under different so-called genera, subfamilies, families, sections, orders, and classes.' And ranking is, of course, the method to express degrees of difference. Clearly, then, a Darwinian classification must be based on two criteria, genealogy and similarity – both of which constitute the evolutionary history of organisms. 'Genealogy alone won't do it,' Darwin stated bluntly in a letter to Hooker (23 December 1859) (Darwin 1857, Correspondence, vol. 7, p. 443) where he comments on Naudin's scheme of classification that 'he cannot have reflected much on subject otherwise he would see that genealogy by itself does not give classification.' Padian's attempt to soften the impact of Darwin's conclusion by reference to the context of Naudin's statement is entirely unconvincing. It is irrelevant what Naudin may have meant in his original statement; the only thing that counts is Darwin's clear-cut conclusion '... that genealogy by itself does not give classification.' The failure of some recent cladifications to provide satisfactory classification fully confirms the validity of Darwin's claim.

An important and generally neglected aspect of classification is that the term genealogical classification is equivocal as these ordering systems can be based either on monophyly (= Haeckelian phylogeny) or on holophyly (= Hennigian phylogeny). It is our claim, very much substantiated by Darwin's barnacle work, that his concept of genealogical classification was based on monophyly. As he stated in a letter (26 March 1843) to Waterhouse, 'when you define your object in classifying, you ... are bound to follow a simple amount of differences of organization ... This is clearly the rule, on the view of classification, being a genealogical process, exhibiting literal or actual relationship.' (p. 354). When we look at 19th century classifications, we find that most of them were based

simply on overall similarity or worse, on single character differences. Whenever a Darwinian (evolutionary) approach was attempted, it was invariably applied to an existing classification that had been previously based on similarity.

11.4. Is a biological classification a theory?

This question has produced an unresolved controversy. The answer depends on one's definition of theory. Darwinian classifications certainly do not have the properties of the causal law explanations that philosophers call universal process theories (= nomological-deductive explanations). However, they are singular theoretical scientific statements (= historical-narrative explanations) about groups of organisms based on the evolutionary theory of common descent (Bock 2000b) and are subject to empirical testing. Hence, Darwinian classifications, Haeckelian phylogenies and Hennigian classifications are theoretical scientific statements and must be properly tested against objective empirical observations.

Using the methods of Darwinian classification, one can sometimes base several different classifications on the same phylogenetic tree (Haeckelian dendrogram) and none of these classifications can be falsified with respect to the others in the strict sense of the word. Acceptance of one or the other of these several classification depends almost entirely on heuristic considerations. Nevertheless, Darwinian classifications have attributes of a genuine theory and have explanatory value as historical narrative explanations. By accepting evolution and by constructing classifications on the basis of homology and joint possession of derived characters, one transfers the explanatory power of evolution to any classification based on it (Bock 2000b). Furthermore, like most theories, all classifications are tentative and thus subject to revision. Classifications thus have many of the traditional properties of theories. When well constructed, they reflect patterns of the evolutionary history of organisms found in nature. Yet a given classification is a human construction, even when every step in the analysis has theory-like qualities. We should add that phylogenetic diagrams or dendrograms are also theoretical scientific statements (= historical-narrative explanations) and are also subject to empirical testing. But we must emphasize that classifications and dendrograms (including cladograms) are not nomological-deductive explanations contrary to the claims of many cladists.

12. Ecological factors of evolution and classification

12.1. The origin of a new higher taxon (splitting or budding)

Critical to ideas about ordering systems of biological organisms is the ecological nature of evolution and especially of the evolutionary origin of new groups. A new higher taxon originates in evolution, according to the traditional view of cladistics, by the splitting of the parental lineage into two daughter lineages, giving rise to two new sister groups. The sister groups diverge to varying degrees from each other and from the parental phenotype. Most important is that such splitting of the parental lineage is considered to be the end of the parental taxon and the beginning of the two sister groups as two new taxa. However, there exists an alternate for the origin of new taxa, which is of great importance for the evaluation of classification. In this process, best designated as *budding*, the new lineage 'buds off' (= separates) from the parental line, enters a new niche or adaptive zone and

establishes a new group that frequently diverges rather quickly (and sometimes drastically) from the parental lineage which continues to exist virtually unchanged. The novel founder lineage may evolve into a new genus and eventually a new family or even higher category. What is important is that this new higher taxon has emancipated itself ecologically from the parental lineage and is now an independent evolutionary/ecological entity. The budding off of a new lineage is of no influence on the continued existence of the essentially unchanged parental taxon. This is beautifully illustrated by geographic speciation within the superspecies *Tanysiptera galatea* (Mayr 1942, p. 153), but it applies also to the budding of the birds from the archosaurian stem, and, in fact, to the origin of any higher taxon in which the parental taxon continues unchanged in its basic characteristics.

12.2. Impact of ecological shifts on classification

The environment in which a group evolves changes usually rather little and very gradually. But there is one situation where the environment changes quite drastically and leads also to drastic changes in the taxon that endeavours to remain adapted to the ecological shift. We refer to the cases where a new lineage has budded off the ancestral lineage and is rapidly evolving into something very different (see Simpson 1944, 1961). The most striking illustrations are (1) the entry of some archosaurian reptiles into the arboreal/aerial environment and thereby evolving into birds, (2) the shift of artiodactyl ungulates to water and giving rise to the Cetacea (whales), and (3) the adoption of a parasitic lifestyle by some lineages of turbellarians which gave rise to trematodes and cestodes, to cite a few particularly illustrative examples. In each case, the parental group is not affected by the evolution of these buds, and the Darwinian systematist, applying the traditional monophyly concept, has no problem in ranking the strikingly different new taxa appropriately. For instance, the Mammalia owing to their large degree of difference from the ancestral Reptilia are raised to the rank of a new class. This ranking is consistent with the basic principle of the first step of Darwinian classification, degree of similarity. As the parental taxon (Reptilia) from which the Mammalia originated has not changed, its categorical rank is not affected. A different choice is made in classification in which the basal reptilian group from which the mammalian arose is included in the mammalians, thereby making the Reptilia a paraphyletic group.

When deciding whether or not to establish a new higher taxon, one must attempt to infer how it had originated. In the large majority of cases, a new higher taxon originates not by splitting but by budding from the parental taxon. When this new taxon enters a new niche or adaptive zone and acquires a new set of characters, it is treated in a Darwinian classification as a genuine novelty rather than as part of the parental lineage. For instance, in such a classification, birds are considered as a separate class rather than as a part of the archosaurs from which they are believed to have been derived, because birds have become a drastically different kind of organism through their conquest of the air. The occupation of the aerial adaptive zone by birds has resulted in numerous fundamental modifications of morphology, physiology, life history, behaviour, and ecology, most of which have been retained by secondarily flightless avian groups. The acquisition of such a striking degree of difference is acknowledged in a Darwinian classification. Pterosaurs and bats have also conquered the air, but as

they have not been modified nearly as much as the birds, they are still classified as orders within the Reptilia and Mammalia, respectively.

Perhaps the greatest advantage of a Darwinian classification is that it calls attention to the ecological significance of the shift in adaptive anagenesis. The basic similarity of the different species of a taxon, particularly at the genus and family level, suggests that they are similarly adapted. They ordinarily occupy the same adaptive zone; thus they are an ecological unit. If two taxa are adapted to strikingly different adaptive zones, like dinosaurs (or thecodonts) and birds, they are members of two very different ecosystems. This difference is obscured when the dinosaurs and birds are placed in the same clade. The groupings recognized by the early naturalists, such as mammals, birds, reptiles, were based on the overall adaptation of these taxa to their place in nature. This provides far more information than placing drastically different taxa in a single clade.

When authors refer to the Darwinian classification as *evolutionary classification*, they want to express their view that a classification must duly consider both aspects of evolution, the ecological adaptiveness through evolutionary divergence (degrees of difference: anagenesis) and the genealogy (branching pattern: cladogenesis) of the taxa. Evolution consists of these two processes: ecological adjustment and origin of new biodiversity. Simpson (1961, p. 52) rightly said: 'Evolutionary taxonomy stems explicitly and almost exclusively from Darwin.'

13. Phylogenetic or genealogical analysis

13.1. Use in biological classifications

The second step of the Darwinian classification consists of the elimination of any species from the provisional taxon that is not a descendant of the nearest common ancestor. A method for ascertaining the phylogeny of taxa within the requirements of evolutionary theory has been outlined by Bock (1977b, 1992). A taxon from which all non-qualifying species have been eliminated is monophyletic. What was usually done was to undertake a special study of any species (or group of species) that were included somewhat doubtfully in the taxon. In particular, it was made sure that the characters of this deviant species were strictly homologous with the characters of the other species placed in this taxon. Yet, classifications based on these guidelines were of rather variable correctness. Superior taxonomists apparently had some other unspoken criteria, rendering 'classification as an useful art', as expressed by Simpson (1961, p. 110), and to which some systematists have objected strongly, feeling that classifications should be strictly 'objective'. Taxonomists, beginning with Darwin in his barnacle work, rarely discussed what principles they used in their classifications. One very important principle, the importance of derived characters, although evidently employed by earlier authors, was first stated formally in print by Hennig (1950, 1966). Experienced taxonomists always seem to have done some weighing even if only in the selection of characteristics used in their analysis. Unfortunately, the judgment of some authors on the weight of different characters was occasionally very poor, but this does not invalidate the general principle of weighing (discussed earlier).

When phylogenetic analyses are based on different kinds of characters, morphological, RNA, mitochondrial genes, nuclear genes, etc., the resulting dendrograms often disagree with

each other. As an organism has only one phylogeny, this means that some of the dendrograms are wrong. When the molecular methods were first introduced, some authors thought that these were automatically superior to morphological characters based on subjective evaluations. But different molecular methods also often led to different results, and it was eventually realized that different molecules may have different rates of change (mosaic evolution) and that morphological characters, the product of large numbers of genes, are usually quite reliable.

13.2. Translating the phylogenetic analysis into an ordering system

Even though some form of phylogenetic analysis is used both in Darwinian classification and in Hennigian cladification, the findings made by these analyses were applied very differently in the two ordering systems.

13.2.1. Darwinian classification

The Darwinian or evolutionary classification is a true classification comprised of similarity classes arranged in a hierarchy. It is defined as: 'A classification based on two criteria – similarity and common descent – and hence the ordered grouping of organisms into classes according to their similarities and consistent with their inferred evolutionary descent.' Not only is a Darwinian classification phylogenetic, but also it is more inclusive than an ordering system based only on branching points because it also considers the amount of evolutionary change after the branching points. Hence, the taxa in a Darwinian classification are classes based on overall similarity. If the phylogenetic analysis reveals an alien element in a taxon, it is removed and then transferred either to the taxon to which it really belongs, or a separate taxon is established for it. Monophyly is carefully maintained or restored through such a shift. For instance, when it was discovered that the South African family of golden moles (*Chrysochloridae*) did not belong to the order *Insectivora* nor to any other recognized mammalian order, a new order was established for it. No change in the rank of the order *Insectivora* was required or any other major disturbance of the previous Darwinian classification. Or to give another example, when it was discovered that the family of the New World vultures (*Cathartidae*) did not belong to the order of the hawks (*Falconiformes*) where it was traditionally classified, but to the storks, it was transferred to the order *Ciconiiformes* without affecting the status of any other family of either order. Scores of such corrections in Darwinian classifications became necessary in recent years, often because of molecular researches, resulting in the shifting of species, genera, families, or higher taxa, but with a minimum of disturbance of the system as a whole.

13.2.2. Hennigian cladification

Groups in a Hennigian cladification are clades based on branching in the phylogeny of the group. These groups are holophyletic. One of the major differences between a Darwinian classification and a Hennigian cladification is that the latter is inherently unstable. If groups such as the golden moles or the New World vultures (mentioned above) are shown to be misplaced in the *Insectivora* or the *Falconiformes*, respectively, then considerable modification of the ordering system of mammals and of birds results. Such instability is highly

undesirable for any ordering system for which heuristics are a prime concern.

14. Graphic representations of ordering systems

Several ordering systems use a particular tree-like diagram (dendrogram) to present their findings on the relationship of the classes in their system. The most frequently used and best known of these dendrograms are the following:

14.1. Phenogram

A phenogram attempts to present graphically the degree of 'overall similarity' of the taxa involved. This presentation is apparently based on the silent assumption that there is a perfect correlation between similarity and nearness of common descent. Phenograms lost favour when it was realized that this correlation often is not very close and that, owing to a deficiency of diagnostic characters, it is often impossible to determine 'overall similarity'.

14.2. Haeckelian–Darwinian dendrogram

This diagram represents both the branching pattern and the degree of divergence (= amount of evolutionary change), and thereby includes the results of both anagenesis and cladogenesis in the past evolutionary history of the group. These diagrams can be termed Haeckelian after the name of the biologist who first proposed the term phylogeny in 1866, or Darwinian since Darwin (without a name) introduced the concept of evolutionary history in 1859. If biologists wish to illustrate relationships of traditional taxa, they use Haeckelian dendrograms. A dendrogram does not necessarily have to have the appearance of a tree. Numerous branches may appear seemingly simultaneously. This is represented by a bush dendrogram (thamnogram).

14.3. Hennigian cladogram

This diagram represents only the branching pattern of descent. Each branch in a cladogram is a clade in a phylogenetic tree, consisting of the stem species and all of its descendants. A cladogram (Hennigian cladification) represents the sequence in which new characters were acquired during phylogeny. Any author who simply wants to illustrate the branching pattern of phylogeny will use a cladogram.

15. Darwinian classification or Hennigian cladification?

The most disturbing finding of our survey is that in biosystematics there are now two widely supported and competing ordering systems, Darwinian classification and Hennigian cladification. Both claim to be classifications and both claim to reflect phylogeny. The disagreement between the followers of the two systems is obviously highly deleterious for the well-being of our understanding and use of classifications. Clearly, an effort must be made to end this controversy. A taxonomist must determine whether the claims of both systems are valid and, if so, which is the better system. To be able to answer these questions it is necessary to make a detailed comparison of the two systems.

15.1. Merits and deficiencies of Darwinian classification

15.1.1. Classification

The procedures of the first step of Darwinian classification follow precisely the prescription of the classical definition of classification being 'the ordered groupings of organisms into classes according to their similarity.' Indeed, no one has ever seriously questioned that a Darwinian classification qualifies as a classification. The grouping of species into tentative similarity classes is relatively easy at the level of species and genera. However, the correct classification of taxa in the higher categories is sometimes quite difficult. A group of species or genera may be adaptively so specialized that the indications of their basic relationship are almost completely obliterated. This is why biologists overlooked for such a long time that the New World Vultures were storks and not Falconiformes (diurnal birds of prey) or that the Pogonophoras were polychaetes. For such cases, 'deep' molecular characters have often been particularly revealing. A Haeckelian dendrogram frequently lacks one special virtue of a cladogram, a precise recording of the sequence in which the characters of a phyletic lineage are acquired. A graphic rendering of such sequences, as presented in a cladogram, would enrich Darwinian classifications.

15.1.2. Phylogeny

The sorting of species into similarity classes is simultaneously also a process of phylogenetic sorting, because usually a class of similar species consists of the descendants of a common ancestor. This sorting depends on the careful establishment of the hierarchical arranged conditional phrases when hypotheses about homologous features are established and tested (see Bock 1989b, and above in 9.2.). Indeed, every correctly formed taxon in a Darwinian classification consists in principle exclusively of the descendants of the nearest common ancestor. Arranging the taxa hierarchically makes a Darwinian classification automatically phylogenetic. However, as we have shown, similarity can be deceiving and the tentative classification based on similarity must be subjected to a detailed genealogical investigation. When there are any doubts, the similarities among diverse species must be tested carefully on whether they are homologous with a high degree of conviction. The result is that any Darwinian classification that had been corrected through a rigorous genealogical analysis, including homology testing, can be considered to be a satisfactory phylogenetic dendrogram. The findings of cladistic analyses are often an important contribution to the genealogical analysis.

One can summarize these findings by stating that the Darwinian (traditional) method of classifying when properly tested, not only qualifies in every respect as a legitimate method of classification, but also that the resulting system strictly reflects phylogeny. Even though Darwin had insisted emphatically that every classification had to be consistent with phylogeny and accurately reflect common descent, this demand was very often ignored in the past. Although authors paid lip service to Darwin's principles, in actual practice they fell back on typology and often based their higher taxa on single characters. Such classifications were not Darwinian.

15.2. Merits and deficiencies of Hennigian cladification

After Hennig's approach to systematics appeared in English (1966), his ideas were rapidly adopted by a large number of

taxonomists. Interestingly, his German text of 1950 had had little influence even in Germany. In more recent years, various computer methods of cladistic analysis were widely adopted and helped to clarify previously doubtful phylogenies. Indeed, Hennigian ordering was so successful that traditional classification was frequently declared to be dead, but criticism was also widespread. Here, we must carefully distinguish criticism of the methodology of cladistic analysis from that of strict cladification, that is, of an ordering system of clades. We will not discuss here any controversies that simply deal with aspects of cladistic analysis, as for instance the advantages (or not) of parsimony or the method of out-group comparison, but deal only with the problems connected with the delimitation and ordering of clades (see, however, Bock 1992).

The same two questions asked about Darwinian classifications have to be asked about Hennigian cladification, namely: (1) Is cladification a valid representation of phylogeny? (2) Does cladification qualify as a classification, in the traditional meaning of the word classification ('consisting of classes of similar entities')?

15.2.1. Phylogeny

There can be no objection to consider cladification as a qualified representation of branching point phylogeny, particularly because this method was developed by Hennig precisely for this purpose. Indeed, clades, the ordering units of a Hennigian cladification, are parts of a phylogenetic dendrogram. A Hennigian cladogram may in part coincide with a Darwinian dendrogram, but in other parts the two phylogenetic representations may differ widely from each other, even though both claim to be phylogenetic.

15.2.2. Classification

As shown by numerous recent critics a cladification, i.e. an ordering system based on clades, cannot qualify as a classification, traditionally defined. It fails because it ignores the fact that a classification must be a hierarchy of groups based on similarity. In addition to the neglect of similarity we distinguish six other aspects of cladification that are in conflict with sound classification. These overlap in part and are in part reinforcements of each other.

Shift to holophyly. The clades produced by holophyly are often highly heterogeneous. The crown portion of a clade may be very different from its base. This makes clades highly unsuitable as units of classification. New characters in a clade often arise in a phyletic lineage between branching points that are chosen for the delimitation of clades. The result is a good deal of arbitrariness in the delimitation of clades.

Selective use of characters As only apomorphic characters can be used in cladistic analysis, plesiomorphies are completely ignored in cladistic ordering. In a traditional classification, as many characters are used as possible, including plesiomorphous ones. Indeed, some ancestral characters are sometimes the most diagnostic features of certain taxa. If some characters are ignored, it is for special reasons; for instance, because they provide no useful information, such as neutral genes or uniformly possessed characters. By contrast, cladifications are based exclusively on derived features (apomorphic) while the information content of plesiomorphies is entirely ignored and that of autapomorphic characters largely so. As clades are delimited by the branching points of the phylogenetic tree,

cladification has no proper method for making use of the differences that develop between branching points.

Theory of ranking. Even though Hennig emphatically rejected the use of degree of similarity in the ranking of taxa, the cladistic method of ranking by sequencing is apparently based primarily on subjectively determined degrees of similarity. Sometimes it is stated that in cladification the rank of a taxon is established by relative inclusiveness. Rank in a Darwinian classification simply indicates level of similarity. Ignoring degree of difference and relying totally on ranking of branching points has led in recent years to many rather absurd classifications. For instance, it induced an author to give the Archaeobacteria a rank as high as the total of the eukaryotes. Actually the Archaeobacteria have nearly all of the characters of the other prokaryotes while the eukaryotes (with nucleated cells, sexual reproduction, cellular organelles, well-defined chromosomes, etc.) are an entirely different kind of organism. Ranking by branching points can lead to highly unbalanced classifications.

Treatment of sister groups. Hennig's original demand that sister groups should be given the same taxonomic rank was unrealistic because sister groups frequently, if not usually, differ in the number and importance of autapomorphic characters. A sister group in the original Hennigian arrangement that had evolved very little after its origin had to be given the same categorical rank as one which had undergone a drastic evolutionary transformation (as for instance the birds from the reptiles). It is for this reason that some present-day cladists have abandoned this Hennigian criterion of ranking. Very similar sister groups are often widely separated in a cladification, because they are assigned to different clades.

Treatment of budding events. In cladistic theory, every split in a cladogram is assumed to produce two sister groups. However, new lineages may be produced through a budding process, not by splitting as discussed above. In such cases, the parental branch continues essentially unchanged. This view of the origin of groups and the principle of holophyly are apt to produce highly heterogeneous clades. According to the principle of splitting, each branch begins with a stem species and includes all of its descendants. The particular species of vertebrates that gave rise to the branch that ultimately became the mammals was an early synapsid reptile of the order Pelycosauria. Hence, the mammalian clade is composed of such highly diverse types as several groups of primitive reptiles and advanced mammals. The same is true for the birds that were derived from archosaurian reptiles (dinosaurs or thecodonts).

Instability. One of the most important properties of a classification is its role in information storage and retrieval. This is the reason why taxonomists have always considered stability one of the chief merits of a good classification. As Simpson (1961, p. 111) has said so rightly, 'The stablest classification is the most useful.' Alas, cladifications tend to have low stability owing to the ease by which new information may result in a shift of the branching point. A system consistently based on clades would obliterate extremely well-known traditional groups, such as reptiles, turbellarians, polychaetes, etc. Any unnecessary destruction of an existing information producing system should be avoided (Mayr and Bock 1994). On the basis of this criterion of strong stability of the information retrieval system, the Darwinian classification is vastly superior to other systems of ordering.

These six points reinforce our basic conclusion that an ordering system ignoring similarity and based on holophyly is unsuited to serve as a classification. This conclusion does not weaken in any way the usefulness of cladistic analysis for phylogenetic studies.

16. Resolution of the conflict

16.1. Stating the conflict

It is now 50 years since Hennig proposed the ordering method of cladification, based on the branching pattern of the phylogenetic tree. Some of his followers have claimed that the adoption of cladification was necessary to escape 'the inconsistencies and ambiguities current in biological taxonomy' (de Queiroz and Gauthier 1992). These authors failed, however, to produce any evidence for their claim. All putative shortcomings cited by them are actually departures from a strict adherence to Darwinian classification.

On the other hand, the numerous weaknesses of cladification have now been widely recognized (see above) and led to criticism. Several critical analyses of the methods of cladification have been presented since the publication of the English edition (1966) of Hennig's work. Among the most recent ones are Cronquist (1987), Mayr and Ashlock (1991), Hedberg (1995), Mayr (1995), Brummitt (1997), Cavalier Smith (1998, pp. 210–215), Knox (1998), and Grant (2001a,b). Most of them accept genealogical analysis, but reject cladification as the basis of biological classification because of its neglect of similarity, its system of ranking, its paraphyly, and its heterogeneity of clades owing to holophyly. Perhaps the greatest deficiency of cladification is that the branching event, responsible for the pattern of the cladogram, is independent of the rate and amount of divergence of the branches.

As a result of these criticisms we must ask ourselves whether Hennig's endeavour was a success? The honest answer must be, only in part. By his emphasis on cladistic analysis, Hennig has strengthened Darwin's and Haeckel's calls for genealogical analysis and this was an important contribution to modern taxonomy, considering the frequent previous neglect of this method. Even though this method has certain weaknesses, as does any method based on inference, a properly conducted phylogenetic analysis is the best method available for the determination of monophyly (traditionally defined). And phylogenetic analysis is as useful in Darwinian classification as it is in Hennig's system. Making use of phylogenetic analysis does not require adoption of cladification (Bock 1992). However, by the introduction of the special methods of the cladistic analysis the cladists have added importantly to phylogenetic analysis.

16.2. Which system is superior?

Whenever there is a conflict between two competing classifications, two general rules help us making the decision which to choose. One is to determine which is more helpful with respect to information storage and retrieval, and the second, which is more apt to preserve stability. On the basis of both of these criteria, Darwinian classification is superior. By first sorting the species by similarity into reasonably homogeneous tentative higher classes (taxa) and by adding the phylogenetic analysis as a second step, Darwinian classification satisfies both requirements of a good biological classification, the delimitation of genera and higher taxa on the basis of the

similarity of the included species, and the demand that each taxon consist exclusively of descendants of the nearest common ancestor. It reflects similarity and yet it is also rigorously phylogenetic. The Darwinian method, thus, leads to a classification, as traditionally defined, which a cladification does not. Cladification cannot replace the Darwinian classification, because it does not have the properties of a classification. Simply stated, a cladification is not a classification. Many traditional taxonomists have paid only lip service to the correct Darwinian method of the two criteria. Henceforth, they must take the phylogenetic analysis much more seriously. Furthermore, they must analyse their morphological characters functionally/adaptively in much more detail and supplement them to a much greater extent by molecular ones, which are available so abundantly. The conflict between the supporters of morphological and molecular methods that existed some years ago has by now largely disappeared. Most museums and systematics laboratories now have a molecular laboratory and do molecular analyses routinely. There is now no longer any difference in the choice of characters between the two camps. Molecular biologists, however, must at all times be aware of mosaic evolution, that is, the probability that different genes (molecules) have different rates of change. They must also remember that mitochondria had started their existence as symbionts and still evolve somewhat independently of the nuclear genes. If the results of mitochondrial analysis are in conflict with the morphological findings, they must be tested against some nuclear genes.

When a clade is rather uniform and had not changed significantly during its phyletic history, it will usually not differ greatly from an equivalent taxon. However, holophyly also may demand that it is still the same clade after it has made a drastic shift into a different adaptive zone, while in a Darwinian classification, a drastically modified clade receives a new rank. A typical example is the 'avian dinosaurs' of the cladists while the Darwinian classifier takes the birds out of the reptiles and gives them the rank of a new class. Hennig's system, even though it is an excellent phylogenetic system, therefore, is not a classification as traditionally defined because its units, the clades, are often highly heterogeneous ('avian dinosaurs') and lack the homogeneity demanded from a class and a classification.

16.3. Termination of the conflict

The taxa delimited by the Darwinian classifier coincide not infrequently with the clades recognized in cladifications. This indicates that there is considerable similarity between the two systems of ordering, particularly in the emphasis by both systems on the Haeckelian monophyly of the recognized taxa. Should it not be possible to remove some of the conflicts between the methodologies of these systems to permit an even closer approach? Both, the Darwinian and the Hennigian, are phylogenetic systems. The basic difference between the two is that the clades, the basic classificatory units of the cladist, are not classes. However, except in the cases of paraphyly, the clades of the cladist are sometimes the same as the taxa of the Darwinian classifier. The cladists have taken some important steps towards a rapprochement. For instance, most cladistic analyses, published in recent issues of *Systematic Biology*, started with a data set of traditional taxonomy (= first step of Darwinian classification) and subjected it to a genealogical

analysis (= second step of Darwinian classification). When the genealogical analysis shows that a taxon of a traditional classification had been placed in the wrong class, it is shifted to its correct position. The basic structure of the ordering system is not destroyed. One could list literally hundreds of such cases from the current literature, but we mention here only the recent reclassification of the Orthoptera resulting from a cladistic analysis (Flook et al. 1999). Most cladists who produce new analyses do not seem to realize that they are actually doing Darwinian classification.

Prum (1988) showed in a very nice analysis of various cryptic morphological characters that the American branch of the tropical avian family of barbets (Capitonidae) is the stem group of the toucans (Ramphastidae) and according to the principles of cladification he placed the several groups of barbets and toucans as subfamilies in the family Ramphastidae. However, Sibley and Ahlquist (1990, pp. 318–319) placed the New World barbets (Capitoninae) and the toucans (Ramphastinae) in the same family (Ramphastidae), which was placed in a different superfamily from the other two superfamilies of barbets. This arrangement was followed in Sibley and Monroe (1990, p. viii). Yet, the American barbets (in spite of their sharing cryptic apomorphies with the toucans) agree so closely with the African and Asian barbets in morphology, general habitat use and niche utilization, that virtually all ornithologists (see Short and Horne 2001, p. 7) have continued to place all barbets in the same family (Capitonidae) separate from the toucans (Ramphastidae).

Similarly, the demonstration that certain families of turbellarians gave rise to the parasitic trematodes and cestodes has not induced most specialists of the Turbellaria to break up this order and transfer to the trematodes and cestodes those non-parasitic families of turbellarians that are the stem groups of the parasitic taxa. Nor have we heard that any polychaete specialist broke up the taxon Polychaeta and transferred certain families to the Pogonophora and Echiura. The advantages of a sound classification won out in these cases over the principles of cladification. Some cladists maintaining the principles of cladification have transferred certain synapsid orders (Pelycosauria, Therapsida, Cynodontia) to the Mammalia, and likewise lowered the rank of a derived group, the Aves, by merging it with its Reptilian stem group (the Archosauria) and thereby breaking up the traditional class Reptilia. But this proposal has not been universally adopted. It seems rather irrational to speak of avian dinosaurs, because birds simply are not dinosaurs. No dinosaur has the diagnostic characteristics of birds, and no bird has the special apomorphies of the dinosaurs. What characters the two taxa have in common are largely old plesiomorphies of the Archosaurians.

To present phylogeny in terms of holophyly precludes any possibility of using the resulting ordering system as a classification. By contrast, the two-criteria method functions well for both Darwinian classification and Haeckelian phylogeny. The method of cladistic analysis fails to lead to a satisfactory classification, but it often improves Darwinian classifications that had been constructed without a rigorous genealogical analysis. The method of cladistic analysis thus will continue to be useful even if one does not use it as an approach to a Hennigian cladification.

Actually, two modifications, one adopted by the Darwinians and the other by the Hennigians, are the steps that would lead to a unified system of classification in biotaxonomy. The

Darwinians must consistently make a proper phylogenetic analysis an integral part of classification. As part of it they should also present the sequence in which diagnostic characters have been acquired in different phyletic lineages. They should also supplement comparison of morphological and molecular characters to a much greater extent with functional/adaptive analyses. The Hennigians must abandon the concept of holophyly and accept classes that are ordered according to the traditional principle of monophyly, accept the fundamental premise that these ordering systems are based on the nomological-deductive theory of evolution, and hence use functional/adaptive analyses in their study of taxonomic characters. The synthesis, however, will be successful only if the participants really understand the meaning of the term classification and its procedures.

17. Glossary

Affinity – The name used by pre-Darwinian taxonomists for the mysterious factor responsible for the cohesion of taxa, now unmasked as common descent. Used for a property of features identical to the original use of homology.

Apomorphic – A derived (newly acquired) character or character state.

Autapomorphous – Characters originating in a new clade.

Budding – The origin of a new higher taxon, by the branching from the parental lineage and entering a new niche or adaptive zone, without having any effect on the existence and attributes of the parental lineage.

Clade – A holophyletic branch of a cladogram.

Cladification – An ordering system in which branches of a cladogram, or parts of such branches, are arranged with reference to the sequence of the branching points in the cladogram and based on the principle of holophyly.

Cladistic analysis – A methodology by which the branching points in a phylogenetic tree or cladogram are discovered. Only derived (apomorphic) characters can be used in these methods.

Cladogram – A diagram of a tree of clades – basically a branching phylogeny. Such a diagram depicts a sequence in the origins of uniquely derived traits that are found in all the members of the clade and not in any others. A cladogram is a diagram of the origin of characters.

Class – (in classification) A group or collection of entities (individuals), possessing attributes or traits in common ('being similar'), a kind or sort, grouped together under a general or class name.

Classification – The arrangement of similar entities (objects) in a hierarchical series of nested classes, in which each more inclusive higher-level class is subdivided comprehensively into less inclusive classes at the next lower level.

Darwinian classification – The ordered grouping of organisms into classes, according to their similarities and consistent with their inferred evolutionary history.

Downward classification – Establishing groups by logical division.

Evolutionary classification – A classification that duly considers both evolutionary processes, the ecological adaptiveness of evolutionary divergence (degree of difference) and the genealogy (phylogeny) of the taxa. Basically equal to a Darwinian classification.

Hierarchical classification – The system of ranks that indicates the categorical level (level of difference) of each taxon.

Convergence – A similarity of a character of two taxa that are only distantly related, when the similar characters are not homologous.

Dichotomy – Dividing a larger group into two by logical division.

Holophyletic – Pertaining to a branch of the phyletic tree (and the species on this branch) derived from a stem species (with the first apomorphy diagnostic of this branch) and all of its descendants, no matter how different.

Homologous – Characters derived phylogenetically from the same character in the nearest common ancestor.

Homoplasy – Similarity in a character shared by two taxa that was independently acquired in their evolutionary history, rather than from their nearest common ancestor.

Identification – The determination of an unknown specimen to the proper class (taxon) to which it belongs.

Logical division – The splitting of a heterogeneous group of entities into two groups by a diagnostic difference (= downward classification).

Monophyletic – Pertaining to a group (taxon) all of whose members are descended from the nearest common ancestor.

Monothetic – Said of a group in which a single feature is both necessary and sufficient for inclusion in that group.

Ordering system – Any arrangement that attempts to place heterogeneous items in order.

Overall similarity – The possession in common of the vast majority of available and logically independent characters.

Parallelphyly – Homoplasy owing to an inherited ancestral propensity (similarity of genotype) to develop these characters.

Paraphyletic – A taxon that includes the stem portion of clades that evolved into new taxa. For instance, the classically circumscribed Reptilia, including the early portion (Therapsida) that led to the Mammalia, and the Archosauria that led to the Aves.

Phylogeny – Traditional (after Haeckel 1866) definition: The inferred lines of descent of a group of organisms, the reconstruction of the common ancestors of a group (monophyly), the amount of divergence among the descendants of the common ancestor – the evolutionary history of a group of organisms. For Hennig (1950, 1966) phylogeny is the study of the descendants of the stem species of a new clade, united by holophyly.

Plesiomorphous – An ancestral character.

Polythetic – Of taxa based on the greatest number of shared characteristics, no single character being either essential or sufficient to make an organism a member of the group; and with no member of the taxon necessarily possessing all the attributes that jointly characterize the taxon.

Ranking – The placement of a taxon in the appropriate category in the hierarchy of categories. This rank indicates the level of distinctness, as compared with other taxa.

Relationship – In Darwinian classification, refers to amount of genetic similarity, as in degrees of relationship in human families. In Hennigian classification relationship means coexistence on the same clade.

Reversal – Return, in a phyletic lineage, to an earlier condition. Reversal is usually caused by the independent loss of the same character or gene in different lineages.

Sequential ordering – Arranging singular entities in a linear sequence.

Taxon – A monophyletic class of organisms that can be recognized by a definite set of shared characters.

Weighing – Crediting, by the use of various criteria, high or low information content to particular taxonomic characters.

Zusammenfassung

Klassifikation und andere Ordnungssysteme

Die ungeheure Mannigfaltigkeit der Dinge in der Natur müssen, bevor sie untersucht und verstanden werden können, geordnet werden. Leider wurden die Methoden des Ordners, trotz ihrer großen Wichtigkeit, von den Philosophen bisher weitgehend vernachlässigt. Wir unterscheiden sechs Ordnungssysteme. Die Klassifikation, in welcher ähnliche Untereinheiten in Klassen (Taxa) zusammengefaßt werden, ist ein solches Ordnungssystem, aber nicht alle Ordnungssysteme sind Klassifikationen. Das Hennigsche System der Kladifikation beruht auf der Anordnung der Äste des phylogenetischen (Stamm-) Baums oder berücksichtigt genauer gesagt nur die Gabelungspunkte der Phylogenie (Holophylie). Es ist kein Klassifikationssystem, da es nicht zu Klassen ähnlicher Entitäten führt. Die Darwinsche Klassifikation erlaubt, indem sie zwei Kriterien, die Ähnlichkeit und die gemeinsame Abstammung berücksichtigt, die Erkennung von Klassen (Taxa) mit ähnlichen Entitäten bei bestehender Konsistenz mit einer gemeinsamen Abstammung (Monophylie).

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