4

SYSTEMATIC RESULTS: CLASSIFICATIONS

CLASSIFICATION: SOME CONCRETE CONSIDERATIONS

This chapter on classification is devoted to analysis of some concrete examples. For any particular classification, there is a corresponding cladogram that specifies the information content of the classification. Consider, for example, the following classification:

Tetrapoda
  Amphibia (A)
  Amniota
    Reptilia (B)
    Aves (C)
    Mammalia (D)

The corresponding cladogram is secondary cladogram 3.7.1, specified by the tertiary component ABCD, and the secondary component BCD. Each of the components is a statement of general synapomorphy, which means that generalizations (homology-synapomorphy statements) are possible (and predicted) for ABCD and BCD. The classification does not specify in what context the components should be interpreted (phyletic, phenetic, gradistic, etc.). Nor does the classification specify that both components should be interpreted in the same context. At most, the classification is a prediction that future research will reveal the same pattern (ABCD, BCD) and no other, such as ACDE, ACD. If the

prediction is corroborated, the classification will doubtlessly prove useful; if the prediction is falsified, the classification will doubtlessly be changed to reflect a more useful pattern.

With respect to this, or any other, classification, the information content may be specified (by specifying the general components of the corresponding cladogram)—without considering any of the specific homology statements (individual synapomorphies) that suggested the existence of the pattern (ABCD, BCD). Indeed, the information content of the classification consists only of the pattern—not the specific homology statements. The component BCD, for example, may be stated thus: Reptilia, Aves, and Mammalia are predicted to be synapomorphic, relative to all other organisms. They may be known to be synapomorphic in numerous ways, in only one way, or in no ways at all: the classification does not tell us, for the classification is merely a hypothesis of general synapomorphy (in exactly the same way as the cladogram). How particular synapomorphies might be conceived, as, for example, anatomical, behavioral, or physiological characters, or in what context the general synapomorphy might be interpreted—in, for example, phyletic, phenetic, or gradistic contexts—is of secondary relevance. Such matters may become relevant, but only if they suggest the existence of some other pattern. Suggestions to that effect, of course, frequently arise, creating the problem of incongruence. But much incongruence is more apparent than real (see above), and is apt to dissipate with further analysis. Persisting incongruence is either noise (random error), or a real indication of a different pattern. But only future research will show which is apt to be the case.

A PHYLETIC EXAMPLE

Simpson's (1945) classification of mammals includes the following major groups († indicates a group known only from fossils):

Class Mammalia
  Subclass Prototheria
 †Subclass Allotheria
  Subclass Theria
    †Infraclass Pantotheria
     Infraclass Metatheria
     Infraclass Eutheria

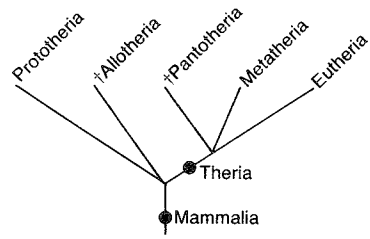


Figure 4.1. A cladogram derived from Simpson's (1945) classification of the major groups of mammals.

For this classification, a cladogram (figure 4.1) may be constructed to portray the information content (two components) of the classification. The two components correspond to the two inclusive taxa (Mammalia and Theria). This cladogram may be compared with the concept upon which Simpson based his classification, and about which he stated:

> The underlying considerations and concrete evidence have been presented here only in the barest possible outline, but they seem to support the following [the above classification] as the most convenient and most natural primary arrangement of mammals. (1945:165)

Simpson did not provide a diagram of his concept, but one may be constructed from his commentary (figure 4.2). With respect to the Theria, he states:

> Although they are too poorly known for certainty, there is good evidence that some of the very primitive and ancient Jurassic mammals, the † Pantotheria, are an offshoot of, and nearly represent, the common placental-marsupial ancestry before it had split up into the Metatheria and Eutheria properly definable. . . . If this is true, these mammals were also Theria but were not Metatheria or Eutheria. These are the conceptions formalized by recognizing a Subclass

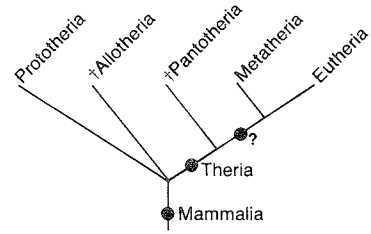


Figure 4.2. A cladogram (phylogram) summarizing the concept upon which Simpson based his classification of the major groups of mammals (cf. figure 4.1).

Theria with three secondary divisions, † Pantotheria, Metatheria, and Eutheria. (1945:165)

With respect to the Mammalia, he states:

There is one great division of fossil mammals that will not enter into either the Prototheria or the Eutheria, although these animals, the †multituberculates, have been referred to both on evidence now unacceptable. Everything now points to their having been distinct from all other mammals since the very beginnings of the Mammalia, and if this is true they can hardly be classified except as another subclass, a conclusion that I have supported and documented elsewhere. . . . The name †Allotheria is available for this subclass. . . . As far as present knowledge shows, the three subclasses have been separate since the beginning of the Class Mammalia, and there is no clear evidence of special relationship between any two of these subclasses exclusive of the third. (1945:165)

A comparison of Simpson's concept (figure 4.2) with the information (two components) actually contained in his classification (figure 4.1) shows that his concept includes three components (1, Mammalia; 2, Theria; and 3, Metatheria-Eutheria), and his classification only two (Mammalia and Theria). The Metatheria-Eutheria component is omitted from his classification.

A recent revision of mammalian classification includes the following major groups (McKenna 1975:40):

Class Mammalia
Subclass Prototheria
Subclass Theria
†Superlegion Kuehneotheria (new)
Superlegion Trechnotheria (new)
†Legion Symmetrodonta (new rank)
Legion Cladotheria (new)
†Sublegion Dryolestoidea (new rank)
Sublegion Zatheria (new)
†Infraclass Peramura (new)
Infraclass Tribosphenida (new)
Supercohort Marsupialia (new rank)
Supercohort Eutheria (new rank)

A cladogram may be constructed from this classification (figure 4.3), and it proves to be identical with the concept upon which the classification is based (figure 4.4). It includes six components, which

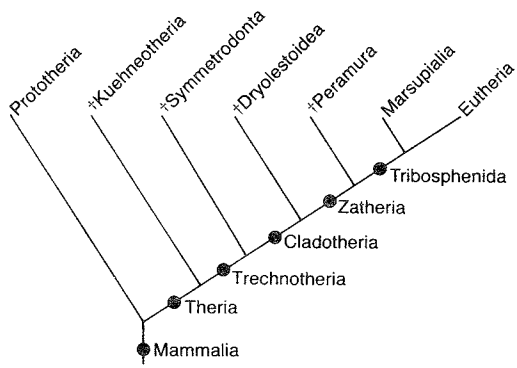


Figure 4.3. A cladogram derived from McKenna's (1975) classification of the major groups of mammals.

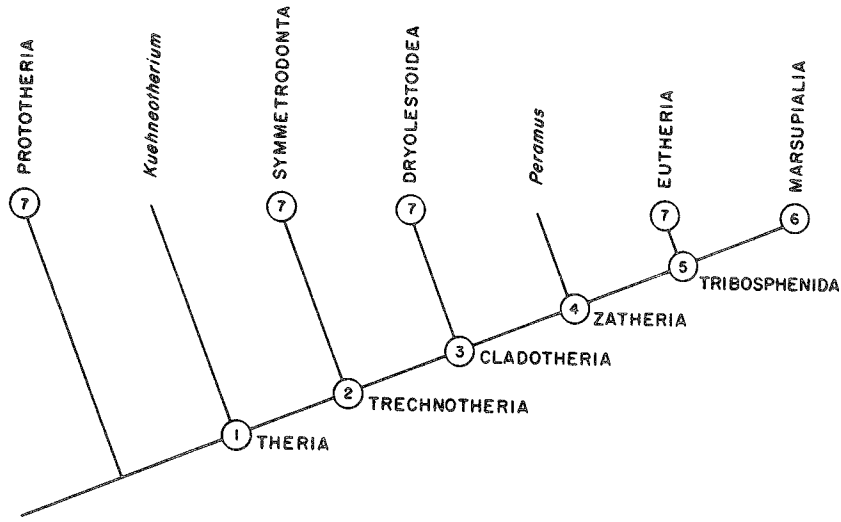


Figure 4.4. A cladogram (phylogram) summarizing the concept upon which McKenna based his classification of the major groups of mammals (cf. figure 4.3). After McKenna (1975), figure 1, p. 25.

correspond to the six inclusive groups (Mammalia, Theria, Trechnotheria, Cladotheria, Zatheria, Tribosphenida).

Comparison of this classification with Simpson's shows many differences: the disappearance of the Allotheria (included by McKenna in the Prototheria); the inclusion of a new taxon (unknown to Simpson), the Kuehneotheria; and the splitting of Simpson's Pantotheria into three taxa, Symmetrodonta, Dryolestoidea, and Peramura (the "Marsupialia" is merely another name for Simpson's Metatheria, and represents no change). Because there are four additional components in the cladogram, four new inclusive taxa are named (Trechnotheria, Cladotheria, Zatheria, Tribosphenida) and new ranks are used to accommodate them (superlegion, legion, sublegion, supercohort). Like that of Simpson, the classification is understandable as cladistic classification in a phyletic context. Unlike that of Simpson, however, the context is explicitly stated:

> I propose here a cladistic reclassification of the therian groups Marsupialia, Eutheria, and Simpson's infraclass Pantotheria, emphasizing kinship and recency of common ancestry. (McKenna 1975:26)

And unlike that of Simpson, the classification includes all of the components of the concept upon which the classification is based. McKenna states:

> To the critics who would ask, "Where will all this proliferation of names and ranks end?" I suggest that if the terms are not found useful to convey exact genealogical meanings dictated by phylogeny, then they can be ignored by those who so choose. They are, however, based upon cladistic principles, not on "art" or caprice. (1975:27)

McKenna's statements are unarguable on the principles of classification developed in this book (but, then, so are Simpson's). Noteworthy is that both of the components of Simpson's classification (Mammalia and Theria) are preserved in McKenna's classification. McKenna also names a component recognized but unnamed by Simpson (Tribosphenida). Thus, it would seem that Simpson's three components, considered as bases for prediction, have been found usefully predictive by McKenna. The components added by McKenna (Trechnotheria, Cladotheria, and Zatheria) may also be considered bases for prediction. Only future research will determine if they are usefully predictive.

McKenna's revision of mammalian classification may be considered

in relation to the stability problem dealt with above, for it might seem that classification of this sort poses a new and serious threat to stability, a threat that might dwarf that posed by the arbitrariness of traditional taxonomy.

The main differences between the concepts and classifications of Simpson and McKenna concern (1) the inclusion of a new group, Kuehneotheria, and (2) different interpretation of Simpson's Pantotheria. Following McKenna's principles, any further reinterpretation, or any discovery of new groups, might cause further revision of the classification, involving new inclusive groups and new ranks.

Devices have been suggested to accommodate such reinterpretation and discovery without resorting to "this proliferation of names and ranks." Most involve discriminating between fossil and recent groups (Brundin 1966; Hennig 1966; Crowson 1970). According to one suggestion, new inclusive taxa are not needed to accommodate purely fossil groups, which may be listed in the order of their branching sequence—a suggestion in agreement with Simpson's omission from his classification of a metatherian-eutherian component distinct from the therian component. According to this suggestion, McKenna's cladogram would result in the following classification with two components (the same two components of Simpson's classification—Mammalia and Theria):

Class Mammalia
  Subclass Prototheria
  Subclass Theria
    †Infraclass Kuehneotheria
    †Infraclass Symmetrodonta
    †Infraclass Dryolestoidea
    †Infraclass Peramura
     Infraclass Eutheria
     Infraclass Marsupialia

Comparison of this classification with that of Simpson shows (1) a new group, Kuehneotheria, (2) in place of Simpson's Pantotheria, the three groups into which the Pantotheria were split, and (3) the same components (Mammalia, Theria).

This suggestion has the advantage that, for reinterpretation of the relationships of fossil groups, no change would result in the basic

structure (the components) of the classification. Consider a reinterpretation (hypothetical) along the lines of figure 4.5. According to the above suggestion—that fossil groups be listed in the order of their branching sequence—fossil groups are, so to speak, free to wander about in the classification. A classification based on this purely hypothetical reinterpretation (figure 4.5) would change only in the rank and position of the fossil groups whose relationships were reinterpreted (Peramura, Symmetrodonta, Kuehneotheria):

Class Mammalia
  †Subclass Peramura
  †Subclass Symmetrodonta
  Subclass Prototheria
  Subclass Theria
    †Infraclass Dryolestoidea
    †Infraclass Kuehneotheria
    Infraclass Eutheria
    Infraclass Marsupialia

As noted above for the Kuehneotheria, this suggestion has the additional advantage that newly discovered fossil groups could be added to the classification in their appropriate position and rank, without change of the components of the classification. This suggestion, in effect, is that components involving one or more fossil groups and only one recent group be omitted from classification. Such omitted

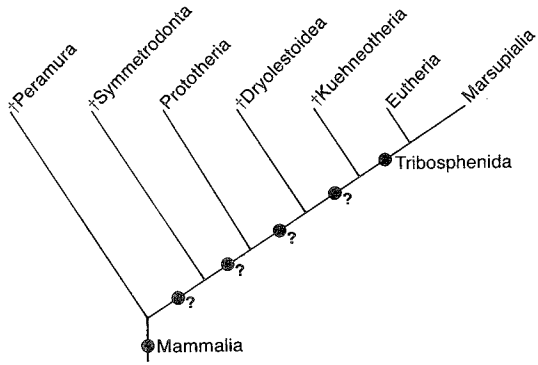


Figure 4.5. A cladogram summarizing a hypothetical reinterpretation of McKenna's concept of the interrelationships of the major groups of mammals (cf. figures 4.3, 4.4).

components constitute no great loss. Even if they were included, they could have only a very restricted generality—restricted to those few characters recoverable from fossils. With a restricted generality, they could never prove very useful, either as summaries of information already acquired or as predictions about information yet to be discovered, for the reason that the amount of information, even in its most complete form, would be meager. And their usefulness, such as it is, would extend only to paleontology. If the sign (†) for fossil groups also indicates use of this convention, the complete cladogram can be reconstructed from the classification with no loss of information content.

It is not the purpose here to argue the pros and cons of various devices that might enhance stability of classification. It is enough to mention that such devices exist (Patterson and Rosen 1977; Wiley 1979). But to mention them does not solve the stability problem. That problem is inherent in usage and custom, which are always at the mercy of future events.

A PHENETIC EXAMPLE

There are very few phenetic classifications in the form of a completely resolved hierarchical arrangement of taxa, for the reason that the phenogram is usually considered a classification in itself. With respect to component analysis, it is difficult to begin with an example of a phenogram for an actual group of species. Although many phenetic studies have been performed, they have usually involved groups of numerous species. Discussion of the many components of even one such phenogram would be tedious. Therefore, an example of a hypothetical group, with a small number of species, will be considered. This group comprises six species, A, B, C, D, E, F, and the results of the study are portrayed as a phenogram (figure 4.6). The components of the phenogram are

ABCDEF
BD
ACEF
ACE
AC

One may inquire what these components represent in the phenetic

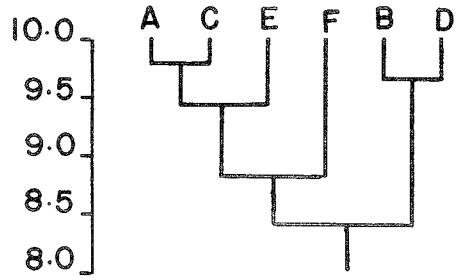


Figure 4.6. A phenogram for six species (A, B, C, D, E, F). After Sokal and Sneath (1963), figure A-2, p. 311. Copyright © 1963, W. H. Freeman.

context. Do the components represent generalizations (statements of general synapomorphy)? If they do, the general synapomorphy would be general phenetic synapomorphy: for example, with respect to "overall similarity" species A and C are more similar to each other than to any other species. Similarly, species A, C, and E are more similar to each other than to any other species; species A, C, E, and F are more similar to each other than to any other species; species B and D are more similar to each other than to any other species; and, finally, species A, B, C, D, E, and F are more similar to each other than to any other species.

Within the phenetic context, the sense of "similarity" is total or "overall" similarity—a concept of similarity that is estimated by sampling numerous characters of each species and combining positive and negative occurrences of them such that a numerical value of "overall similarity" can be computed for comparisons between species. A characteristic of the phenetic approach is that the similarity statements (components) can be associated with numerical levels of similarity. For example, species A and C are similar at a level of 9.8. The level of similarity may, therefore, be considered a generalization for each component:

ABCDEF: 8.4
BD: 9.6
ACEF: 8.8
ACE: 9.4
AC: 9.8

These components allow two types of predictions: that independent samples of information will reveal (1) the same components at (2) the

same levels. To date, neither type of prediction has proved useful, because in actual examples the components and the levels depend upon the characters sampled and the particular numerical methods used to compare and group the species (Farris 1977, 1979, 1980; Mickevich 1978). Different methods yield different phenograms with different components, or the same components at different levels (figures 4.7, 4.8).

In expositions of phenetic theory, "prediction" is considered important:

> Gilmour's dictum—that a system of classification is the more natural the more propositions can be made regarding its constituent classes—admits of objective measurement and testing, in contradistinction to Simpson's natural system. Furthermore, Gilmour's system has powerful predictive properties; it is therefore the one we recommend. (Sneath and Sokal 1973:27, also Sokal and Sneath 1963:19)

The nature of this "prediction" has been further clarified in expositions of phenetic theory, but it seems to have no relation with the two types of phenetic prediction considered above:

> We can neither list nor remember all the characteristics of various organisms and higher taxa, and we therefore need a system of grouping them into a manageable number of groups whose characters are preponderantly constant. Because of high constancy and mutual intercorrelations of characters, such a grouping will carry a high predictive value. Thus, if we read of a new aphid species we can immediately predict a number of characteristics that this species is expected to possess. An aphid will with almost complete certainty be a plant feeder, possess a particular type of wing venation, be parthenogenetic in part of its life cycle, produce males by nondisjunction of the sex chromosomes, produce honeydew, secrete wax from cornicles or other glands, and so on. Since an aphid is a homopteran, we can forecast with some accuracy the general construction of its mouth parts, the texture of its wings, and other homopteran characteristics. This type of argument can, of course, be extended to the hexapod and arthropod levels of classification and even higher. It is obviously much easier for us to remember this of the group Aphididae than of each individual aphid or species of aphid. Furthermore, it is impossible to remember or appreciate the innumerable relations between the various OTU's [species] to be classified, but this is easier when they are grouped into fewer inclusive taxa.
>
> It is clear that such considerations lead to a second, closely related purpose of taxonomy, namely predictive power. The more natural a taxonomy is, the more predictive it will be about characters known from part of the group that have not yet been investigated in another part. (Sneath and Sokal 1973:188–189)

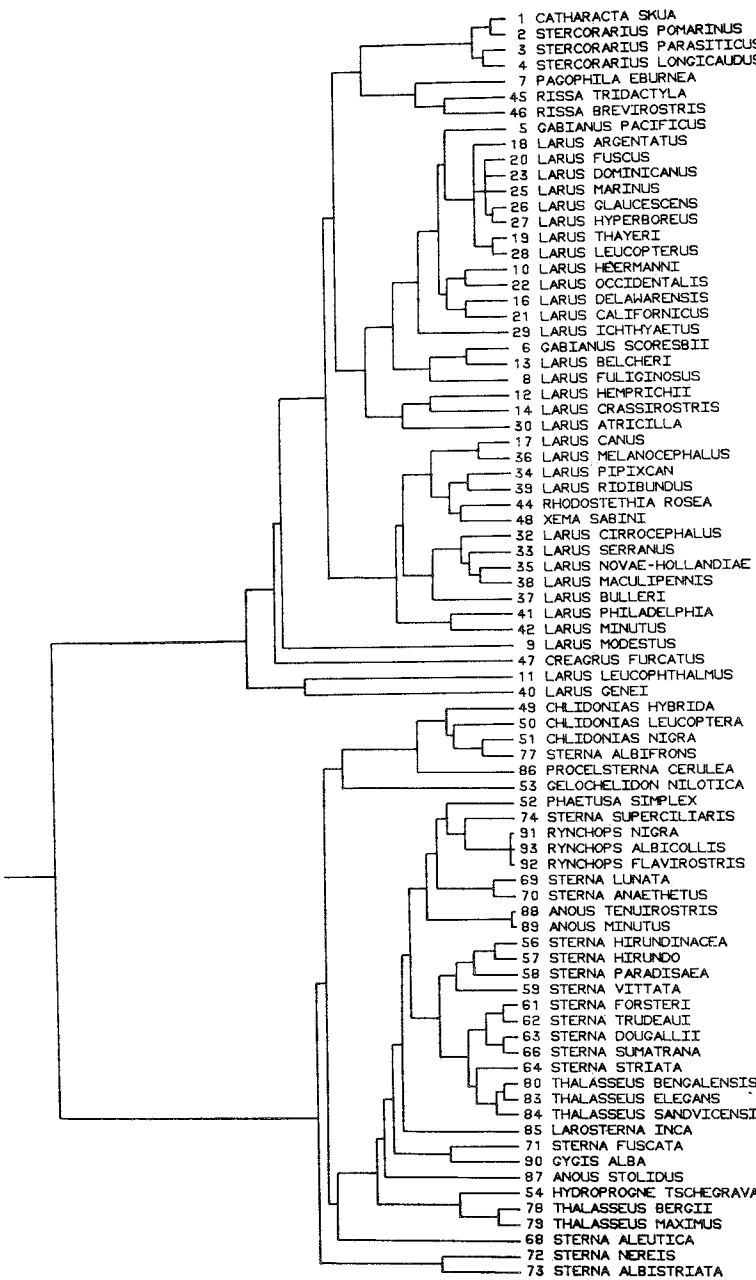


Figure 4.7. One phenogram for 81 species of birds, based on variation of 51 skeletal characters. The phenogram was constructed using correlation of "arithmetic averages (UPGMA)." After G. D. Schnell (1970), A phenetic study of the Suborder Lari (Aves). Syst. Zool. 19:264–302; figure 12, p. 266.

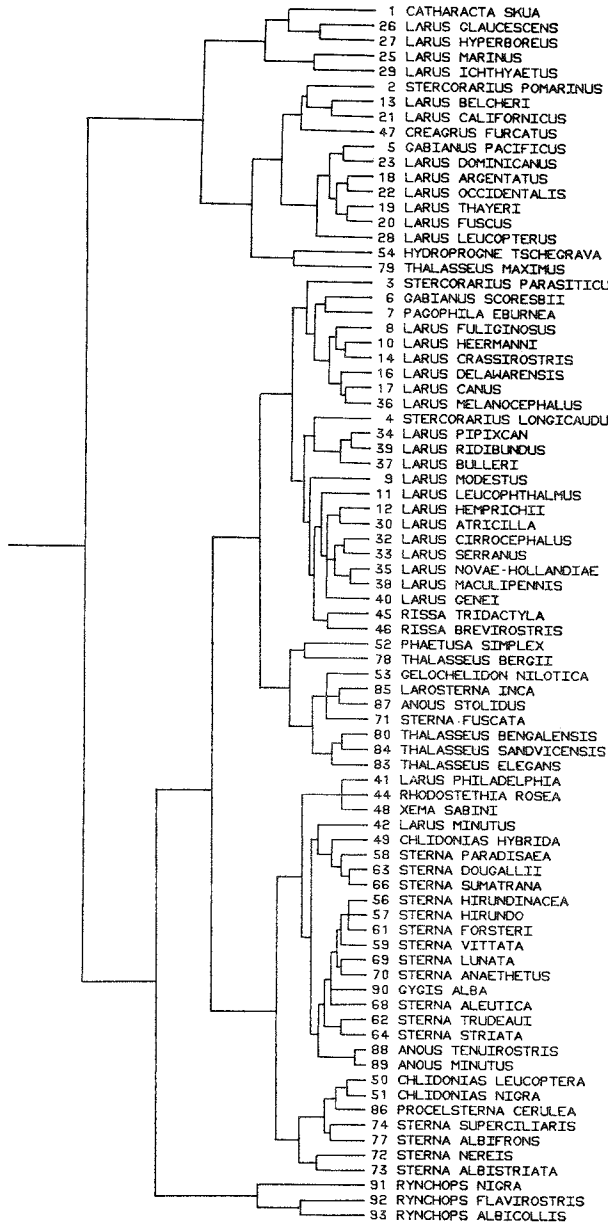


Figure 4.8. Another phenogram for 81 species of birds, based on variation of 51 skeletal characters. The phenogram was constructed using distance in relation to the "UPGMA method." After Schnell (1970; see caption for figure 4.7), figure 13, p. 267.

The key element in the above quotation is: " . . . if we read of a new aphid species we can immediately predict a number of characteristics that this species is expected to possess." This statement contains no reference to overall similarity, nor to levels of overall similarity. The statement does not, therefore, refer to prediction in the phenetic context. It is merely a statement that there are already known some generalizations (synapomorphies) for a group called Aphididae, generalizations that might apply to a presently unknown member (a species) of the group. To be recognized as a member of the Aphididae, the "new aphid species" would, of course, have to display at least some of the characters considered synapomorphic for the Aphididae (the element of prediction applies only to those aphid synapomorphies not already detected in the new species). In any event, the generalizations that pertain to the Aphididae are merely synapomorphies in the sense that that term has been used throughout this book. Considered as a basis for prediction, the generalizations would lead to the hypothesis of congruence: that a certain group of species, observed to be synapomorphic in one respect, with further study will be observed to be synapomorphic in other respects not yet discovered.

It seems, therefore, that in expositions of phenetic theory, the hypothesis of congruence has been confused with phenetic prediction. And although phenetic prediction of two types is possible, phenetic predictions are seldom if ever realized in practice. Predictions of overall similarity and the levels of overall similarity appear to be artifacts of the particular numerical methods used on particular sets of data.

These comments constitute something of a critique of phenetic taxonomy, but their main purpose is to relate component analysis to phenograms. The example shows that a phenogram has cladistic components. And the significance of the components, considered as a basis either of generalization or prediction, is the same significance as that considered earlier in relation to the hypothesis of congruence—a claim that the reader might like to explore independently, by reading the literature of phenetic taxonomy (an excellent bibliography is contained in Sneath and Sokal 1973).

A GRADISTIC EXAMPLE

As stated above, the concept of grade is not very well defined and, for all practical purposes, may be undefinable. This difficulty aside, some

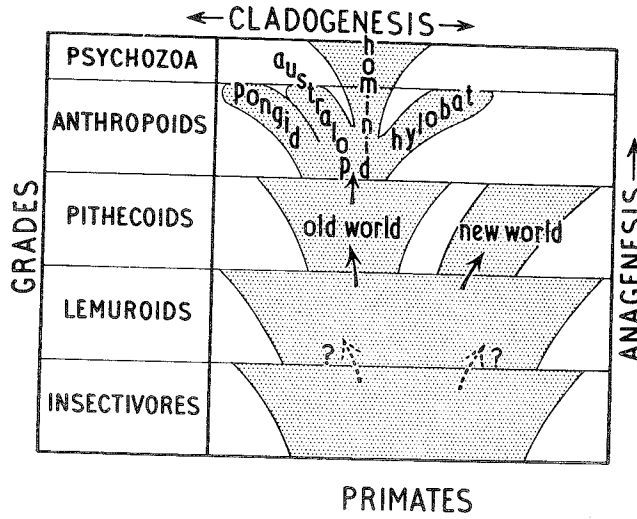


Figure 4.9. A diagram illustrating grades, published by Huxley in 1958. His legend reads: "Grades and clades in primate evolution. The Lemuroids are possibly and the Pithecoids certainly grades but not monophyletic clades. Cladogenetically, Man constitutes the family Hominidae, but anagenetically the major grade Psychozoa." After Huxley (1958), figure 12, p. 37.

attempts at gradistic taxonomy may be considered. A good place to begin is with Huxley's (1958: 36) concept of grade: "I consider that *grade* is the best general term to denote readily delimitable or definable anagenetic units or assemblages." Huxley provided several diagrams of grades, one of which may be used here to illustrate component analysis of gradograms. Huxley's figure (figure 4.9) can be simplified to a gradistic tree (figure 4.10), and the general components of the tree may be summarized as a gradogram (figure 4.11):

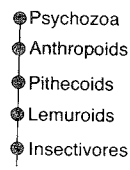


Figure 4.10. A gradistic tree derived from Huxley's diagram (figure 4.9).

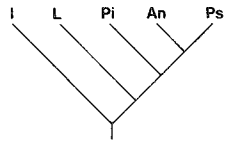


Figure 4.11. A gradogram derived from the gradistic tree of figure 4.10.

ILPiAnPs
LPiAnPs
PiAnPs
AnPs

These components do not, however, reflect Huxley's concept about these particular grades. With reference to the grade Psychozoa (including only *Homo*), he states: "Cladogenetically man constitutes only the single family Hominidae: but anagenetically he constitutes a grade equivalent in evolutionary importance to all other organisms taken together" (1957:455). The gradistic tree expressing this concept is that of figure 4.12; and the corresponding gradogram is that of figure 4.13.

It is unnecessary here to belabor the inconsistency between Huxley's diagrams and his concepts. But the nature of gradistic prediction may be briefly considered with reference to figure 4.13. The unique properties of humankind (Huxley's Psychozoa), such as intelligence, culture, language, etc., are a basis for the hypothesis of congruence respecting the psychozoans (e.g., the various kinds of humans): psychozoans are synapomorphic generally, relative to all other forms of life; therefore, they will prove synapomorphic in other ways not yet discovered. All other forms of life (here termed the "Apsychota"), however, are a group lacking any basis for generalization, except the negative generalization that "Apsychota" lack the unique properties of Psychozoa. Indeed, for the "Apsychota" there are known no generalizations that would not

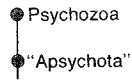


Figure 4.12. A gradistic tree exemplifying Huxley's concept of the grade Psychozoa (including *Homo*) and the grade including all other organisms (here termed the "Apsychota").

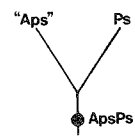


Figure 4.13. A gradogram derived from the gradistic tree of figure 4.12.

apply also to Psychozoa. For the "Apsychota," therefore, the only possible "prediction" is that future research will demonstrate that newly discovered traits unique to Psychozoa will be absent among "Apsychota"—a prediction that in reality is a tautology. It is not surprising that Huxley's comments about the "Apsychota" have not been productive; indeed, they have been ignored, presumably because the "Apsychota" are a group for which useful prediction is not possible. Huxley's concept of grade, however, has been used, with whatever degree of success, despite the tautological nature of gradistic "prediction," which seems an ever-present problem and a serious defect of the gradistic approach.

For example, Simpson, in a branching diagram, has elaborated a more detailed gradistic scheme for humankind and its near relatives (figure 4.14), in which grades are considered "adaptive-structural-functional zones." He states (1963) that the diagram is a

> combination of a dendrogram and an adaptive grid. . . . Interpretation of probable closeness of genetic connection is indicated by depth of branching, although it is to be emphasized that such a diagram is not a phylogenetic tree and has no time dimension. (p. 25)

Whatever Simpson meant by "genetic connection," the gradistic elements may be portrayed in a gradogram (figure 4.15) with the following components:

HoHyPoPa
HyPoPa: Pongid Zone
PoPa: *Pongo-Pan* Subzone

The components correspond to Simpson's zones, subzones, and subsubzones (all of which are grades), and the gradogram is consistent with his concepts, in contradistinction to Huxley's diagrams and concepts, as may be appreciated by a complete listing (including implicit components):

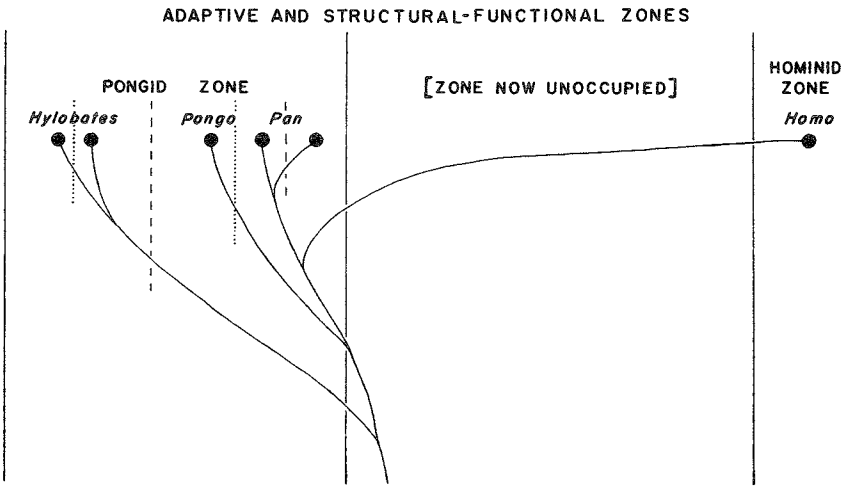


Figure 4.14. A diagram illustrating grades, published by Simpson in 1963. His legend reads: "Dendrogram of probable affinities of recent hominoids in relationship to their radiation into adaptive-structural-functional zones. The two major adaptive zones are bordered by solid lines. Pongid radiation into sub- and sub-sub-zones is schematically suggested by broken and dotted lines. A dendrogram of this sort has no time dimension and does not indicate lineages, but it is probable that divergences of lines showing affinities are topologically similar to the phylogenetic lineage pattern." After Simpson (1963), figure 5, p. 26. Reprinted from S. L. Washburn, ed., Classification and Human Evolution. Viking Fund Publications in Anthropology, no. 37. Copyright © 1963, Wenner-Gren Foundation for Anthropological Research, Inc., New York.

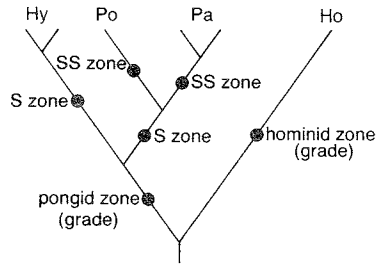


Figure 4.15. A gradogram derived from Simpson's diagram (figure 4.14).

HoHyPoPa
Ho: Hominid Zone
HyPoPa: Pongid Zone
Hy: *Hylobates* Subzone
PoPa: *Pongo-Pan* Subzone
Po: *Pongo* Subsubzone
Pa: *Pan* Subsubzone

Simpson has further developed his gradistic interpretation in another figure (figure 4.16), which has a time axis. The gradistic elements may, nevertheless, be isolated in a gradogram (figure 4.17), for which a listing of components seems superfluous.

The question may be asked, what is the relation between these gradistic interpretations and classification? Simpson's (1945) classification is as follows:

Order Primates
Suborder Prosimii
Suborder Anthropoidea
Superfamily Ceboidea
Superfamily Cercopithecoidea

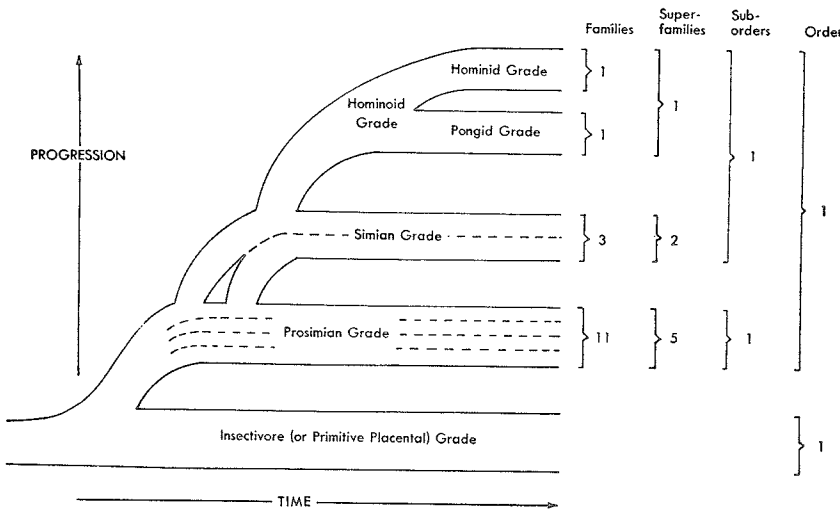


Figure 4.16. A diagram illustrating grades and their relation to taxa. After Simpson (1961), figure 29, p. 215.

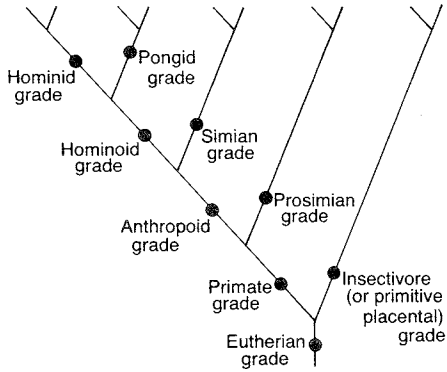


Figure 4.17. A gradogram derived from figure 4.16. The Anthropoid and Primate grades are represented in Simpson's diagram (figure 4.16) by the inclusive suborder and order (brackets). The Eutherian grade is not represented in Simpson's diagram.

Superfamily Hominoidea
Family Pongidae
Subfamily Hylobatinae
Subfamily Ponginae
Family Hominidae

The cladogram derived from this classification is that of figure 4.18. A comparison of this cladogram with the gradograms (figures 4.15, 4.17) shows many common components (the Simian grade, Ceboidea+ Cercopithecoidea, is the only grade unrepresented by a taxon, and all taxa represent grades). The conclusion is that Simpson's groups are all

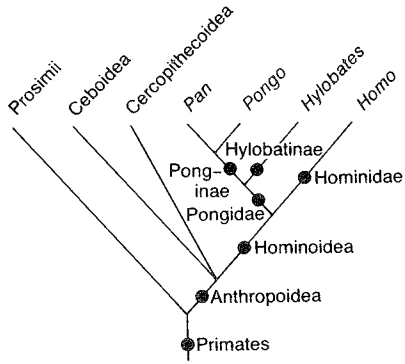


Figure 4.18. A cladogram derived from Simpson's classification of Primates.

grades, relative to his concepts. But Simpson had phyletic concepts as well (figures 4.14 and 4.16), and the phyletic concepts may be summarized in a phylogram (figure 4.19). Comparison of the phylogram (figure 4.19), gradograms (figures 4.15, 4.17), and the cladogram derived from his classification (figure 4.18) reveals the following:

Grades Unrepresented by Taxa	Monogradistic Taxa	Monophyletic Taxa	Polyphyletic Taxa
	Primates	Primates	
	Prosimii		Prosimii
	Anthropoidea	Anthropoidea	
Simian	Ceboidea	Ceboidea	
	Cercopithecoidea	Cercopithecoidea	
	Hominoidea	Hominoidea	
	Pongidae		Pongidae
	Ponginae		Ponginae
	Hylobatinae	Hylobatinae	
	Hominidae	Hominidae	

One hundred percent of these taxa are grades according to Simpson's concepts (figures 4.14–4.17), however clearly formulated they might be; 70 percent are also monophyletic according to Simpson's concept of

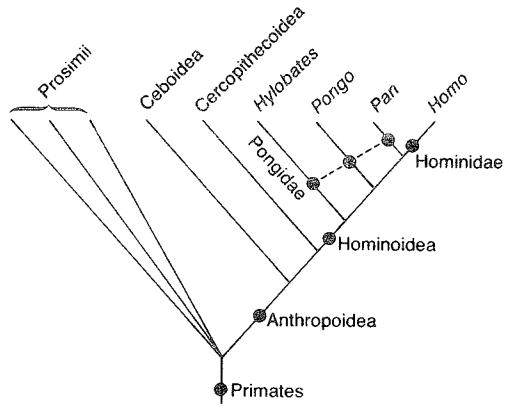


Figure 4.19. A cladogram (phylogram) derived from Simpson's phylogeny of Primates (figures 4.14, 4.16).

their phylogeny. The reader may independently investigate the reasons, if any can be discovered, for this mixture of taxa. Here it is enough to show that gradistic concepts may be analyzed into their components. Once isolated, the components may be considered in relation to classification, on the one hand, and phyletic components on the other. These considerations have importance for the problem of prediction.

Of interest in this regard are the developments in primate research during the twenty to thirty years since Simpson's publications. The summary of Goodman (1975) may be considered an example, in order to explore the predictive aspects of the various taxa recognized by Simpson. Goodman's figure of primate interrelationships (figure 4.20), based on studies of proteins and other molecules, may be simplified into

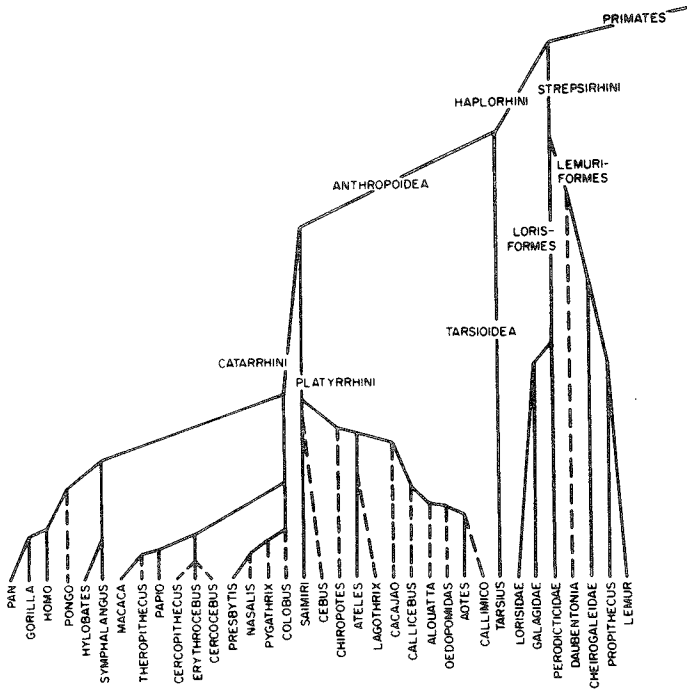


Figure 4.20. A cladogram of the Primates, based on molecular data. After Goodman (1975), part of figure 1, p. 226.

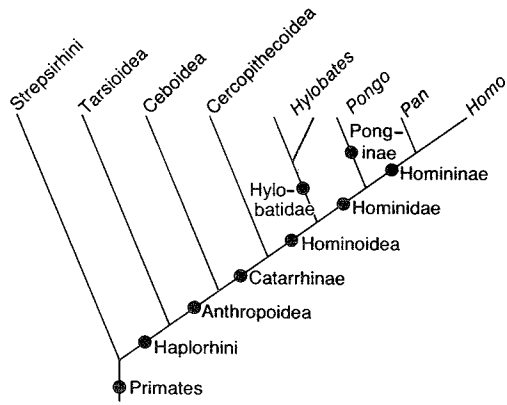


Figure 4.21. A simplified cladogram derived from Goodman's cladogram (figure 4.20), identical to one derived from Goodman's classification (see text).

a cladogram (figure 4.21) comparable in its level of detail with Simpson's figures.

Comparison between Simpson's concepts and Goodman's diagram shows the following: Simpson's Prosimii are divided into Strepsirhini and Tarsioidea; Goodman recognizes two new inclusive taxa, Haplorhini and Catarrhini; and there are two groups with a more inclusive composition, Hominidae and Homininae. Goodman's classification is as follows:

Order Primates
- Semiorder Strepsirhini
- Semiorder Haplorhini
  - Suborder Tarsioidea
  - Suborder Anthropoidea
    - Infraorder Platyrrhini (Ceboidea)
    - Infraorder Catarrhini
      - Superfamily Cercopithecoidea
      - Superfamily Hominoidea
        - Family Hylobatidae
        - Family Hominidae
          - Subfamily Ponginae (*Pongo*)
          - Subfamily Homininae (*Pan* and *Homo*)

Comparison between Goodman's and Simpson's classification shows

that Goodman's contains two ranks (semiorder and infraorder) absent in Simpson's, and certain names not used by Simpson. It is not the purpose here to decide which is the better classification. But we may ask which of Simpson's taxa have been retained, i.e., which taxa have proven predictive with respect to the new information about molecules, information unavailable to Simpson when he composed his classification? What is important for this question is not change of rank, or change in name, but change in composition (change in components).

Simpson's Taxa	Goodman's Taxa
Primates, unchanged	Primates
*Prosimii, split into	Strepsirhini Tarsioidea
Anthropoidea, unchanged	Anthropoidea
Ceboidea, unchanged	Platyrrhini (Ceboidea)
Cercopithecoidea, unchanged	Cercopithecoidea
Hominoidea, unchanged	Hominoidea
*Pongidae, split into	Hylobatidae Ponginae Homininae (in part: *Pan*)
*Ponginae, split into	Ponginae Homininae (in part: *Pan*)
Hylobatinae, unchanged	Hylobatidae
Hominidae, unchanged	*Homo*

*Taxa changed in composition (components).

The taxa that proved predictive were all of those visualized by Simpson as monophyletic. The only taxa that proved nonpredictive were those visualized by Simpson as polyphyletic (nonmonophyletic). Simpson, of course, viewed all of his taxa as grades, but one grade (Simian) visualized by Simpson, though not recognized as a taxon, proved nonpredictive.

It is not surprising that the only nonpredictive taxa are polyphyletic, i.e., groups that Simpson could not generally visualize as real (that is, groups that he thought were grades but not also monophyletic groups). It is not surprising because gradistic "prediction" seems to be tautological, rather than useful, prediction—a point that is not proved, however, by this discussion. Indeed, one might argue that, for one reason or another, Goodman's cladogram and classification do not

constitute a useful test of gradistic prediction. Simpson, in fact, has already provided an argument of that kind. Referring to an earlier paper by Goodman and Moore (1971), he stated:

> Those authors report that . . . their results confirm the "established" taxonomic (classificatory) arrangement but show the "classical Pongidae" (i.e., the living apes) to be polyphyletic and require the reference of *Pongo*, subfamily Ponginae, to the Hominidae and of "*Pan*" . . . not only to the Hominidae but also to the Homininae.
>
> Those are subjective interpretations of data that are summed up in their Fig. 6, a "cladogram" or, as it should be designated not to prejudice interpretation, a dendrogram based on elaborately measured antigenic distances.
>
> The data of Goodman and Moore and the resulting dendrogram do not in fact show the classical Pongidae (or Pongidae plus Hylobatidae) to be polyphyletic. They are indicated as strictly monophyletic from the stem labeled "Hominoids" on the dendrogram. That dendrogram neither contradicts nor adds to the classical and still current consensus about relationships within the Catarrhini. It is interesting that as regards relationships of living catarrhines Goodman and Moore's dendrogram, although drawn in a different and unusual form, is topologically absolutely identical with that already presented by Haeckel (1866 . . .) more than a century ago. (1971:369)

With respect to Goodman's concept of primate interrelationships (figure 4.20), Simpson stated:

> The "classical" arrangement, with Hominoidea divided into Pongidae (all living apes) . . . and Hominidae (*Homo* only among living animals), is consistent with those relationships and was arrived at with them in mind. (*Ibid.*)

The relevant part of Haeckel's phyletic "tree" is reproduced here (figure 4.22) and summarized in a simplified cladogram (figure 4.23). The relevant part of Haeckel's classification is as follows (see figure 4.24 for a cladogram derived from this classification):

Order Simiae
- Suborder Arctopitheci
- Suborder Platyrrhinae
- Suborder Catarrhinae
  - Section Menocerca
  - Section Lipocerca
    - Family Tylogluta (*Hylobates*)
    - Family Lipotyla (*Pongo, Pan*)
    - Family Erecta (*Homo*)

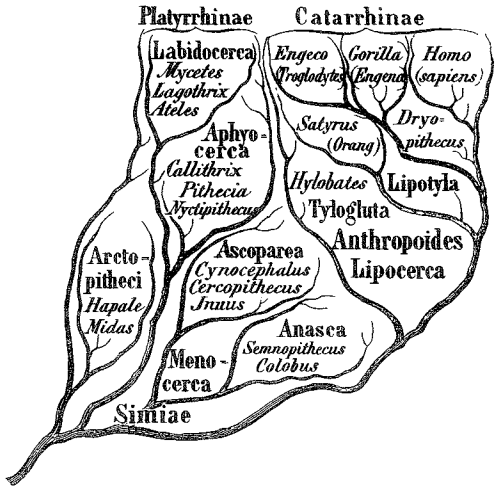


Figure 4.22. Part of a phyletic tree, published by Haeckel in 1866, showing the interrelationships of some primates as he conceived them. After E. Haeckel (1866), Allgemeine Entwicklungsgeschichte der Organismen (Berlin: Reimer), part of plate 8.

Haeckel's taxa may be compared with those of Goodman:

Haeckel's Monophyletic Taxa	Haeckel's Polyphyletic Taxa	Equivalent Taxa in Goodman's Classification
Simiae, unchanged		Anthropoidea
Arctopitheci, Platyrrhinae	lumped as	Platyrrhini
Catarrhinae, unchanged		Catarrhini
Menocerca, unchanged		Cercopithecoidea
Lipocerca, unchanged		Hominoidea
Tylogluta, unchanged		Hylobatidae
	*Lipotyla, split into	Ponginae (*Pongo*); Homininae (in part: *Pan*)
Erecta, unchanged		*Homo*

*Taxon changed in composition (components)

Comparison between these classifications, concepts, and diagrams leads to the conclusion that Simpson is correct in asserting that a *Pongo-Pan* component was recognized by Haeckel in his classification, that the component was maintained by Simpson (who added a

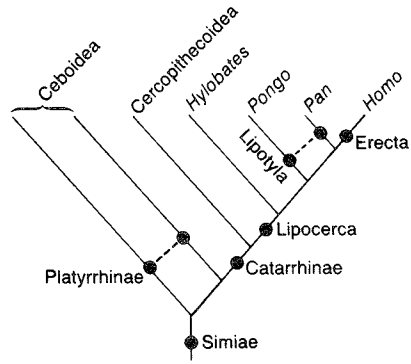


Figure 4.23. A cladogram derived from Haeckel's tree (figure 4.22). Along the top are the modern names of the groups recognized by Haeckel. Names of the inclusive taxa are the names in Haeckel's classification (see text).

Hylobates-Pongo-Pan component as well), and that the component was abandoned by Goodman (who abandoned Simpson's *Hylobates-Pongo-Pan* component as well).

Haeckel did not elaborate his reasons for grouping *Pongo* and *Pan*. Indeed, not much was known about the organisms in Haeckel's time. Simpson, of course, did elaborate his reasons to some extent, in relation to his concepts of grades (his zones, subzones, and subsubzones). These reasons and concepts are put into question by Goodman's results. It is not argued here that the *Pongo-Pan* controversy involving Simpson and

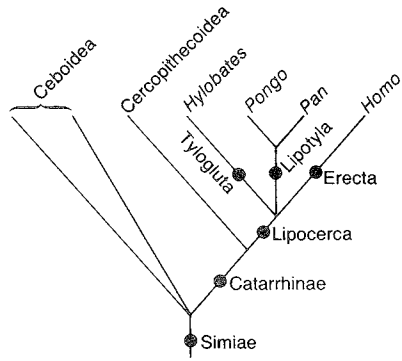


Figure 4.24. A cladogram derived from Haeckel's (1866, see caption for figure 4.22) classification of Primates.

Goodman has great intrinsic interest, but only that the controversy allows some general exploration of gradistic taxonomy.

Goodman's results, in effect, raise a question about the usefulness of the *Pongo-Pan* component: why was it not resolved by Goodman's study? And why did his study resolve instead a *Pan-Homo* component?

If gradistic prediction were possible, it would imply some generalization that would lead to the hypothesis of congruence. For example, a person might state that *Pongo* and *Pan* are gradistically synapomorphic, relative to all other organisms; and that independent samples of information will resolve a *Pongo-Pan* component rather than any other component involving those taxa. Such prediction presumes that this gradistic component has already been resolved at least once, or that it is potentially resolvable—a presumption that may have no basis in fact because of the apparently tautological nature of gradistic generalization and "prediction" (see above).

Simpson seems to have approached the problem of prediction. He stated:

> It is abundantly established that anatomically, behaviorally, and in other ways controlled or influenced by total genetic makeup *Homo* is very much more distant from either "*Pan*" or [*Pongo*] . . . than they are from each other. That fact is not overbalanced by the failure of just one kind of data to reflect that distinction clearly or in equal degree. The distinction is real, and it still justifies the classical separation of Pongidae and Hominidae in classification. (1971:370)

One problem with Simpson's generalization, and any "predictions" that might arise from it, is that it is a phenetic, rather than gradistic, prediction, and is subject to the difficulties of the phenetic approach. If it is not a phenetic "prediction," then it is a statement whose meaning will become clear when and if the "total genetic makeup" of these organisms becomes known. Simpson did not attempt to make a distinct gradistic prediction, in order to determine if it is realized or realizable, with particular reference to molecular information, but he did invoke a principle supposedly underlying all classification. With respect to Goodman's classification, Simpson stated:

> The difference of opinion might thus be taken as purely formal and subjective.
>
> Where does one prefer to draw arbitrary family lines? The consensus puts the division Pongidae-Hominidae at the dendrogram point of divergence between a line leading to "*Pan*" . . . and another leading to *Homo*. Goodman and Moore

simply have a personal preference to draw it at the dendrogram point of divergence of a line leading to the gibbons from one leading to . . . [*Pan* and *Homo*] plus *Pongo*. (1971:369)

Here Simpson avoids the main problem (what groups to recognize) to focus on a trivial problem (what names should apply to the groups).

It is not the purpose here to discredit the gradistic approach, but rather to try to understand it. Simpson's words are quoted not to show that they are inadequate, but rather to inquire about their meaning and adequacy and, more precisely, to determine if they contain an element of useful gradistic prediction. They seem not to contain such, inasmuch as they lead into the area of phenetic "prediction" on the one hand, and arbitrariness of classification on the other.

An attempt to isolate gradistic synapomorphy for a group composed, say, of *Pongo* and *Pan* leads immediately to an appraisal of synapomorphy of organisms, such as *Homo*, distinct from the *Pongo-Pan* group. Interestingly, a statement of general synapomorphy for *Homo* is a statement that the various forms of *Homo* are synapomorphic relative not merely to *Pongo* and *Pan*, but to these as well as all other forms of life. In order to isolate *Pongo* and *Pan* from all other forms of life, and in effect to group them with *Homo*, another statement of general synapomorphy is required, or at least implied: that *Pongo, Pan,* and *Homo* are generally synapomorphic, relative to all other forms of life.

Gradistic "synapomorphy" (G_s), therefore, seems to be analyzable into two elements of general synapomorphy (S_1, S_2):

(1) S_1 (*Pongo, Pan, Homo*) – S_2(*Homo*) = G_s (*Pongo, Pan*)

Or, with reference to Simpson's classification:

(2) S_1 (Hominoidea) – S_2 (Hominidae) = G_{s1} ("Pongidae")

This conception of gradistic "synapomorphy" allows the possibility of numerous alternative grades (again, with reference to Simpson's classification):

(3) S_{1a} (Anthropoidea) – S_2 (Hominidae) = G_{s2} (nonhuman anthropoids)
(4) S_{1b} (Primates) – S_2 (Hominidae) = G_{s3} (nonhuman primates)
(5) S_{1c} (Eutheria) – S_2 (Hominidae) = G_{s4} (nonhuman eutherians)
(6) S_{1d} (Mammalia) – S_2 (Hominidae) = G_{s5} (nonhuman mammals)

(7) S_{1c} (Animalia) – S_2 (Hominidae) = G_{s6} (nonhuman animals)
(n) S_{1n} (All of life) – S_2 (Hominidae)
= G_{sn} (nonhuman organisms: "Apsychota")

If gradistic "synapomorphy" is as described above, analyzable into two elements of general synapomorphy, then there is a contradiction at a fundamental level in gradistic theory, at least as it is conceived and applied by Simpson: the groups Hominoidea, Anthropoidea, Primates, etc., if they include *Homo*, cannot be grades (figure 4.25). This conclusion suggests that a group characterized by gradistic "synapomorphy" (synapomorphy that is analyzable into two elements of general synapomorphy) cannot also be a monophyletic group. Neither can it be generally predictive. If so, there can be no generality of classification, based on congruence between grades and monophyletic groups, because such congruence is impossible. Indeed, such may be the case. Such would not be the case if some useful gradistic synapomorphy actually existed and could be resolved.

These considerations suggest various possibilities: (1) that, for example, the various taxa visualized by Simpson as both grades and monophyletic groups are either one or the other, but not both; (2) that the taxa he visualized as grades and polyphyletic groups may be both; (3) that there may be two kinds of grades, (*a*) those defined by gradistic synapomorphy (those that might also be monophyletic groups), and (*b*) those defined by gradistic "synapomorphy" (those that cannot also be monophyletic groups).

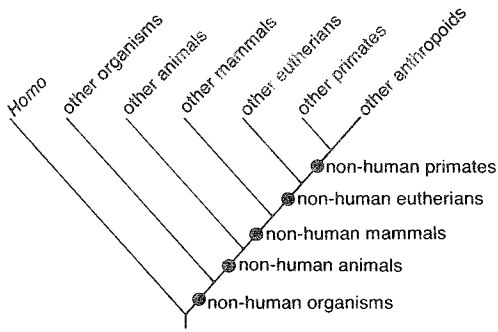


Figure 4.25. A gradogram of some grades (inclusive groups), defined with reference to two statements of general synapomorphy (see text).

Possibility (3) seems to reflect the actual situation, namely that some groups visualized as grades are predictive (monophyletic grades) and some are not (polyphyletic grades). Examples are furnished by Simpson's Hominidae (*Homo*) and Pongidae (*Pongo, Pan*), respectively. But if some grades are not usefully predictive, what then is their use? And why do taxonomists sometimes recognize them? In this case, Simpson has attempted to make clear his reasons. With reference to *Pongo, Pan,* and *Homo,* he stated:

> Wilder boldly united all these forms in a single family, Hominidae, and Gregory and Hellman (e.g., 1939d) have adopted this arrangement. On the basis of usual diagnostic characters, such as the teeth, viewed with complete objectivity, this union seems warranted. I nevertheless reject it, for two reasons: (a) mentality is also a zoological character to be weighed in classification and evidently entitling man to some distinction, without leaning over backward to minimize our own importance, and (b) there is not the slightest chance that zoologists and teachers generally, however convinced of man's consanguinity with the apes, will agree on the didactic or practical use of one family embracing both. (1945:187–188)

It is doubtful that these reasons have much significance for gradistic taxonomy in general.

The previous examples, (l)–(n), involved comparisons of pairs of groups, both monophyletic, in order to resolve elements of gradistic "synapomorphy" (G_s). A more complex situation is discussed by Huxley (figure 4.26). His figure can be simplified to a gradistic tree (figure 4.27), and the general components of the tree can be summarized in a gradogram (figure 4.28):

AgPlOsAmReHo
PlOsAmReHo
OsAmReHo
AmReHo
ReHo
Ho

Of interest is the group "Homotherma," considered by Huxley to be polyphyletic ("diplyletic"). As subgroups it includes Aves and Mammalia. Because each of the two subgroups is monophyletic according to his conception, elements of gradistic "synapomorphy" can be resolved by comparing each of them with a more inclusive group, either individually:

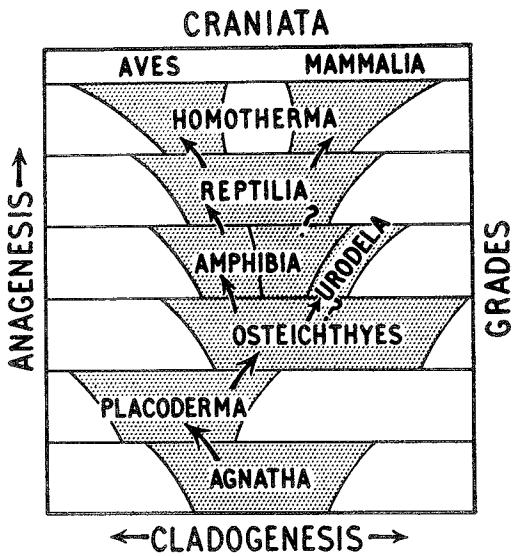


Figure 4.26. A diagram illustrating grades, published by Huxley in 1958. His legend reads: "Anagenesis and cladogenesis in Craniate evolution . . . . The grade Homotherma is diphyletic, consisting of the separate classes Aves and Mammalia." After Huxley (1958), figure 5, p. 28.

(1) S_1 (Amniota) – S_2 (Mammalia) = G_{s1} (nonmammalian amniotes)
(2) S_1 (Amniota) – S_3 (Aves) = G_{s2} (nonavian amniotes),

or jointly:

(3) S_1 (Amniota) – S_2 (Mammalia) – S_3 (Aves) = G_{s3} ("Reptilia").

Thus is it possible to create gradistic "synapomorphy" by subtracting from an inclusive group two or more of its included subgroups. Such

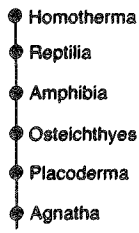


Figure 4.27. A gradistic tree derived from Huxley's diagram (figure 4.26).

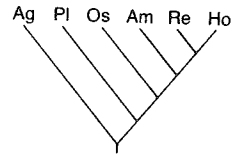


Figure 4.28. A gradogram derived from the gradistic tree of figure 4.27.

subgroups can also be combined in a "grade," which can be defined if the subgroups have characters in common:

(4) S_2 (Mammalia) + S_3 (Aves) = G_{s4} ("Homotherma").

Combining the subgroups produces another kind of gradistic "synapomorphy":

S_2 (Mammalia): a, b, c, d, e,
S_3 (Aves): d, e, f, g, h, i,
G_s ("Homotherma"): d, e

According to Huxley's concept in this case, the two subgroups together do not form a monophyletic group. The "Homotherma" are not, therefore, generally synapomorphic, and the defining characters of the group are parallelisms or convergences.

In another case, the combined subgroups might, however, form a monophyletic group, in which case the combined group will be generally synapomorphic. An example is furnished by Simpson's "Hominoid Grade," which is subdivided into the "Hominid Grade" and the "Pongid Grade" (figure 4.16):

(5) G_{s1} ("Hominoid Grade") = G_{s2}("Hominid Grade") + G_{s3} ("Pongid Grade").

The gradistic "synapomorphy" of the "Hominid Grade" is merely the general synapomorphy of the Hominidae (*Homo*):

(6) G_{s2} ("Hominid Grade") = S_2 (Hominidae).

The gradistic "synapomorphy" of the "Pongid Grade" is derived by comparison of two groups:

(7) S_1 (Hominoidea) – S_2 (Hominidae) = G_{s3} ("Pongid Grade").

It follows, therefore, that

(8) G_{s3} ("Pongid Grade") + S_2 (Hominidae) = S_1 (Hominoidea)
= G_{s1} ("Hominoid Grade").

Various types of gradistic "synapomorphy" may, therefore, be distinguished:

1. General: $G_s = S$
   Example: "Psychozoa" = *Homo*
2. Simple gradistic: $G_s = S_1 - S_2$
   Example: "Pongidae" = Hominoidea – Hominidae
3. Compound gradistic: $G_s = S_1 - S_2 - S_3$
   Example: "Reptilia" = Amniota – Mammalia – Aves
4. Complex gradistic:
   General: $G_{s1} = G_{s2} + G_{s3} = S$
   Example: "Hominoid Grade" = "Hominid Grade" + "Pongid Grade" = Hominoidea
   Convergent: $G_s = S_2 + S_3 \neq S$
   Example: "Homotherma" = Aves + Mammalia

One may compare the possibilities of prediction of these four types of gradistic "synapomorphy" (P_g) and the possibilities of prediction for general synapomorphy (P_s):

1. General: $P_g = P_s$
2. Simple gradistic: $P_g = P_{s1} - P_{s2}$
3. Compound gradistic: $P_g = P_{s1} - P_{s2} - P_{s3}$
4. Complex gradistic:
   General: $P_{g1} = P_{g2} + P_{g3} = P_s$
   Convergent: $P_g = P_{s2} + P_{s3} \neq P_s$

The only type of gradistic "prediction" that is conceivably different from that of general synapomorphy is that of convergent gradistic "synapomorphy." In this case, the "prediction" is limited to parallel or convergent characters.

The above analysis of gradistics is a preliminary attempt, not only to formulate gradistic principles, but to follow their implications. The anaylsis should not be considered definitive, but it does indicate severe weaknesses in gradistics, as exemplified in the writings of gradistic theorists. Either the weaknesses are misconstrued in the above analysis, or gradistic theory suffers from them.

In a recent discussion of grades, Schaefer (1976:4) asserts that "A

higher group is the evolutionary result not merely of an accumulation of character differences (a clade), but also represents a new level of organization (a grade)." Paraphrased, Schaefer's assertion is that all grades are monophyletic. This assertion runs counter to Huxley's and Simpson's usages, which provide for grades that are explicitly nonmonophyletic. Schaefer's assertion thereby exemplifies the presently confused state of gradistic theory.

Inasmuch as Simpson's classification of mammals has served here in numerous discussions, both of phyletic and gradistic taxonomy, and his comments have been extensively quoted, it is appropriate to call attention to the overall nature of his classification. It cannot be argued that Simpson's classification is predominantly gradistic, even though Simpson may have tended to view his taxa as grades from time to time. Most of his taxa have precedents in older classifications of mammals. Moreover, most of his taxa are predictive, and have proven themselves so on numerous occasions through history, even if Simpson may on occasion have argued in ways that might suggest otherwise.

Simpson's classification can generally be interpreted as cladistic classification in a phyletic context, and his classification is, perhaps, best viewed as such—within the limitations imposed on any one person's ability fully to grasp or to explain taxonomic endeavors when applied on so broad a scale.

CLASSIFICATION AND GENERAL CHARACTERS

Having explored phyletic, phenetic, and gradistic classifications in relation to their components, we now turn to the obvious question: is there a way to resolve the differences? In particular, can the differences be resolved in a way that might be satisfactory to phyleticists, to pheneticists, and to gradists? One might ask if there is any common ground at all that is shared by workers of all three persuasions. Perhaps all systematists might agree that they wish to be able to predict from the components of their classifications the maximum possible number of unknown characters, in both studied and yet unstudied taxa. The views of Sneath and Sokal on such predictions (with regard to aphids) have been noted above. And Mayr (1969) says that

one of the greatest assets of a sound classification is its predictive value. It permits extrapolation from known to previously unstudied characters. (p. 7)

If systematists can agree on this, the original question can be rephrased: is there a concept of "character" that might be satisfactory to all three schools? For if there is, the question of what kind of classification is best (i.e., is most successful at predicting unknown characters) becomes an empirical one, on which agreement should be attainable. This section will explore the possibility that the concept alternately called a general character, a synapomorphy, a homology-synapomorphy statement, or a defining character of a group, may provide such a resolution.

What, after all, is a taxonomic character? The conventional analysis indicates that a character consists of two or more different attributes (character states) found in two or more specimens that, despite their differences, can be considered alternate forms of the same thing (the character). A character is thus a theory, a theory that two attributes which appear different in some way are nonetheless the same (homologous). As such, a character is not empirically observable, and the hope of pheneticists to reduce taxonomy to mere empirical observation seems futile; to be able to consider the distance between two setae on the back of a mite a character, for example, one must hypothesize that given pairs of setae on two or more mite specimens, despite their different relative positions and interdistances, are nonetheless the *same* setae. But if alternate character states are in some sense the same, how can they be different? There seem to be only two possibilities: either one state is a modified form of the other, or both are modified forms of a third state. The "sameness" that constitutes the character (the homology) is thus the *unmodified* state, which all the organisms that show the character share, either in its original or in some modified form.

What, then, are the possibilities for prediction? Suppose that we have recognized a group (spiders) on the basis of seven character states believed unique to spiders, and that we find a new specimen about which we know only that it has one of these unique character states. Can we predict that the new specimen will have the other six character states as well? The new specimen might well have a different state of any or all of the six remaining characters, providing the different state represents a modified form of the character state found in all other spiders. Thus, given the information

Character A: State 1 (nonspiders)
State 2 (spiders),

we can predict that all new spiders will have state 2, but they might have instead a different character state:

Character A: State 1 (nonspiders)
State 2 (most spiders)
State 3 (some spiders),

if that different state is actually a further modification of state 2:

Character A: State 1 (nonspiders)
State 2 (spiders): Substate 1 (most spiders)
Substate 2 (some modified spiders).

In this situation, of course, state 2 is functioning as a character (a unit of "sameness"), not a character state; just like character A, it is divided into an original and a modified form. If we agree that for the character (the "sameness") to exist, the character states must be modifications, it is apparent that predictions cannot really function at the level of character states. Because of the ever-present possibility of further modifications, predictions will hold only for characters (i.e., only for sets of original plus modified character states).

In this sense, then, the concept of character states is misleading. To view character A as being "composed" of three character states:

Character A
---State 1--- ---State 2--- ---State 3---

implies that the character states are alternatives, when they are actually additions:

---State 1----------
---State 2----------
---State 3---

In this case, character A is actually equivalent to state 1 (i.e., it defines a group, all the members of which have state 1, either in its original or some modified form). States 2 and 3 are best regarded as new characters (B and C), for which the same provisions hold. Further, state 1 itself is a modification of some other character (state) and represents a restricted subset of some other, more general, character. Thus, all characters can

be seen as modifications (or restrictions) of other characters, and the groupings of character states within characters can be seen as arbitrarily delimited clusters of separate characters that are increasingly more restricted in generality (i.e., that form nested sets of increasingly modified versions of other characters).

The implications of this for prediction can be readily seen in a simple example involving tetrapod and nontetrapod vertebrates. Systematists have long been in agreement that the limbs of tetrapods are homologous with the fins of nontetrapod vertebrates ("fishes"). If we regard fins and limbs as alternative states of a character (paired appendages), we might thereby sort out vertebrates into two groups:

```
                    ---Vertebrata (paired appendages)---
---Pisces (fins)-------                    ---Tetrapoda (limbs)---
```

and vertebrates were indeed classified in this way for many years. However, one of these groups (Pisces) proved not to be maximally predictive, in that many characters were found that are shared uniquely by tetrapods and some (but not all) fishes. If, however, the limbs of tetrapods are not only homologous with, but are also modifications of fins, the problem disappears:

```
---Vertebrata (paired appendages: fins) ----------
      ---Tetrapoda (modified paired appendages: limbs) ----------
```

We can now predict that any vertebrate will have fins, and that only some vertebrates (tetrapods) will have modified fins. The phyleticist should presumably be happy, because the groups that are recognized *are* believed to be monophyletic. The pheneticist should presumably be happy, because all of the phenetic information (that tetrapod vertebrates have limbs and nontetrapod vertebrates do not) *is* included. The gradist should presumably be happy, because the available phenetic and phyletic data *are* combined in the classification. If so, then all systematists can agree that what they are seeking are synapomorphies: hypotheses that particular groups, defined by particular characters, are synapomorphic generally, with respect to all other organisms, and will prove to be so, no matter what other characters we may eventually discover or consider.

One possible source of difficulty here is that some types of properties

or attributes of organisms that have traditionally been used as characters by taxonomists may actually not be usable as defining characters of groups (even though they may still be useful for the practical task of identifying specimens). Size, for example, may fall into this category: we might say that a family of spiders is characterized by a total length of between 2 and 4 mm. But this is not a defining character of that family, for there are many other spiders, and many other organisms, with a total length of between 2 and 4 mm. Color might pose similar problems: we might say that a family of bugs is characterized by green wings, but many other insects have green wings. Of course, we may be able to show that bugs of this family have wings that are green because they contain a pigment not found in other organisms; if so, the pigment could be a defining character. Similarly, if a given pigment is found in two groups but we can show that the enzymatic pathways by which the pigment is synthesized are different in the two groups, then the two enzymatic pathways could each be defining characters. It is clear, at any rate, that the "best" groups, those that have proved maximally predictive through the years, have been explicitly based on general characters, like the spinnerets of spiders or mammary glands of mammals, which define groups (in the sense that any organism with spinnerets is a spider) that are generally synapomorphic with respect to all other organisms.

It would appear, then, that systematics in general consists of the search for defining characters of groups. Admittedly, the search seems to have been abandoned, on occasion, by persons who would search instead for overall phenetic similarity, or overall gradistic similarity. But what justification is there for abandoning the search for defining characters? Certainly we can make mistakes; we may fail to recognize that one character is a modified form of another, and thereby underestimate the generality of the latter one (plesiomorphy), or we may confuse two different characters as one (convergence), or we may mistakenly consider attributes (such as absences, or physical properties like total length and color) defining characters when they're not. But we do not need to fear such mistakes: should we make them, future research will reveal them quickly enough, through incongruences with other characters. Indeed, one might contend that the utility of cladograms is

precisely that: to point up incongruences and allow us to predict that mistakes have been made, and that more intensive study will reveal them.

CLASSIFICATION AND GENERAL CLADOGRAMS

The preceding section explored the possibility of a synthesis of phyletics, phenetics, and gradistics involving the concept of a general character. In this section, we will explore another possibility for synthesis based on the concept of a general cladogram, using as an example a recent paper by Michener (1977) on the classification of bees.

Briefly summarized, Michener's paper includes five cladograms and three classifications of 14 genera of allodapine bees. The cladograms include what Michener terms a "cladogram . . . developed using the methods of Hennig" (his figure 1), and four diagrams, each of which he terms a "cladogram on which are shown certain distance coefficients" (his figures 7–10). These are the five cladograms, which include one phylogram (redrawn here as figure 4.29.1) and four phenograms (figures 4.29.2–5). Of each of Michener's figures 7–10, he states that "nested rings indicate subjective levels of similarity." The nested rings are the basis of the four phenograms of figures 4.29.2–5: one based on "54 characters of mature larvae" (his figure 7; cf. figure 4.29.2); a second, on "46 characters of pupae" (his figure 8; cf. figure 4.29.3); a third, on "144 external characters of adults" (his figure 9; cf. figure 4.29.4); and a fourth, on "25 genital and associated characters of adult males" (his figure 10; cf. figure 4.29.5). The five cladograms constitute a study of 14 genera coded as follows: A, *Halterapis*. B, *Compsomelissa*. C, *Allodape*. D, *Braunsapis*. E, *Nasutapis*. F, *Allodapulodes*. G, *Dalloapula*. H, *Allodapula*. I, *Eucondylops*. J, *Exoneurella*. K, *Brevineura*. L, *Inquilina*. M, *Exoneura*. N, *Macrogalea*. The classifications include what Michener terms "different lists of genera," of which there are three, specified by the cladograms of figure 4.30: one based on "all variables so far analyzed" (figure 4.30.1); a second, on "larval variables only (Fig. 7)" (figure 4.30.2); and a third, on "adult external variables only (Fig. 9)" (figure 4.30.3).

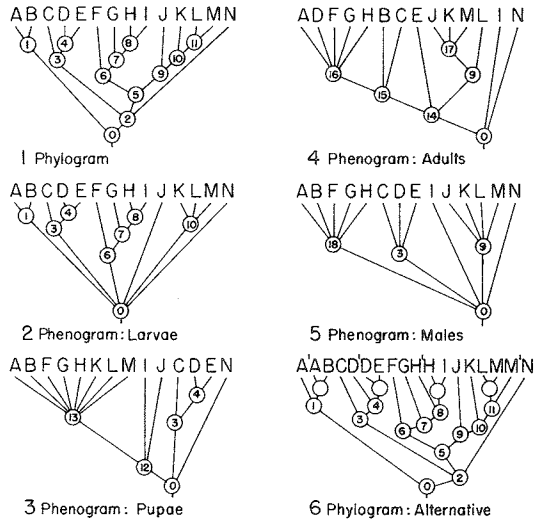


Figure 4.29. Cladograms based on information from Michener's (1977, figures 1, 7–10) study of allodapine bees (cladograms 1–5) and an alternative phylogram (cladogram 6).

There are 21 different components in the cladograms of figures 4.29 and 4.30. Twenty are listed in table 4.1, along with their distribution among the various cladograms. Component 0, defined as that branch point leading to all branch tips, has properties unlike components 1–20, for it appears in all cladograms of the 14 taxa. Components 1-20 need not appear in all cladograms, and, indeed, none of them does. For cladistic analysis, component 0 is irrelevant.

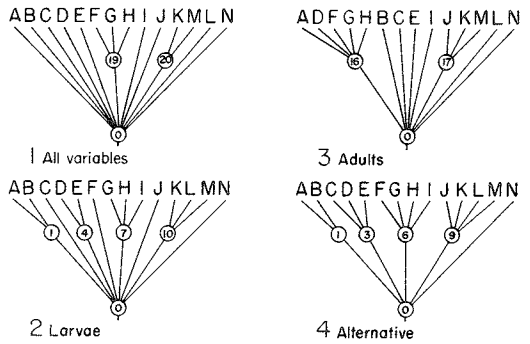


Figure 4.30. Cladograms based on classifications from Michener's (1977:51–52) study of allodapine bees (cladograms 1–3) and an alternative classification (cladogram 4).

The information of a component relates to the number of taxa in its definition. A branch point leading to two branch tips (terminal taxa, or terms) has an information content of one unit (one 3-taxon problem solved); a branch point leading to 12 branch tips, 11 units; and so on. The number of terms and the information of each of the 20 components are listed in table 4.1.

FUNDAMENTAL AND DERIVATIVE CLADOGRAMS

Two major types of cladograms may be distinguished: (1) fundamental cladograms, such as those of figure 4.29, which summarize data about the interrelationships of organisms; and (2) derivative cladograms (classifications), such as those of figure 4.30, which specify the cladistic aspect of hierarchical classifications. Systematic study of the interrelationships of the species of a given group generally results first in one or more fundamental cladogram, which is used as a basis for constructing one or more derivative cladogram. In a given study, the fundamental and derivative cladograms may agree or differ. If they agree, they agree because they include the same components. If they differ, they differ only because they include different components, or different sets of components. Of the cladograms in figures 4.29–4.30, each specifies a different set of components (table 4.1).

Figure 4.29 includes an additional fundamental cladogram (4.29.6), which is an alternative phylogram somewhat more detailed than Michener's (cf. figures 4.29.1, 4.29.6) obtained by splitting four of Michener's genera and creating four new taxa (A′, D′, H′, M′). Figure 4.30 includes an additional derivative cladogram (4.30.4) derived from the alternative phylogram by omitting the new taxa mentioned above. Omitting them makes for easier comparison among the different classifications.

INFORMATION CONTENT OF A CLADOGRAM

The information of a cladogram has two parts: the component information and the term information. The component information, which relates to the number of components in the definition of a cladogram, is one unit less than the total (N–1, 3-taxon problems solved). A cladogram defined by 12 components has a component information of 11 units; a cladogram defined by 8 components, 7 units; and so on. The component information of the cladograms is listed in table 4.1.

Table 4.1. Analysis of Cladistic Components of Cladograms, and of Their Information and Efficiency[a]

Components				*Fundamental Cladograms*					*Derivative Cladograms*			
					Phenograms							
Number	*Definition*	*Terms/ Information*	*Probability of Replication (%)*	*Phylogram* Fig. 4.29.1	*Larvae* Fig. 4.29.2	*Pupae* Fig. 4.29.3	*Adults* Fig. 4.29.4	*Males* Fig. 4.29.5	*All Variables* Fig. 4.30.1	*Larvae* Fig. 4.30.2	*Adults* Fig. 4.30.3	*Alternative* Fig. 4.30.4
1	AB	2/1	1.1	+	+	–	–	–	–	+	–	+
2	C-N	12/11	1.1	+	–	–	–	–	–	–	–	–
3	C-E	3/2	0.27	+	+	+	–	+	–	–	–	+
4	DE	2/1	1.1	+	+	+	–	–	–	+	–	–
5	F-M	8/7	0.033	+	–	–	–	–	–	–	–	–
6	F-I	4/3	0.10	+	+	–	–	–	–	–	–	+
7	G-I	3/2	0.27	+	+	–	–	–	–	+	–	–
8	HI	2/1	1.1	+	+	–	–	–	–	–	–	–
9	J-M	4/3	0.10	+	–	–	+	+	–	–	–	+
10	K-M	3/2	0.27	+	+	–	–	–	–	+	–	–
11	LM	2/1	1.1	+	–	–	–	–	–	–	–	–
12	ABFG-M	10/9	0.27	–	–	+	–	–	–	–	–	–
13	ABF-HK-M	8/7	0.033	–	–	+	–	–	–	–	–	–
14	A-HJ-M	12/11	1.1	–	–	–	+	–	–	–	–	–
15	A-DF-H	7/6	0.029	–	–	–	+	–	–	–	–	–
16	ADF-H	5/4	0.050	–	–	–	+	–	–	–	+	–
17	JKM	3/2	0.27	–	–	–	+	–	–	–	+	–
18	ABF-H	5/4	0.050	–	–	–	–	+	–	–	–	–
19	FGH	3/2	–	–	–	–	–	–	+	–	–	–
20	KM	2/1	–	–	–	–	–	–	+	–	–	–
Information, Component:				11	7	4	5	3	2	4	2	4
Information, Term:				34	12	19	26	9	3	6	6	9
Information, Total:				45	19	23	31	12	5	10	8	13
Efficiency, Component (%):[b]				–	–	–	–	–	0	57	40	36
Efficiency, Term (%):[b]				–	–	–	–	–	0	50	23	26
Efficiency, Total (%):[b]				–	–	–	–	–	0	53	26	29

[a]Component present (+); component absent (–).

[b]Efficiency for cladogram 4.30.4 is computed by comparison with cladogram 4.29.1.

The term information is the sum of the information of all informative components of a cladogram. Consider cladogram 4.29.1. It has 11 informative components (components other than component 0). Component 1, with two terms, has an information content of 1 unit; component 2, with 12 terms, 11 units; component 3, with 3 terms, 2 units; etc. For cladogram 4.29.1 the total term information is the sum of 1 + 11 + 2 etc., = 34 units. The term information of the cladograms is listed in table 4.1.

The component information plus term information is the total information, which is equal to the sum of the terms of all informative components. Consider cladogram 4.29.1. Its component information is 11 units; its term information is 34 units; its total information is 45 units. The total equals the sum of terms of all informative components: 2 + 12 + 3 etc., = 45 units. The total information of the cladograms is listed in table 4.1.

DERIVATIVE CLADOGRAMS AND EFFICIENCY

The three derivative cladograms (4.30.1–3) may be compared with the fundamental cladograms (4.29.1–6); two of the three invite comparison with particular fundamental cladograms (4.30.2 with 4.29.2, and 4.30.3 with 4.29.4).

Comparison 1 (4.30.2 and 4.29.2): The classification of larvae contains components 1, 4, 7, 10. The phenogram for larvae contains components 1, 3, 4, 6, 7, 8, 10. The classification may be said to be derived by accepting components 1, 4, 7, 10 and rejecting components 3, 6, 8.

Comparison 2 (4.30.3 and 4.29.4): The classification of adults contains components 16 and 17. The phenogram for adults contains components 9, 14, 15, 16, 17. The classification may be said to be derived by accepting components 16 and 17 and rejecting components 9, 14, 15.

Comparison 3 (4.30.1 and all fundamental cladograms): The classification based on all variables contains two components (19, 20), which are absent from all fundamental cladograms (4.29.1–6). The classification may be said to be derived by accepting components 19 and 20 (from unknown sources) and rejecting components 1–18.

Other comparisons are of course possible; they would reveal various agreements or the lack thereof.

Inasmuch as derivative cladograms invite comparison with particular fundamental cladograms, such that one might be said to be derived from the other, a given derivative cladogram may be said to be more or less efficient in representing a given fundamental cladogram. Component efficiency may be expressed as the fraction of derived to fundamental component information. Consider derivative cladogram 4.30.2 in relation to fundamental cladogram 4.29.2: four of seven units of component information are represented; the derivative cladogram may be said to have a component efficiency of 4/7, or 57 percent. Term efficiency may be expressed as the fraction of derived to fundamental term information. Consider again cladograms 4.30.2 and 4.29.2: 6 of 12 units of term information are represented; the derivative cladogram may be said to have a term efficiency of 50 percent. Total efficiency may be expressed as the fraction of derived to fundamental total information, 53 percent. Efficiency (component, term, and total) of the derivative cladograms is listed in table 4.1.

CHAOS VERSUS ORDER

Consider derivative cladogram 4.30.2 (the classification of larvae). All of its components are represented in fundamental cladogram 4.29.2 (the phenogram for larvae); all of its components are represented also in fundamental cladogram 4.29.1 (the phylogram). One may ask: what is the nature of the classification? Is it purely phenetic, purely phyletic, or both? It would seem to be both.

Consider derivative cladogram 4.30.3 (the classification of adults). Its components are represented only in fundamental cladogram 4.29.4 (the phenogram for adults). What is the nature of the classification? It would seem to be purely phenetic.

Consider derivative cladogram 4.30.1 (the classification based on all variables). Its components are represented in no fundamental cladogram. What is the nature of the classification? It would seem to have no nature that can be specified, except to say that it is derived from unknown sources.

That Michener presented three classifications, all differently derived, might be considered curious or unusual. One may ask, why three and three only? Or alternatively, why not just one? Confronted with five different fundamental cladograms, one might assume that each tells a

different story of its own: that nature is chaotic; evolution, discordant; convergence, common; etc. This assumption might lead to the idea that the task of systematics is to impose order upon a chaotic nature (in which case many classifications would be justifiable). An alternative assumption is that each cladogram tells the same, or part of the same, story: that nature is ordered; that discordant evolution and convergence are mere artifacts of human perception. This assumption might lead to the idea that the task of systematics is to discover and record nature's order and to embody it in (a single) classification. Thus, different philosophies of systematics are possible, as exemplified in the discussion of artificial vs. natural systems—a discussion some 200 years old.

To some extent, one may try to avoid the pitfalls of metaphysics by a judicious choice of questions. For example, rather than assume that nature is chaotic (and opt for some artificial system), or that nature is ordered (and ponder the one and only natural system), one may ask how chaos or order might be discovered, granting the possibility that each might exist. For chaos, an immediate (but facile) answer is possible, with reference to the diversity of fundamental cladograms that might be at hand (figure 4.29). For order, in contrast, an immediate answer is problematical. The question, however, can be restated: given a diversity of fundamental cladograms, what single story might they all be telling?

The question could be answered if diverse fundamental cladograms can be combined to form a single general cladogram. There might seem to be various approaches to this objective. One might assume, for example, that the phylogram (figure 4.29.1), if it has been derived by combining various data according to some phyletic clustering technique, is *the* general cladogram, and that any departure from it is discordance, convergence, etc. Alternatively, one might assume that some phenogram (figures 4.29.2–5), if it has been derived by combining various data according to some phenetic clustering technique, is *the* general cladogram. One might question, however, whether such assumptions are satisfactory at a general level.

Again, one may turn toward a judicious choice of questions. Rather than assume that the general cladogram must be phyletic, or phenetic, or gradistic, or whatever, one may ask how a general cladogram might be discovered, given the possibility that it exists? What follows is an attempt to answer this question.

COMPONENT RELATIONS

One component is more or less like another, such that any two components share one of four possible relations:

Exclusion:

components are combinable and exclusive if their definitions are different and nonoverlapping. Example: component 1, with the definition AB, and component 4, with the definition DE.

Inclusion:

components are combinable and inclusive if their definitions are different and overlapping, such that one is included in the other. Example: component 3, with the definition CDE, and component 4, with the definition DE. For each inclusive relation one component is a whole (3), and the other (4) is a part.

Noncombinability:

components are noncombinable if their definitions are different and overlapping, such that neither is completely included in the other. Example: component 11, with the definition LM, and component 17, with the definition JKM.

Replication:

components are replicated if their definitions are the same, in which case there are not two components, but merely one that is replicated.

These four relations may alternatively be viewed as two:

Combinability (Inclusion, Exclusion, and Replication):

components are combinable if they can be parts of the same cladogram.

Noncombinability:

components are noncombinable if they cannot be parts of the same cladogram.

Replicated components are significant because the probability of replication for any given component, due to chance alone, is small. In this case (Michener's 14 genera of bees) the probability is 1 percent or less (table 4.1). Of interest is the fact that the probability is not a function of the fundamental cladogram in which a component appears, but rather a function of the number of terms in the component's definition. Consider, for example, component 1, with two terms. It is one of 91 possible 2-term components that might result from clustering 14 terminal taxa. Hence its probability of replication, due to chance alone, is about 1 percent.

In the fundamental cladograms (table 4.2), there are eight 2-term

Table 4.2. Probabilities (P) of Replication of Components (C) in Fundamental Cladograms [a]

Number of Terms	*Number of Possible Components*	*Fundamental Cladograms* 4.29.1 C	4.29.1 P:%	4.29.2 C	4.29.2 P:%	4.29.3 C	4.29.3 P:%	4.29.4 C	4.29.4 P:%	4.29.5 C	4.29.5 P:%	*P for components of same number of terms, %*	*P cumulative %*
		1	–	1	4.40								
2	91	4	–	4	4.55	4	4.40					3.90×10^{-4}	3.90×10^{-4}
		8	–	8	4.44								
		11	–										
		3	–	3	3.75	3	1.29			3	1.10		
3	364	7	–	7	4.08							8.37×10^{-7}	3.27×10^{-12}
		10	–	10	3.85			17	–				
		6	–	6	16.7							5.73×10^{-4}	1.87×10^{-17}
4	1001	9	–					9	0.59	9	0.59		
5	2002							16	–	18	–	–	10^{-17}
7	3432							15	–			–	10^{-17}
8	3003	5	–			13	–					–	10^{-17}
10	1001					12	–					–	10^{-17}
12	91	2	–					14	–			–	10^{-17}

[a]For a component that replicates a previously resolved component, the probability is that of replication due to chance alone, under the assumption that the components are resolved one at a time in the order listed for each cladogram. The probability fractions for replicates are: cladogram 4.29.2 (4/91, 3/66, 2/45, 3/80, 2/49, 1/26, 2/12); 4.29.3 (4/91, 3/232); 4.29.4 (2/341); 4.29.5 (4/364, 2/341). A component that is resolved for the first time has 0 probability of replicating a previously resolved component.

components, of which four are replicates ($P = 10^{-4}$ percent); there are nine 3-term components, of which five are replicates ($P = 10^{-7}$ percent); and there are five 4-term components, of which three are replicates ($P = 10^{-4}$ percent). One may doubt that these replicates are due to chance alone ($P = 10^{-17}$ percent). There are three different 2-term components that are replicated; three different 3-term components; and two different 4-term components. The replicated components may be combined in one cladogram (figures 4.31.1–2). One may doubt that this combination is due to chance alone ($P = 10^{-17}$ percent).

The cladogram specified by the replicates may be considered a first step toward a general cladogram. Inspection of the definitions of components (table 4.1) shows that several are noncombinable with the replicates (cladogram 4.31.2): components 13, 14, 15, 16, 17, 18. There is no reason to doubt that these components are due to chance alone. Of the remaining components (2, 5, 11, 12), each is combinable (either exclusively or inclusively) with all replicates, but components 2 and 12 are mutually noncombinable. There is no reason to doubt that these components are due to chance alone. Nevertheless, four categories of components may be recognized: (1) replicates (1, 3, 4, 6, 7, 8, 9, 10); (2) components noncombinable with replicates (13, 14, 15, 16, 17, 18); (3) components combinable with replicates and with each other (5, 11); (4) components individually combinable with replicates, but not with each other (2, 12). Only category (3) is combinable with the replicates in a single cladogram. Hence, categories (1) and (3) may be combined in a general cladogram (figure 4.32), which may be considered a best estimate of one, and the only apparent, cladistic parameter.

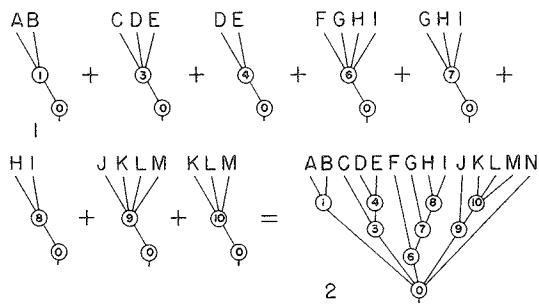


Figure 4.31. Replicated components (1) and their resulting cladogram (2).

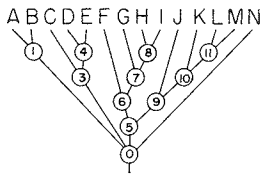


Figure 4.32. The general cladogram derived from the fundamental cladograms of figure 4.29.

Consider cladogram 4.31.2 (replicates) and cladogram 4.32 (general cladogram). Category (3) contributes two additional components (5 and 11)—25 percent of the replicates. What can be said on behalf of the added components? Not much beyond the statement that they are combinable with the replicates and with each other—a statement of less significance than, and a statement of which the significance depends upon, the phenomenon of improbable replication. Component 5 is one of 15 possible components that could be formed by component 6 (or component 9) in exclusive relation with components 1 and 3 and term N. Component 11 is one of three possible components in inclusive relation with component 10. Hence, there are $15 \times 3 = 45$ possible combinations. And there is only 1 chance in 45 that components 5 and 11 might accurately estimate the cladistic parameter, under the assumption that the replicates are an accurate estimation. That the probability is on the order of 2 percent, rather than 10^{-3} percent, is due wholly to the improbable pattern of replication, which determines that there are 45, rather than 400,000, possible combinations.

The general cladogram (figure 4.32) may be compared with the fundamental cladograms (figure 4.29.1–6). Its components are all included in the phylogram (figure 4.29.1), and it might, therefore, be termed purely "phyletic." Most of its components are included also in the phenogram for larvae (figure 4.29.2), and at least one of its components appears in each of the other phenograms (figures 4.29.3–5), and it might, therefore, also be termed somewhat "phenetic." In what follows, the components of the general cladogram are termed "true components"; those noncombinable with the general cladogram (category 2), "false components"; those mutually noncombinable (category 4), "ambiguous components."

Given a general cladogram with its "true components," it may be

compared with fundamental and derivative cladograms (table 4.3), and their information content may be broken down into three categories: true, false, ambiguous (by "true" and "false" we mean only agreement or disagreement with the general cladogram). For fundamental cladogram 4.29.1, which includes 11 components, 10 components are true, and one is ambiguous (component 2). One-half of the ambiguity may be allocated to the true category, resulting in 10.5 true units. For fundamental cladogram 4.29.3, which includes four components, two components are true; one is false; and one, ambiguous. The false may be subtracted from the true, and the ambiguous allocated as above, resulting in 1.5 true units. General component information for all cladograms is listed in table 4.3. General term information and general total information may be treated in a similar way. They are listed in table 4.3.

Efficiency is calculable when there is a cladogram that can serve as a standard for comparison. General efficiency is calculable for both fundamental and derivative cladograms, with the general cladogram serving as a standard (10 component-units + 23 term-units = 33 units of information). Consider fundamental cladogram 4.29.1, with 10.5 component-units and 28.5 term-units, for a total of 39 units. The general component efficiency is 10.5/10, or 105 percent; and the general term efficiency is 28.5/23, or 124 percent. General total efficiency is 39/33, or 118 percent. Consider fundamental cladogram 4.29.3, with 1.5 component-units and 0.5 term-units. Its general component efficiency is 1.5/10, or 15 percent. Its general term efficiency is 0.5/23, or 2 percent. And its general total efficiency is 2/33, or 6 percent. In cladograms with ambiguity, general efficiency may exceed 100 percent—indicating that the cladograms are, in some sense, too efficient. In cladograms with false information, both general information and general efficiency may achieve negative values (table 4.3).

OPTIMUM CLASSIFICATION

What is the optimum, or best, kind of classification? A variety of answers is possible, in accordance with the variety of possible taxonomic philosophies. According to one such philosophy, there is no optimum at all. The assumption that there is an optimum defines a philosophy that we call cladistics—a modern version of an old tradition in systematics,

Table 4.3. Analysis of General Information and General Efficiency of Cladograms

	Component Information					*Term Information*					*Total C + T True*	*Efficiency (%)*		
	Total	*Units That Are:*			*Total*	*Total*	*Units That Are:*			*Total*				
Cladograms	*Units*	*True*	*False*	*Ambiguous*	*True*	*Units*	*True*	*False*	*Ambiguous*	*True*		*Component*	*Term*	*Total*
4.29.1	11	10	0	1	10.5	34	23	0	11	28.5	39	105	124	118
4.29.2	7	7	0	0	7	12	12	0	0	12	19	70	52	58
4.29.3	4	2	1	1	1.5	19	3	7	9	0.5	2	15	2	6
4.29.4	5	1	4	0	−3	26	3	23	0	−20	−23	−30	−87	−70
4.29.5	3	2	1	0	1	9	5	4	0	1	2	10	4	6
4.30.1	2	0	2	0	−2	3	0	3	0	−3	−5	−20	−13	−15
4.30.2	4	4	0	0	4	6	6	0	0	6	10	40	26	30
4.30.3	2	0	2	0	−2	6	0	6	0	−6	−8	−20	−26	−24
4.30.4	4	4	0	0	4	9	9	0	0	9	13	40	39	39
General	10	10	0	0	10	23	23	0	0	23	33	100	100	100

namely the theory and practice of methods to resolve *the* natural system, or classification.

Discussion of optimality has generated a dispute between adherents of phyletic, phenetic, and gradistic philosophies, all of which are cladistic—under the assumption that any optimal classification has a cladistic aspect that may be represented by a cladogram, which is true for all attempts at hierarchical classification. Thus, there is a generally optimal classification—of which the cladistic aspect is represented in a general cladogram.

It is entirely possible, of course, that some methods are more efficient than others in estimating a general cladogram. To judge from Michener's bee study, his phyletic methods are more efficient than his phenetic methods. But his phenetic methods are not without value. They contribute replications and apparently generate random variation (i.e., noncombinable components) that may be discriminated as such and set aside. Without methods that generate random variation, there would be no need for cladistic analysis and synthesis, for their results would be intuitively self-evident in advance (which is near the truth anyway, for much of the general cladogram can be immediately apprehended by anyone inspecting the fundamental cladograms with an eye for the replications that they contain; in short, cladistic analysis and synthesis can operate at an intuitive level).

Michener (1977) provided three classifications of bees, one based on all variables, one based on larvae, and one based on external features of adults. He did not say so explicitly, but we assume that the classification based on all variables was offered by him as a general classification. The three classifications, plus an alternative one (figure 4.30.4) are analyzed in table 4.3. They differ widely in their information and efficiency. What are the conclusions to be drawn?

The basic question is about optimal classification: is classification to reflect a parameter? If yes, then one may judge one classification better than another in accordance with its agreement with some standard estimate of that parameter. If no, then one may not. To date, various parameters have been suggested: phyletic, phenetic, gradistic, etc., all of which are cladistic in the sense that each may be represented by a cladogram. We suggest the parameter estimated by the general cladogram—the cladistic parameter.

There is no necessary correlation between the cladistic parameter and any one discipline, such as phyletics, phenetics, or gradistics. In the case of Michener's bees, the general cladogram agrees better with Michener's phylogram than with three of his four phenograms, but it agrees better with one phenogram than with the other three. The agreement between estimates of the cladistic parameter and phyletics may prove general, at least in theory, but who knows? In another case, phyletic methods, applied ineptly but with the best of intentions, might generate pure noise; and phenetic methods, with a careful analysis of characters, pure signal.

GENERAL PATTERN

Traditionally conceived, systematics is the search for general pattern in the living world. During the history of systematics, pattern has been resolved piecemeal, and its resolution has never been claimed to be complete. Discovery of pattern has depended upon sampling, and confidence in the results has been a function of prediction and replication. Traditionally, sample size has been small.

With the advent of phenetic methods, stress was placed on large samples, in the hope that their results would be imperturbable with further sampling, and in the hope that the results would estimate a parametric "overall similarity." The recommendation was made that further samples be pooled with the original data, with the consequence that prediction dissolves into nonfalsifiability, which may be the Achilles' heel of purely phenetic philosophy. Hence, the time is ripe for consideration of small samples, the extent to which elements of cladistic pattern (components) are replicated therein, and the probability of their occurrence due to chance alone. These are the traditional virtues of systematics.

The obvious weakness of phenetics is its assumption of parametric "overall similarity"—the reason for the recommendation for pooling further samples with the original data (presumably resulting in a more reliable estimate of "overall similarity"). The usefulness of the idea of "overall similarity" would seem to consist only in its implication that, given estimates of the "overall similarities" for the species of a certain group (a phenogram), the estimates specify a cladogram, i.e., an estimate of the cladistic parameter. But there is no reason to believe that

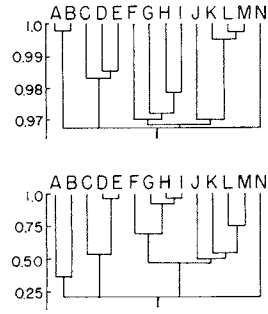


Figure 4.33. Two hypothetical phenograms that differ in their statements about levels of "overall similarity" but specify the same components.

either purported estimate depends for its existence upon the other. Even if there is no parametric overall similarity, there may yet be a cladistic parameter. Consider, for example, the hypothetical phenograms of figure 4.33. Each specifies estimates of the overall similarities for 14 taxa of a certain group. The estimates of the two phenograms differ in all particulars, but the cladistic aspect is the same for both.

Of interest is a comparison between the efficiency of the fundamental cladograms and the number of characters upon which each cladogram is based:

Cladogram	Characters	Efficiency
4.29.1	about 30	118 percent
4.29.2	54	58 percent
4.29.3	46	6 percent
4.29.4	144	−70 percent
4.29.5	25	6 percent

There seems to be no positive correlation, but there might be a negative one, with the implication that, with large numbers of characters processed by phenetic techniques, virtually all resolved components might be due to chance alone—a possibility enhanced by the findings of Mickevich (1978).

Suppose that a general cladogram is derived (figure 4.32). What does it mean? It specifies a nonrandom pattern of interrelationships. One may ask, what is the cause of the nonrandom pattern? Two possibilities come to mind: (1) the pattern is a methodological artifact; (2) the pattern reflects (and, therefore, estimates) an aspect (parameter) of the real

world that is method-independent. Given these two possibilities, how might the truth be ascertained? Consider possibility (1): if the pattern is artifact, different methods, to the extent that they are truly independent, should produce different (randomly noncombinable) patterns. Consider possibility (2): if the pattern is method-independent, different methods, even if they are truly independent, should produce the same nonrandom pattern, or combinable parts of the same pattern, in addition to some random variation.

There is already available enough information to assert that different clustering methods produce fundamental cladograms that are to some extent different and to some extent the same. If the differences are artifact, and the samenesses method-independent, then the problem is only distinguishing signal from noise. Deriving a general cladogram merely specifies what is signal, given a number of fundamental cladograms that are to some extent the same, and to some extent different. As here conceived, its derivation amounts to asking, and answering in the affirmative and in detail, this question: given some fundamental cladograms, do they exhibit a nonrandom pattern of cladistic components?

One may ask, in addition, how this question might best be explored and answered. Suppose that a certain clustering method is applied to different data sets in order to generate various fundamental cladograms for the species of a certain group, one cladogram for each data set. A general cladogram might be derived. It could be an artifact of the clustering method. To explore the possible bias of a single clustering method, different methods might be applied, each method to a different data set, or all methods to the same data set. Another general cladogram might be derived. What might be expected in the way of agreement between the two general cladograms? The present study suggests that both general cladograms would estimate the same cladistic parameter.

Suppose that a general cladogram is derived (figure 4.32). What then? Is it artifact or knowledge of the real world? The bolder, and nontrivial, hypothesis is the latter. How might this hypothesis be falsified in a given case? The answer seems clear: by deriving a second, and independent, general cladogram from a different, and independent, set of fundamental cladograms. The prediction is that the two general cladograms, even though independently derived, will estimate the same cladistic

parameter. The prediction is a null hypothesis: the two general cladograms will not significantly differ. The null hypothesis may be tested by sampling.

Suppose that the sampling is done, and that, in one's judgment, the two general cladograms differ significantly (we pass over the problem of what might constitute a significant difference). There seem to be four possibilities for an alternative: (1) there are two different cladistic parameters, each estimated by one general cladogram; (2) there is one cladistic parameter, estimated by one, or the other, or neither, of the general cladograms; (3) there is one cladistic parameter, estimated by the sameness (replication and combinability), if any, exhibited jointly by the two general cladograms; (4) there is no cladistic parameter, or parameters; and all pattern is artifact.

Possibility (1) seems purely ad hoc: "I still believe that there is one cladistic parameter (estimated by my first general cladogram), but now I believe that there is another." Possibility (2) also seems purely ad hoc: "I still believe that there is one cladistic parameter, but I have different estimates of it; I know not which to choose, but my first estimate might still be correct." Possibility (3) seems partly ad hoc, but is, nevertheless, interesting: "I still believe that there is one cladistic parameter, but I have revised my estimate of it; the revised estimate might prove more reliable." Possibility (4) seems trivial: "I no longer believe that there is a cladistic parameter, because my prediction was unfulfilled; and my hypothesis, falsified."

Possibility (3) seems unrejectable as an alternative, if there is some replication of components in the two general cladograms. The replicates, and components combinable with them, may be specified in a second-order general cladogram, i.e., a unique estimate of the cladistic parameter. Therefore, some replication between different general cladograms implies that possibility (3) is unrejectable, and that possibility (4) is merely false. We conclude that, even if the null hypothesis is falsified, the only alternatives are either partly ad hoc or trivial. Of the ad hoc possibilities, only (3) seems interesting.

We have asserted that possibility (4) seems trivial. It is a statement that replication of results (if any) is artifact, and noncombinability is an estimate of the real world. As such, it contradicts one of the premises of

the falsification argument: namely, that the two general cladograms are, or should be, independently derived. If independence is assumed, and significant replication is the result, the result is *not* artifact. Significant artifact can mean *only* nonindependence in the derivation of the two general cladograms. Hence, possibility (4) is a misstatement. It purports to say something about the world, but in reality contradicts the premise of independence.

What then of the initial hypothesis: that a general cladogram is knowledge of the real world? Is it falsifiable? We conclude that it is not in a general sense, but that it is in a particular sense. In the general sense, all that a person can do is to search, but if one fails to find, the failure is no falsification. In the particular sense, a person may find one pattern rather than another.

What are the implications? The initial hypothesis can only be presumed. Once presumed, it may lead to particular null hypotheses that may be tested and, perhaps, falsified, and an alternative may be entertained. If this is the only implication, what is there in the way of a general theory of systematics? The answer seems clear: the theory of general cladograms. As here conceived, the theory includes phenetics, phyletics, gradistics, and any other theory that might be proposed, if its applications lead to results that might be rendered as hierarchically branching diagrams.

At present it is difficult to evaluate the completeness of the theory of general cladograms. Two areas of theoretical problems are evident: (1) levels of significance of difference between two or more general cladograms; (2) criteria of independence in derivation of general cladograms. We do not consider either area particularly important in a practical sense; such a judgment would presuppose that systematic data are necessarily so noisy in themselves that only mathematical treatment can isolate a nonrandom pattern. The history of systematics belies that presupposition. Systematic data are simply not in themselves necessarily noisy. So more practical significance may arise from a theoretical consideration of systematic data (characters). If some data sets are noisy, why so? Could it be that they include "characters" that are not general characters? Are there remedies? Could an explicit search for general characters suffice? Only time will tell.

EPILOGUE

A NOTE ON TERMINOLOGY

Persons may think it strange to use words beginning with "clado-" in a sense divorced from evolution and phylogeny. Their attention may be called to the definition of the term: "A combining form from Gr. *klados*, a shoot, branch, signifying branched or having branches." Persons may also doubt that cladistic analysis can be divorced from evolution and phylogeny. Their attention may be called to the numerous successful homology statements made by pre-evolutionary systematists, and to the fact that every homology statement implies one or more synapomorphy statements.

To state that a cladogram is a synapomorphy scheme invites the rejoinder that a cladogram must, therefore, be a phyletic concept. Not so, for by "synapomorphy" we mean "defining character" of an inclusive taxon. True, all defining characters, in the phyletic context, may be assumed to be evolutionary novelties. But making that assumption does not render it automatically true; nor does it change the characters, the observations on which the characters are based, or the structure of the branching diagram that expresses the general sense of the characters: i.e., that there exist certain inclusive taxa (components 1, 2, . . .) that have defining characters. That the taxa may be assumed to be "monophyletic" (derived from a single ancestral species) does not change the structure of the branching diagram, but merely adds the phyletic context of interpretation; hence the diagram becomes a phylogram. It is still atemporal in the sense that it is necessarily nonreticulate and that its branch points are mistakenly construed as speciation events. To equate "synapomorphy" and "defining character" invites the rejoinder that a branching diagram specifying only "polythetic" inclusive taxa is no cladogram, because no defining characters are present. Not so. Even if the inclusive taxa are assumed to lack defining characters (because none is yet known), that assumption does not change the fact that the branching diagram expresses the general sense of defining characters even in their absence: i.e., "if there were some defining characters, these are the inclusive taxa (components 1, 2, . . .) that the characters would define." In short, finding defining characters for each of the "polythetic" taxa would not change the

structure of the branching diagram, but merely add replications of components.

A NOTE ON HISTORY

Rosa (1918) and Hennig (1950) may be considered among the many independent inventors of cladograms, at least in the phyletic context. Rosa's work is not widely known, and an excerpt of it is translated here, to illustrate the trend of his thought (even though Rosa's figure [Fig. 4.34] in this case is properly a tree, not a cladogram):

. . . to the following scheme [Fig. 4.34], which represents the connections of affinity between the species of a group, such as they would be if the species were the result of dichotomous speciation. . . . Having before us 32 terminal species, represented by the black dots above, we would be able to make four groups (such as genera): A, B, C, D.

It is clear that, even without paleontological knowledge of the connections, an adequate knowledge of the morphology of these species would suffice to indicate that genus B is more closely related to genus A than to genus C; and that, before grouping the 32 species into four genera, it would be necessary to group them

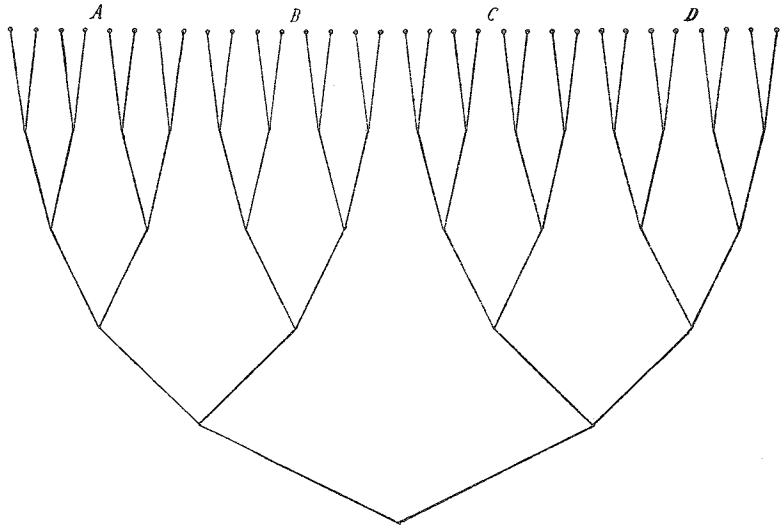


Figure 4.34. A cladogram (phylogram) showing the hypothetical relationships of 32 species of four groups (A, B, C, D). After Rosa (1918), figure on p. 138; also Rosa (1931), figure on p. 174.

into two "supergenera" or subfamilies: AB and CD. And within each genus it would be possible also to recognize subgenera and even smaller groups of more closely related species.

If this scheme corresponds to reality, one may conclude that the distinction between groups of equal taxonomic rank cannot be arbitrary; and, also, that the distinctions are not caused by gaps in the system, gaps produced by extinctions. Even in the absence of extinction, the distinctions would be quite clear. And while it might be arbitrary to consider group A a genus, rather than to consider group AB a genus, no good systematist would ever combine some species of group C with AB, and the other species of group C with D. (Rosa 1918: 137–38, 1931:174–75, translated)

Mitchell (1901) and Hennig (1950) may be considered among the many independent inventors of the concepts of synapomorphy and of classification as a nested set of synapomorphies, at least in the phyletic context. Mitchell's work is not widely known, and an excerpt of it is presented here, to illustrate the trend of his thought:

In the description of the structure of an organ or anatomical part as it occurs in a large series of different forms, it becomes necessary from simple convenience to attempt some kind of valuation according to which the series of facts shall fall into definitely-named groups. When there is attempted the difficult passage from descriptive anatomy to morphology, it is necessary that the valuation and nomenclature should be in relation to the theory of descent with modification. I assume that birds were monophyletic in origin, and that the existing forms have branched out in diverging directions from the ancestral group. The members of this ancestral group, at the stage when they first might have been called birds, possessed an heritage of characters and tendencies, and these characters and tendencies have undergone modifications different in amount and nature in the different groups. The first business is to come to a decision as precise as possible as to the ground-plan, or archetype, the most ancestral condition of the structures under consideration. . . . I propose to call such a condition "archecentric," implying that it represents a primitive, ancestral, or central condition, from which the conditions to be found in the other cases have diverged. It is obvious that the possession by two or more groups of birds of a character in its archecentric form cannot be an indication in itself that these groups are more closely related to one another than they are to groups possessing the character in another form; for if the diagnosis of archecentricity be correct, the condition has been present in all birds, and may be retained by any. . . .

When the ancestral condition is modified, it may be regarded as having moved outwards along some radius from the archecentric position. Such modified conditions I propose to call "apocentric." Again, it must be obvious that the mere apocentricity of a character can be no guide to the affinities of its possessor. . . . Before deciding as to the value of eutaxy [a putatively apocentric character of bird wings] in a natural classification, it would be necessary to

decide whether the modification of the archecentric condition were a simple change that we might expect to occur in independent cases, or if it involved intricate and precisely combined anatomical changes that we could not expect to occur twice independently. In fact, having come to the conclusion that a character is apocentric, we must pass on to consideration of the problem whether or no the apocentricity be *uniradial* or *multiradial* [synapomorphic or convergent]. . . . Similar and common multiradial apocentricities, from which no direct argument of kinship is to be drawn, are to be found in conditions depending on the degeneration of a structure. . . . In the case of the alimentary canal, it is easy to set apart certain modifications as directly adaptive, and as therefore of no value when the character of an organ is being considered as an indication of the natural affinities of its possessor. For the apocentric modifications in question have been produced in different mammals as well as in different birds, and hence in birds these modifications must be multiradial and no indication of relationship. . . .

A complex apocentric modification of a kind that we cannot well expect to be repeated independently, and that may be designated as uniradial, must be the most certain guide to affinity. It happens frequently that such a modification forms a new centre around which new diverging modifications are produced. Such a centre I propose to call a "Metacentre," borrowing a convenient term from physics. It is obvious that the condition of a character, archecentric so far as the whole group of birds is concerned, is metacentric with regard to the common stock of birds and reptiles, and that the transformation of an apocentric character into a metacentre is simply an event in the general process of divergent evolution. I justify the nomenclature which I am proposing largely because it brings the valuation and classification of characters into line with our conception of the general processes of evolution. . . .

I trust that the ideas underlying this attempt at the valuation and nomenclature of characters, so far from being novel, are merely a codification of criteria in common employment among naturalists. I find, however, that such a codification was necessary when I tried to arrange systematically the modifications of the characters with which this memoir deals. So far as I have used them in my own work, I have found them illuminating, and I offer them in the conviction that the rigorous discipline which their use entails would prove of general utility. (Mitchell 1901:178–82)

That anyone in particular could be recognized as the inventor of cladistic analysis is moot, for all of its formal properties are not yet clearly established. It is doubtful that either Mitchell, Rosa, or Hennig is the inventor of "cladistics" as a philosophy of classification, for all, or almost all, systematists seem to be, and seem ever to have been, "cladists." At least cladistic elements are discernible in systematic work of whatever age. However, Hennig's diagrams, as portrayed in his books and in the scientific papers of various European systematists (Brundin,

Schlee et al.), did provide a focus of general interest and an impetus to apply Hennig's type of diagram to the systematic study of various groups of organisms, both fossil and recent. And there is little doubt that Hennig's diagrams in particular, because of the widespread attention paid to them, have been a progressive factor beneficial to systematics generally. But the argument over "cladistics" has not centered on the diagram as much as on the "problem" of classification. In reality, no real "problem" ever existed. The argument developed, so it now seems, because of misapprehension on the part of the critics, due to their inability to understand the statements of the exponents, which were not, it is true, framed in their widest generality. The exponents can, perhaps, be forgiven for not realizing at once the full generality of cladistics and for not stating it clearly. It may prove more difficult to forgive certain of the critics—those who repeatedly failed to apprehend any generality at all.

A NOTE ON PHILOSOPHY

Since the advent of the so-called New Systematics, it has become popular to deprecate as "essentialistic" or "typological" the notions that species (and hence groups of them) have defining characters, and that it is the business of systematics to find them (see, for example, Mayr 1957; Hull 1965; Ghiselin 1969). The rationale for this deprecation seems to be that if evolution occurs, the characters of species (and hence groups) may change in the future; therefore, species and groups cannot be permanently characterized by means of a single character or set of characters such that the character or set is necessary and sufficient for membership in the species or group. The argument seems to rest on the misleading use of character states: it assumes that when a species is modified, and acquires a new apomorphic character (state), it no longer has, or is no longer recognizable as having, the original plesiomorphic character (state). In other words, according to this argument, we cannot use characters (such as fins) to define groups (such as Vertebrata), because some members of those groups (such as tetrapods) may acquire apomorphies (such as limbs). If one accepts the validity of ontogeny or outgroup comparison (i.e., parsimony) or any other possible test of hypotheses about character transformation, the argument is obviated. In this sense, systematists always have been, are, will be, and should be, typologists.