

TAXONOMIC CHARACTERS

Taxonomic characters provide the evidence from which relationship between taxa is inferred. The more characters two taxa have in common and the more similar they appear to the taxonomist, the more closely related they are considered to be (Chapter 6). In taxonomic practice, however, it is actually more productive to look for differences between taxa. The definition of a taxonomic character is based on this experience: *A taxonomic character is any attribute by which a member of a taxon differs or may differ from a member of another taxon.*

Any difference between two individuals is a character, but not all characters are useful for taxonomic purposes. Knowing where useful characters are to be found and establishing their specific value is perhaps the most important skill of a systematist, requiring not only a good theoretical knowledge but experience as well.

Defining a taxonomic character as "any attribute of an organism" is incorrect. Differences between phena (Chapter 4) are not taxonomic characters. Therefore, features by which individuals of the same population differ—that is, differences between sexes, age classes, and other polymorphisms—are not taxonomic characters. However, differences between corresponding phena of different species are taxonomic characters.

CHARACTERS AND SIGNIFIERS

The word *character* is not the exclusive property of systematics. The letters in a type alphabet are called characters, and the moral attitudes of a

person constitute that person's character. The word's meaning in systematics is derived from one of its most common uses: *A character is a property, attribute, or feature that distinguishes one thing, individual, or group from another.* Black feathers are a character of Australian swans, and white feathers are a character of European swans. This use of the word predates Linnaeus.

In the late 1950s, numerical taxonomists encountered a difficulty with the word. To be handled by a computer, all characters must be assembled into a table called a data matrix (Chapter 11). Typically, the columns of the table are for taxa, and each row of cells contains the numerical codes for characters. The problem was what to call the rows.

To solve this problem, these workers unfortunately transferred the meaning of the term *character* from the difference between taxa (e.g., black versus white feathers in swans) to the structure that varies (e.g., feather color) in order to have a term to designate the rows in their tabulations. The datum in each cell, traditionally a character, came to be called a *character state*. As explained by Sokal and Michener (1958a:1410):

Our use of the word "character" will require some elaboration. In its commonest taxonomic usage, a character is any feature of one kind of organism that differentiates it from another kind. Thus the red abdomen of one bee is a character distinguishing it from another bee with the abdomen black. In this paper we use the word in a second connotation only; that is, as a feature which varies from one kind of organism to another. Now, to use the above example, abdominal color is the character, which occurs in two "states" or alternatives, red and black.

This proposal had the unfortunate result that the term *character* is now used in taxonomy in two very different senses. In computer taxonomy it is used in the transferred sense of Sokal and Michener, while in ordinary taxonomic discussions it is used in the classical sense of the word. This equivocation has caused considerable confusion in the taxonomic literature.

Problems caused by the dual use of this word are frequently found in studies done by numerical taxonomists. For example, in phenetics (Chapters 8 and 11), some formulas used to measure difference between taxa produce results that also reflect how many actual characters are used in a study. This makes it difficult to compare a study using few characters with a study using many. Pheneticists suggested that each similarity value be divided by the number of "characters" in each study to find an average distance. What they intended was to divide by the number of distinct characters, but the correction factor actually employed in their formulas and computer programs was the number of variables. The result

of this confusion of terms was that the newly made and supposedly comparable phenograms were nothing of the sort. Numerous errors of this type can be found in the recent numerical literature.

To end this confusion Ashlock (1985) proposed restoring the term *character* to its traditional meaning and introducing a new term, the *signifier*, for a feature that varies from one organism to another. The feather, then, would be the signifier (sign bearer), and "feather white" and "feather black" would be the character. As desirable as such a restoration of the traditional meaning of the word *character* would be, the transferred meaning has been so firmly established after 30 years that all our consultants strongly advised against the adoption of the term *signifier*. Thus *character*, particularly in regard to numerical methods, refers to a variable feature, and *character state* is defined as an attribute by which a member of a taxon differs from a member of another taxon.

KINDS OF CHARACTERS

Almost any attribute of an organism may be useful as a taxonomic character if it differs from the equivalent feature in members of another taxon. However, proper classifying work is possible only when adequate material from many species is simultaneously available for comparison. Museums provide this opportunity, and this is why the taxonomist prefers characters that can be easily observed in preserved specimens (e.g., morphological characters) (Table 7-1).

In each group of organisms, whether birds, butterflies, sea urchins, or snails, different taxonomic characters exist. It is part of the training of a taxonomist to become familiar with the characters that are most useful in the particular taxon in which that taxonomist plans to specialize. Monographs and handbooks usually give detailed descriptions of the characters used. In his revision of the North African scorpions, for instance, Vachon (1952) devoted 27 pages to a detailed description and illustration of the taxonomic characters of that group.

Morphological Characters

Features of external morphology vary according to kinds of animals. They range from such superficial features as plumage and pelage characters of birds and mammals through scale counts of fishes and reptiles to the highly conservative and phylogenetically significant sutures and sclerites of the arthropod body. Internal anatomy provides many taxonomic characters in practically all groups of higher animals. The extent to which such characters are used routinely varies from group to group, generally in inverse proportion to the abundance and usefulness of easily

TABLE 7-1
KINDS OF TAXONOMIC CHARACTERS

- 1 Morphological characters
 - a General external morphology
 - b Special structures (e.g., genitalia)
 - c Internal morphology (anatomy)
 - d Embryology
 - e Karyology and other cytological differences
- 2 Physiological characters
 - a Metabolic factors
 - b Body secretions
 - c Genic sterility factors
- 3 Molecular characters
 - a Immunological distance
 - b Electrophoretic differences
 - c Amino acid sequences of proteins
 - d DNA hybridization
 - e DNA and RNA sequences
 - f Restriction endonuclease analyses
 - g Other molecular differences
- 4 Behavioral characters *behavior*
 - a Courtship and other ethological isolating mechanisms
 - b Other behavior patterns
- 5 Ecological characters
 - a Habitats and hosts
 - b Food
 - c Seasonal variations
 - d Parasites
 - e Host reactions
- 6 Geographic characters
 - a General biogeographic distribution patterns
 - b Sympatric-allopatric relationship of populations

observed external characters. In the preparation of mammal skins, the skull (with teeth) is routinely preserved and used in classification, while reptiles, amphibians, and fish are normally preserved in alcohol and are always available for dissection. On the whole, aspects of internal anatomy supply characters for the classification of the higher taxa more often than they do for discrimination at the species level. Fossils consist almost entirely of preserved hard parts; in the case of Mesozoic mammals, for instance, they consist largely of teeth.

Even in this traditional area great advances have been made in recent decades. Descriptions have become more detailed and better standardized. Careful microscopic analysis of lower invertebrates has revealed an abundance of characters even in such seemingly nondescript forms as nematodes. The development of new silver impregnation techniques has

revealed a wealth of characters even among protozoans, particularly ciliates. Scanning electron microscopy has added enormously to our knowledge of the morphology of insects, arachnids, and other small organisms.

New organs and structures are steadily added to those which show taxonomically important differences. The spermatozoa of many taxa, for instance, have a highly peculiar and specific morphology and may serve as useful indicators of relationship.

Hard Parts and the Work of Animals It would be senseless to worry about whether the items referred to as hard parts (shells, external skeletons, etc.) are morphological, physiological, or behavioral characters. Much of the classification of invertebrates is based on characters of exoskeletons and shells. Similarly, among the protozoans, tests, shells, thecal plates, cysts, and other hard parts are vital in the classification of foraminiferans, radiolarians, testaceous rhizopods, flagellates, and other organisms. The orientation types of calcite crystals in the skeletons of echinoderms agree well with their classification in families and orders (Raup 1962).

The description of many taxa of dinosaurs has been based on fossil tracks. In the classification of gall insects, the gall sometimes yields as good a clue to relationship as do the insects themselves. The form of the mines is an important taxonomic character in mining insects, and it even sheds light on their history since these mines are sometimes well preserved in fossil leaves (Figure 7-1). However, since 1930 it has not been permissible to base the name of new species exclusively "on the work of an animal" [Articles 12b (8) and 23f (iii) of the International Code of Zoological Nomenclature].

Coloration Color pattern and other aspects of coloration are among the most easily recognized and thus most convenient characters in certain groups of animals. Every species of bird can be recognized by its coloration except for a few genera with sibling species (e.g., *Collocalia*, *Empidonax*). The same is true of certain reef fishes and butterflies. Even where coloration is not completely diagnostic, it often helps narrow down drastically the number of species to be considered. In groups in which subspecies are recognized routinely, such as mammals, birds, butterflies, and some wasps, color again plays an important role; many subspecies are identified entirely on the basis of coloration.

The quality of color is not easy to describe in words. In original revisionary work, therefore, it is preferable not to rely on descriptions but to base one's judgment on the comparison of specimens if possible. There are, however, various ways in which greater precision can be given to color determination and description (Chapter 12).



FIGURE 7-1 Diagnostic mine patterns caused by six species of leaf miners of the genus *Phytomyza* on the leaves of *Angelica* (50, 51) and *Aquilegia* (54). The letters a, b, and c refer to different species of *Phytomyza* on the same host plant. (From Hering 1957.)

Genital Structures For reasons that are not yet fully understood (Mayr 1963:103; Eberhard 1985), the genitalia of many animals, particularly arthropods, not only show a great deal of structural detail but are also highly species-specific (Figure 7-2). Because they are three-dimensional structures, genitalia have to be carefully prepared to be strictly comparable. In many groups of insects and spiders genital structures are more important for species diagnosis than is any other character. However, even here it has been found that a single species may have a good deal of variation or that two related species may have

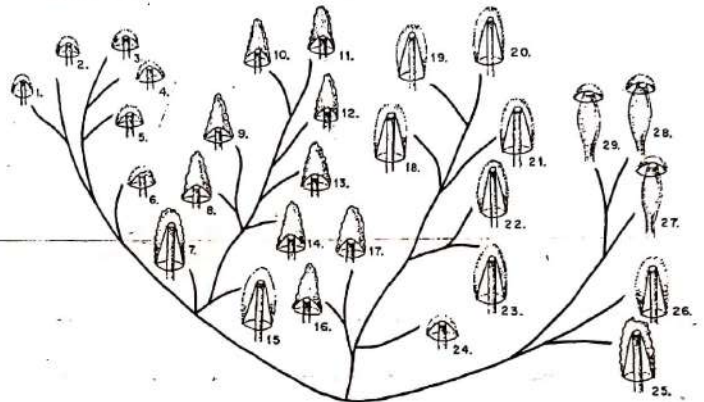


FIGURE 7-2 Types of spermathecae in the *Drosophila repleta* group placed on a phylogenetic tree constructed on the basis of chromosomal characters. (After Throckmorton 1962.)

indistinguishable structures. In most vertebrates the genitalia are soft, but the gonopodium of some fishes, the hemipenis of snakes, and the baculum of mammals may supply good taxonomic information.

Other Characters Morphological characters of adult specimens are still used more frequently than are any others, but they are supplemented to an increasing extent by other characters, as listed and discussed below (Blair 1962; Munroe 1960). This is particularly true for "difficult" species, genera, and families in which the evidence from morphology has been equivocal or contradictory. The increasing utilization of new characters is justified because (1) morphology reflects only part of the genotype and may not reflect genetic relationship accurately, (2) morphology in certain taxa does not supply sufficient characters, and (3) any character may be misleading because of special adaptations. The introduction of new kinds of taxonomic characters has been one feature of the so-called new systematics. These characters (molecules, chromosomes, behavior, etc.) supplement but do not displace the use of morphological characters.

A particularly important reason for the utilization of new characters is that they serve as a check on the conventional morphological characters. When discrepancies occur between a classification that is based on morphology and one that is not, still other sets of taxonomic characters must be used. Fortunately, the newer characters usually confirm classifica-

pericentric inversions, translocations, Robertsonian changes, sex-determining mechanisms, the presence of diffuse or concentrated heterochromatin, and the presence of supernumerary chromosomes (White 1973). The fine structure of chromosomes can be brought out by appropriate staining methods that show G bands, C bands, or Q bands. Not only do these banding patterns reveal a wealth of detail, they are also highly conservative in some groups, convincingly documenting relationship (Baker, Qumsieh, and Hood 1987). Bickham and Carr (1983) have demonstrated the importance of chromosomal information for the determination of turtle phylogeny. Robertsonian changes (fusions and fissions) are not necessarily unique events in phylogeny. Even this chromosomal phenomenon is subject to homoplasy.

The phylogeny of horses, asses, and zebras (genus *Equus*) has been greatly clarified by means of a comparison of their chromosomes. The dendrogram of the karyotypes agrees remarkably well with the dendrogram based on morphology. What no one understands, however, is why there are such drastic numerical differences among closest relatives in this taxon. The chromosomal number (2n) ranges from 66 in *Equus przewalskyi* to 32 in *E. zebra*. *E. przewalskyi* has 40 acrocentric and 24 metacentric autosomes (and a pair of sex chromosomes), while *E. hemionus onager* has only 8 acrocentrics and 46 metacentrics. Fusions and translocations must have been rampant within this genus. By contrast, in the camel family the two old world species and the four South American species (llama, etc.) have 74 very similar chromosomes, documenting great chromosomal conservatism. In numerous orders and families of animals, for instance, bats and turtles, the study of chromosomes has led to a considerable improvement in our understanding of relationship. The greatest value of chromosomal information is that it can serve as a check on morphological, molecular, and other types of information.

Chromosomes are particularly useful on two different levels. At the lower level, they aid in the comparison of closely related species. Sibling species are often far more different in chromosomes than they are in external morphology (Mayr 1963, Chapter 3). In higher taxa, chromosomal patterns may be of extreme importance in establishing phyletic lines. Most chromosomal changes are unique events; once the new pattern is established, it is characteristic of all descendants of the ancestral population. Changes in sex determination; rearrangements of chromosomes and centromeres through fusions, fissions, or translocations; and the acquisition of supernumeraries often supply unequivocal clues to relationship. For instance, the similarity in the spermatogenesis of Mallophaga and that of Anoplura (true lice) strongly supports the belief in a close relationship of these taxa. The giant salivary gland chromosomes of certain

larval dipterans permit the construction of very precise dendrograms of related species.

Polyploidy is rare in animals compared with plants, but there are numerous other ways in which an increase or decrease in chromosome number may occur. Curiously, the most frequent evolutionary trend in many groups is from high to low chromosome number through chromosomal fusion. Even though the chromosomes represent the genetic material, it is not true that the amount of chromosomal change reflects the amount of genetic change. Close relatives may show considerable rearrangement; indeed, many species are polymorphic for various types of chromosomal rearrangements. However, cases are known in which a considerable degree of genic change is not reflected or is only lightly reflected in the chromosomal pattern, as in some Hawaiian *Drosophila* (Carson 1967).

Physiological Characters

This group of characters is hard to define. All structures are the product of growth, that is, of physiological processes, and are thus ultimately physiological characters. Also, physiology is regulated by enzymes and other macromolecules and thus is not separable from biochemical characters. Physiological characters generally include growth constants, temperature tolerances, and the various other processes studied by the comparative physiologist. Species differences are abundant in these characters, but since they are not present in preserved material and their study usually requires special apparatus, they are rarely used by the taxonomist. Some representative cases are discussed by Mayr (1963:60-65), and fuller treatments are given in textbooks of comparative physiology (Prosser and Brown 1973; Schmidt-Nielsen 1979).

Molecular Characters

The major molecular inventions were made by the earliest living organisms. Even the most primitive prokaryotes have on the whole the same kinds of macromolecules and metabolic processes that are found in the highest animals and plants. Still, there is enormous specificity at every taxonomic level, and this specificity is being increasingly exploited by taxonomists.

Serology provided the earliest widely used method of comparing proteins. This method is based on the principle that the proteins of one organism will show a stronger antibody reaction to the proteins of a closely related organism than they will to those of a more distantly related or-

ganism. Unfortunately, this method has various technical difficulties. Though used for more than 60 years, it has not contributed as much to a clarification of otherwise ambiguous cases as had been hoped. A summary of some of the achievements of this method can be found in Leone (1964). As a result of improvements in these techniques, there has recently been a revival of interest in the quantitative study of antigenic reactions. An extension of this work is the method of microcomplement fixation (Champion et al. 1974). The study of blood-group genes (immunogenetics) has shed light on relationships among species of pigeons (Irwin 1947 and later authors of his school) and has been used in the study of primates.

Much recent work has been devoted to developing a taxonomy of specific chemical components and macromolecules. The early technique of diffusion chromatography used capillary action to separate molecules on filter paper. In this method a sample (e.g., a body fluid or macerated tissue) is spotted on the paper, which is dipped in a solvent. Movement of the solvent carries different molecules at different rates, so that different samples produce different patterns of spots that represent various components of the samples. Diffusion chromatography has largely been replaced by electrophoresis, which uses an electrical potential instead of capillary action and hydrolyzed starch or polyacrylamide instead of filter paper. Improved resolution has been obtained by processing samples a second time at 90 degrees to the first run to produce a two-dimensional separation. Most components are colorless and must be stained to show differences or must be viewed under ultraviolet light, which may be absorbed or cause fluorescence. Improvements are constantly being introduced, and the newest literature must be consulted for the latest techniques and instrumentation (Brewer 1970; Harris and Hopkinson 1976).

A large number of new molecular techniques have been introduced since the early days of serology and electrophoresis. They make use of proteins, nuclear DNA, mitochondrial DNA, and ribosomal nucleic acids. A study of the restriction site mapping of ribosomal DNA showed the value of this method in establishing relationships in the genus *Rana* (Hillis and Davis 1986). A comparison of 18S ribosomal RNA permitted a provisional reclassification of the invertebrate phyla (Field et al. 1988), but subsequent findings led to considerable modifications. Ribosomal RNA has been particularly useful for an understanding of the relationship of the lower eukaryotes and the various branches of the prokaryotes.

The molecular method that provides the greatest amount of information is the sequencing of proteins and nucleic acids. The number of differences in the base pairs of two nucleic acids reflects the number of mutational steps that separate them (except for transposons and other insertions). By comparing the sequence of base pairs of two homologous

DNAs or RNAs, one can determine the number of mutational differences (Goodman 1982). The same technique can be applied to amino acid replacements in proteins, but this provides much less information. The complete amino acid sequence is now known for many macromolecules (Dayhoff 1973, 1976, 1979), and the degree of relationship of two species can be inferred from the amount of difference. The close relationship of humans and chimpanzees, for instance, is indicated by the fact that their hemoglobins and fibrinopeptides are still identical (King and Wilson 1975). Different macromolecules change at different rates—histones very slowly, cytochrome C quite slowly, globins at an average rate, and fibrinopeptides very rapidly.

A given macromolecule usually changes in a particular phyletic lineage at a rather constant rate. This observation led Zuckerkandl and Pauling (1962) to propose the idea of a molecular clock. The clock is calibrated by estimating the age of certain branching points between higher taxa with the help of the fossil record or biogeographic evidence and then calculating from these dates and the known difference in the amino acids the average number of amino acid replacements per 10 million years. The resulting time frame permits the construction of dendrograms that depict the inferred phylogeny (Fitch and Margoliash 1967).

Use of molecular evolution permits inferences on the probable time of the splitting of phyletic lines and sometimes even on the geography of the splitting event. For instance, the immunological distance of the hemolymph proteins of the Hawaiian drosophilids from those of their North American relatives is consistent with a colonization of the islands about 40 million years ago, that is, before any of the currently existing islands had emerged (the older islands are now submerged sea mounts) (Beverley and Wilson 1985). This confirms the previous reconstruction of the history of the Hawaiian biota by Zimmermann (1948).

The assumption of a completely constant molecular clock is, of course, unrealistic (Britten 1986). The same molecule may evolve at quite different rates in different phyletic lines. The less affected by selection certain molecular changes are, the more likely it is that they will occur at a constant rate; this seems to be the case with many enzyme genes, as revealed by electrophoresis (Kimura 1983). Regulatory genes, introns, transposons, and gene families may experience considerable deviations from a molecular clock constancy. The molecular clock thus is only a first approximation, and its results must be fine-tuned through the use of additional methods.

Chronologies can also sometimes be established through an analysis of particularly stable molecular changes. For instance, in the echinoderm phylum a certain gene regulatory mechanism (alpha subtype histone maternal mtRNA) originated in the late Triassic and is now found in all the

orders of echinoids that originated after that date (about 200 million years ago) (Raff et al. 1984). In doing such calculations one must always remember not only that different molecules may evolve at different rates but also that within a lineage the rate may change drastically. For instance, nucleotide substitutions for seven mammalian proteins seem to have occurred in the primates at a distinctly slower rate than was the case in most other organisms (Fitch 1976). It is now known that several molecules change as much as five times as fast in some phyletic lineages as they do in others.

The ideal of the pheneticists has always been to determine the total overall similarity of two taxa. This is what the technique of DNA hybridization attempts to achieve at the molecular level (Sibley and Ahlquist 1983, 1985). The method is fairly complex. The DNA is freed of all protein and RNA, and then the purified DNA is sheared into fragments with an average length of 500 base pairs. The DNA is then melted at about 100°C so that the two strands of double-stranded DNA separate. Then the repeated sequences are removed so that only the pieces of a single-copy DNA are left. When the DNA of two species is mixed (one DNA is labeled with a radioactive isotope) and the mixture is gradually cooled, homologous single-stranded pieces of the two DNAs will pair while the nonmatching pieces will remain in solution. This indicates what percentage of the DNA pairs and what percentage has become sufficiently different during evolution to pair no longer. A delta (Δ) value can be determined which reflects the degree of difference. (This is a greatly abbreviated account of a considerably more elaborate procedure.) Sibley at first postulated the rate of DNA evolution (i.e., nucleotide substitution) to be the same in all lineages of birds and stated that it took about 5 million years of divergence for the genomes of two species to become different in 1 percent of their base pairs. On the basis of these assumptions he constructed a dendrogram of all avian families. The discovery of considerable inequalities of rates has necessitated certain modifications (Britten 1986). Since Sibley's dendrogram is based on a phenetic method, it is really a phenogram, even though it is quite different from Sokal's overall morphological similarity. Mitochondrial DNA is of considerable help in the comparison of populations of a single species, for such DNA is inherited directly from the maternal parent and is not subject to sexual recombination, as is nuclear DNA (Awise and Lansman 1983).

Different molecular techniques are useful at different taxonomic levels. The study of mitochondrial DNA and that of electrophoretically discovered enzyme differences are most useful for the comparison of populations and closely related species (Barrowclough 1983; Patton and Yang 1977; Selander and Whittam 1983), while protein and nucleic acid

sequencing, immunological methods, and DNA hybridization are most informative in the study of distantly related species and higher taxa, that is, in the construction of phylogenetic trees. One of the first molecular trees, that of Fitch and Margoliash (1967), was so close to the traditional phylogenetic tree of the vertebrates that it made taxonomists aware of the importance of molecular methods. Unfortunately, the methods that are most precise and informative, such as protein and DNA sequencing, are also the most time-consuming.

The thoroughly documented demonstration by Davis (1964), based on morphological characters, that the giant panda is a bear and is not related to the raccoons was doubted by a few scientists until Sarich and O'Brien confirmed the validity of Davis's conclusion by using several molecular methods (Mayr 1986). In a similar manner the findings of comparative anatomists have been confirmed again and again in recent years by molecular methods. However, there are exceptions. The cheetah (*Aconyx*) has always been considered by morphologists to be the most aberrant of all the cats, but molecular studies have revealed that it actually is a rather close relative of the lion-tiger group, with other genera of the cat family being far more distant (Collier and O'Brien 1985).

The study of structural characters has revealed that each organ or organ system may have its own specific rate of evolutionary change (mosaic evolution) (Chapter 6). Much evidence indicates that this principle is equally valid for molecular characters. A comparison of the human being (*Homo*) with the chimpanzee (*Pan*) shows, for instance, that there has been little evolutionary divergence in the hemoglobins and some other molecules since they branched from each other, even though the hominid line has since entered an entirely new adaptive zone (Figure 7-3). When one uses taxonomic characters to draw inferences about classification, one must always balance the potentially conflicting information derived from different character domains. One must also understand the subtle difference between evolutionary phenomena at the molecular level and the organismic level (Mayr 1964; Simpson 1964).

Molecular taxonomy permits the analysis of a wholly new set of characters that are seemingly independent of more traditional characters (Barrowclough 1985). While molecular characters are subject to the same problems of convergence, parallelism, and reversal that any character set may have, it is highly unlikely that morphological and molecular characters will be affected in the same manner. Where the molecular characters are superior in the extraordinary detail they can supply. The genome of a mammal consists of about 2 billion nucleotide base pairs. In many cases where the morphological evidence is ambiguous, molecular methods have produced totally unequivocal conclusions. The study of evolving

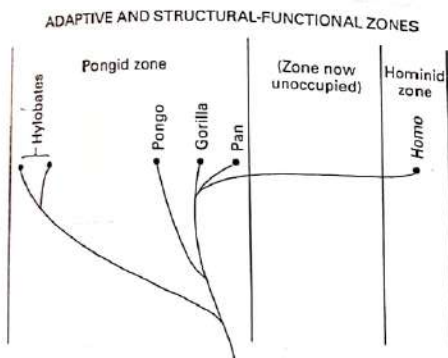


FIGURE 7-3
Recency of descent versus degree of adaptive divergence. Dendrogram of inferred affinities of recent hominoids in relation to their radiation into adaptive and structural-functional zones. (After Simpson 1963.)

molecules superimposed on the background of classical taxonomy is bound to reveal discrepancies and inaccuracies which will lead to improvements in classification (Hillis 1987).

Molecular methods are not a panacea. In almost every case (particularly among more distant relatives) where taxa were classified with the help of different molecular methods, different classifications were arrived at. This is not surprising in view of the universality of mosaic evolution. Such conflicts pinpoint the branches in a phylogeny that are in need of further analysis. Instead of concentrating on such trouble spots, some molecular biologists have wasted time and valuable resources by confirming totally uncontroversial findings of taxonomists.

The most important aspect of some of the molecular methods is that they do not determine relationship by the presence or absence of shared characters but permit one to calculate the distance (degree of difference) between two taxa. The special numerical methods required for such calculations are described in Chapter 11. These methods are so new and there are so many competing ones that it is still uncertain which the best methods are and in what circumstances a distance determination is superior to a character analysis.

The increasing need for suitable material for taxonomic analysis has induced many museums to establish molecular collections, that is, col-

lections of material suitable for molecular analysis. Such material consists of whole specimens, tissues, or body fluids preserved in such a way that they are suitable for the study of proteins, nucleic acids, or other molecular constituents or for chromosome analysis. For information on methods for the preservation and use of such material, see Chapter 13.

Behavior

Behavior is undoubtedly one of the most important sources of taxonomic characters. Indeed, behavioral characters are often clearly superior to morphological characters in the study of closely related species, particularly sibling species (Mayr 1963). However, there are two major technical drawbacks. Behavior cannot be studied in preserved material, and it is intermittent even in a living animal. Some types of behavior occur only during the breeding season; others, only during part of the 24-hour period. The comparative study of the behavior of related species has become an autonomous discipline known as comparative ethology. It has already made major contributions to the improvement of classifications of birds, bees, wasps, orthopterans, frogs, fishes, and other groups.

The reason for the importance of behavior is obvious. Behavioral characteristics are the most important isolating mechanisms in most animals, and new adaptations are often initiated by changes in behavior. The rapidly expanding literature on behavioral systematics has in part been summarized in a number of reviews, including those of Mayr (1958), Alexander (1962), and Wickler (1967). Exemplary studies include those of Evans (1957, 1966) on the digger wasps (Sphecidae), Spieth (1952) on the genus *Drosophila*, Tinbergen (1959) and Moynihan (1959) on gulls (Laridae), Eickwort and Sakagami (1979) on halictid bees, and Gordl and DeBach (1978) on chalcid wasps. Flash patterns are species-specific in most genera of fireflies (Figure 7-4) and have been used by systematists to unmask sibling species (Barber 1951; Lloyd 1983). However, in the genus *Photinus* males may mimic the signal of sympatric species of other genera (*Photinus*, *Pyroctomena*, etc.). When one encounters several flash patterns in the repertory of a single mimicking species (Lloyd 1985), one must not conclude that one has discovered several sibling species.

A great technical advance in the study of behavior has been the development of devices for accurate sound recording and the translation of sounds into graphic patterns (the sonograph (Figure 7-5)). More than 40 species of North American crickets were either discovered or rediscovered by B. B. Fulton and his followers as a result of a careful analysis of their songs. The classification of species in several avian genera (for instance, *Myiarchus*, *Empidonax*, *Tyrannus*) has been greatly helped by an analysis of sound recordings. A comparison of the calls of frogs and

Not study
at my lab

study
of Animal
behavior

comparative
eth.

Comparative
Ethology

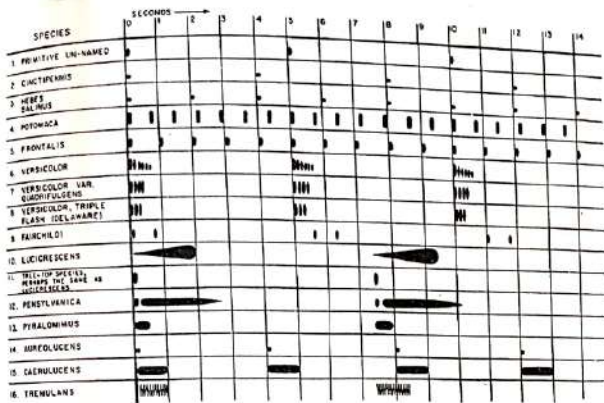


FIGURE 7-4 Patterns of light flashes in North American fireflies (*Photuris*). Height and length of the marks indicate intensity and pattern of the flashes. (From Barber 1951.)

toads not only has led to the discovery of previously unrecognized sibling species but also has shed light on the relationship between previously established species. Important studies of comparative sound analysis in anurans were done by Barrio, Blair, Bogert, Littlejohn, Main, and Mecham. The acoustics of animal behavior has been summarized in a number of recent volumes (Tavolga and Lanyon 1960; Busnel 1963; Sebeok 1977; Claridge 1985). The importance of bird song in avian systematics has been reviewed by Payne (1986).

In addition to courtship and acoustic behavior, various other kinds of behavioral elements have taxonomic value. For example, the pattern of the webbing constructed by various mites and caterpillars may be used at various levels in the classification. The two bee genera *Anthidium* and *Dianthidium* were slow to be recognized on morphological grounds, yet all known species of *Anthidium* construct nests from cottony plant fibers while those of *Dianthidium* construct nests from resinous plant exudations and sand or small pebbles.

The use of extraneous materials in the construction of nests or of larval or pupal cases provides characters at various levels in the classification of caddisworms and bagworms. The egg cases of praying mantids have a species-specific form.

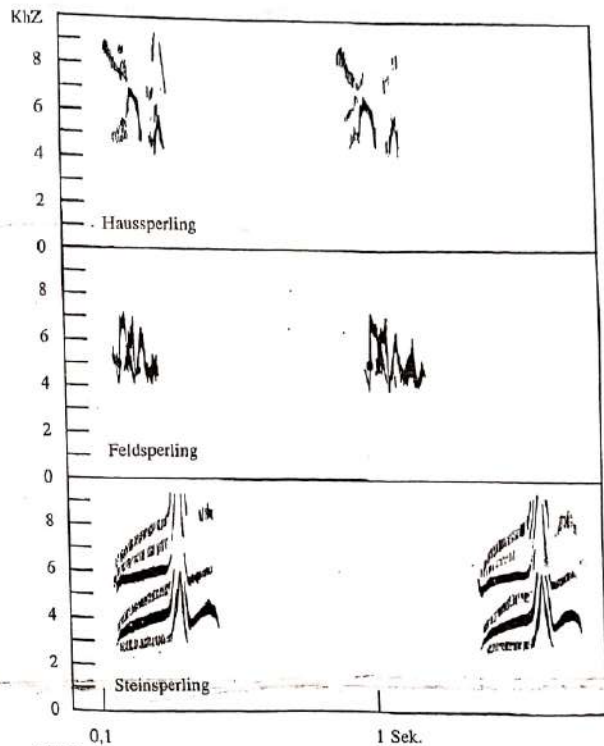


FIGURE 7-5 Different vocalizations of related species of sparrows. (After Thielcke 1964.)

Behavior patterns that are characteristic of higher taxa are far more rare. Examples are the use of mud in nest building by barn swallows and crag martins (*Hirundo*), certain "comfort movements" (scratching, stretching, bathing, etc.) in birds (McKinnéy 1965), and grooming movements in insects. Attention up to now has been directed so strongly at the

comparison of closely related species that the diagnostic value of behavior patterns at the level of higher taxa has gone largely unexplored. However, Eberhard (1982) showed that web structure is diagnostic for certain genera or even higher taxa of spiders; this permitted the construction of a cladogram of the orb-weaving behavior of the araneoid spiders. Behavior cladograms have also been published for other groups, for instance, the nest architecture of halictine bees (Eickwort and Sakagami 1979).

Ecological Characters

It is now well established that every species has its own niche in nature, tending to differ from its nearest relatives in food preference, habitat selection, breeding season, tolerance to various physical factors, altitudinal distribution, resistance to predators, competitors, and pathogens; and other ecological factors. When two closely related species coexist in the same general area, they avoid fatal competition by means of these species-specific niche characteristics (principle of competitive exclusion; see Mayr 1963, Chapter 4). A number of sibling species were discovered as a result of discrepancies in food preference (host specificity)—for example, the apple and blueberry maggot—or habitat preference (Mayr 1963, Chapter 3). Many aspects of the life cycle, such as life span, fecundity, and length or time of breeding season, may be different in closely related species (Mayr 1963).

Niche specificity is quite pronounced even in species that are not particularly substrate-specific, such as birds, mammals, and mollusks. Kohn (1959) found that every species of the genus *Conus* in the Hawaiian Islands differs ecologically from related species. Two sibling species (*ebraeus* and *chaldaeus*) feed on nereid polychaetes, but of 199 *ebraeus*, 136 contained nereid species *a* and none contained species *b*, while of 106 *chaldaeus*, 5 contained species *a* and 98 contained species *b*. The larvae of *Drosophila mulleri* and *D. aldrichi* live simultaneously in the decaying pulp of the fruits of the cactus *Opuntia lindheimeri*. However, the two species differ markedly in their preference for certain yeasts and bacteria (Wagner 1944).

Niche specialization is even more pronounced in animals that are substrate-specific, including host-specific plant feeders among insects and mites and host-specific parasites. Some of this information can be found in recent books on coevolution (Nitecki 1982; Futuyma and Slatkin 1983). There is also the excellent treatment by Dethier (1947), who emphasized the sensory aspects of host selection. Many new species of insects were discovered by comparing populations of the "same" species occurring on different plant hosts. Some enthusiasts, however, carried this principle too far and made any occurrence on a different host an ex-

cuse for the naming of a new species. In the North American Cryphalini (bark beetles) alone, 53 of the species described by Hopkins turned out to be synonyms. Downey (1962) and Kohn and Orians (1962) have given useful summaries of some of the relevant literature. Host specificity of external parasites has been discussed by Clay (1949), Hopkins (1949), and Holland (1964).

Ecological differences also occur among populations of the same species. Indeed, most widespread species exhibit differences in the ecology of local populations, particularly of peripherally isolated populations (Mayr 1963:312ff, 355).

Again, as with behavioral characters, differences at the species level have been studied far more extensively than have ecological differences between higher taxa, many of which are simply taken for granted. The fact that whales occupy a different adaptive zone than do bats is too obvious to be mentioned, yet a close study shows that even most genera, when well founded, occupy definably different niches or adaptive zones. Lack (1947) showed, for instance, that each genus of Galápagos finches is characterized by its utilization of the environment. *Geospiza* is a ground finch (chief food, seeds), *Camarhynchus* is a tree finch (chief food, insects), and *Certhidea* is a warbler finch (chief food, small insects) (Grant 1986).

Mytilus
Blaschke
R. mulleri
Blaschke
R. mulleri

Parasites and Symbionts In several instances sibling species were discovered because their parasites were different. A previously undiscriminated species of *Octopus* was discovered in California because it had its own set of mesozoan parasites. A new species of termites was discovered because its nests contained a different set of termitophile staphylinid beetles than did the nests of a previously known species. Parasites are also important in contributing to our knowledge of the relationship of higher taxa. Parasites evolve together with their hosts and are in some cases more conservative than the hosts. Unfortunately, they shift to new hosts more frequently than is sometimes admitted, and so evidence based on parasites must be evaluated very carefully (Baer 1957). For instance, flamingos (Phoenicopterii) exhibit characteristics which they share with both storks and geese. Their bird lice (Mallophaga) are of the same genera as those which occur on geese. At first this might suggest a close relationship, but it actually indicates merely a comparatively recent transfer of the lice from geese to flamingos. If the bird lice had been derived from a common ancestor, we would expect related but slightly different parasites in the two orders of birds. Neither anatomic nor molecular evidence indicates a close relationship of flamingos and geese. Human beings (*Homo*) and the African apes (*Pan* and *Gorilla*) share more external and internal parasites with each other than the Afri-

can apes do with the orang (*Pongo*). This strengthens the case for a close relationship between *Homo* and *Pan* (established on other grounds).

The fact that intracellular symbionts supply important taxonomic characters was discovered by Buchner (1966a) and his school. For instance, the most primitive tribes of the coccids (Steingelini, etc.) have no symbionts, but once a coccid taxon has acquired one, this symbiont (with all its highly specific adaptations) will be found in the derived phyletic lines of coccids. Repeatedly, unnatural taxa of coccids could be unmasked because they had heterogeneous complements of symbionts (Buchner 1966b). The same is true of symbionts in other groups of insects. The protozoan faunas in the intestines of termites evolved together with their hosts and are potentially useful indicators of relationship in cases of ambiguity in termite classification (Kirby 1950b).

Geographic Characters

Each taxon, from the species to the highest taxon, has a geographic range. Since this range changes as the taxon evolves, an intimate relation exists between systematics and biogeography. Most great biogeographers were systematists. Patterns of distribution often provide decisive clues for clarifying a confused taxonomic picture and for testing taxonomic hypotheses. The distributions of most taxa display patterns that permit conclusions about their past history. Because geographic range provides such useful taxonomic characters, every taxonomist needs to become familiar with the literature in the field of biogeography. The following works should be mentioned: Briggs (1974), Brown and Gibson (1983), Carlquist (1974), Darlington (1957, 1965), Mayr (1976), Pielou (1979), Raven and Axelrod (1974), Simpson (1965), and Udvardy (1969).

Geographic characters are important on two levels. In microtaxonomy the sympatric-allopatric relationship of populations is often decisive in the determination of species status. Two sympatric populations in reproductive condition can never be conspecific. The mapping of populations, subspecies, and allopatric species is indispensable in the delimitation of polytypic species and superspecies.

In macrotaxonomy an understanding of the relationship of higher taxa is often helped by an analysis of their distributions. Two questions are particularly important: (1) What is the distribution of the nearest relative (the sister group) of the studied taxon? and (2) If the taxon has a disjunct range, what is the probable cause of the range disjunction?

Since Darwin, we know that there are potentially two causes for disjunction:

1 Primary isolation (establishment of a founder population through dispersal)

2 Secondary isolation, that is, the fracture of a previously continuous range by a new distributional barrier across the previously continuous range (vicariance)

A knowledge of the Earth's history and the geological record often permits one to decide whether the isolation is primary or secondary and, more important, for how long a time the two isolates have been separated. The fact that the mockingbirds on the volcanic Galápagos Islands had flown across from the adjacent South American continent was perfectly clear to Darwin. The fact that the fauna and flora of the volcanic Hawaiian Islands had gotten there by transoceanic colonization has also been long evident; the same conclusion was inevitable for all volcanic oceanic islands in any ocean. Some continental islands, however, for instance, Madagascar and New Zealand, have a mixture of old vicariant elements that are remnants of the biota of the continents or plates to which these islands had formerly been attached and of more recent elements that reached them by transoceanic colonization.

Depending on the dispersal facility of a taxon, either primary or secondary isolation is the more important cause of range disjunctions. Some groups, such as earthworms (except when passively transported) and primary freshwater fishes, have very low dispersal facilities. In such groups almost any range disjunction is secondary, caused either by geological events (plate movements, mountain building) or by climatic-vegetational shifts such as range disjunctions caused by the Pleistocene ice caps or by post-Pleistocene habitat shifts.

Groups with poor dispersal facilities are particularly useful in determining the age of taxa. If such a group is found in South America and Australia but not on the northern continents, it is probably an old Gondwana element that goes back to the time when Australia was still connected with South America across Antarctica. If poorly dispersing groups are found in Africa and South America, they presumably go back to the time before Africa separated from South America. Most faunas, however, are a mixture of old and more recent elements (Mayr 1976:552-564) and these elements have to be carefully discriminated to establish a reliable chronology. The New Zealand kiwis and moas, for instance, are among the remnants of the old Gondwana fauna that ruled when New Zealand was still in contact with Antarctica, but most or all of the other birds of that island are descendants of more recent transoceanic immigrants from Australia or Melanesia.

The facility with which certain groups can cross water gaps is documented by the numerous colonizations of the Hawaiian Islands or of

even more remote Pacific islands such as the Marquesas and the Australs. In the case of easy dispersers, it is often difficult to determine the source area of colonization and thus the nearest relative. Some biogeographers tend to underestimate the dispersal ability of most organisms. The lizard family Iguanidae is otherwise restricted to the Americas, but surprisingly there is a species in Tonga and a superspecies in Fiji. All careful students of former land connections have come to the unexpected conclusion that these lizards could have reached these outposts only by long-distance dispersal.

The question is often asked, How can a pattern of distribution help in determining the nearest relative of a higher taxon? Here the basic rule is as follows: In case of doubt, the nearest relative is in the same geographic region or continent. This is well illustrated by the taxonomy of numerous Australian songbirds. When warblers, flycatchers, shrikes, nuthatches, tree creepers, and (wood) swallows were found in Australia, it was only natural that they were placed with the corresponding groups of the holarctic region. There were, however, enough puzzling aspects of the ecology and distribution of these Australian taxa to raise doubts. Could they not all be convergent adaptive radiations of indigenous Australian stocks? That this seems to be the case was eventually shown by Sibley and Ahlquist (1983) with the help of DNA hybridization.

The nearest relative, however, is not always found in the same geographic region. The nearest relative of the llamas is not a South American animal but the old world camel. The story of the marsupials is more complex. Today they are restricted to South America and Australia (except for the opossum that successfully reinvaded North America). Fossil marsupials, however, have been found in North America, Europe, Africa, and Asia. Geologists are now able to date the age of fossils and of all former land connections after the Pennsylvanian rather accurately. As far as the marsupials are concerned, this leads to the well-substantiated conclusion that North America was the original source area. From there, one radiation invaded Europe (and from there Africa and Asia) early in the Tertiary across a north Atlantic land bridge; this radiation soon became extinct. A far more successful radiation colonized South America and from there expanded across Antarctica to the Australian region. We are fortunate that it is now possible to provide reasonably accurate dates for the biota of the various plates and plate remnants.

A primitive relic sometimes survives in peripherally isolated areas, such as the tuatara on New Zealand and the rich fauna of lemurs on Madagascar, a phenomenon used by Matthew (1915) and other zoogeographers as a basis for broad generalizations. On the whole, however, the more primitive branches of a major radiation are most likely to be found

Am. cont.
Subcontinent
bridge
Peninsular

exotic sp.
Native sp.

near the original source area, with the expanding colonizations evolving farther and farther away from the ancestral location.

The theory of plate tectonics has shed considerable light on the evolutionary history of many animal taxa, particularly that of poor dispersers. It has helped resolve a number of taxonomic puzzles. In 1922 Michaelsen made the unexpected discovery that the earthworm fauna of India is more closely related to that of Africa and South America than it is to that of the rest of Asia. He explained this on the basis of Wegener's theory of continental drift, according to which the Indian plate was formerly part of Gondwanaland and established contact with the Asian plate only in the middle of the Tertiary. Many other biogeographic puzzles have since then been explained in the light of plate tectonics. However, even today there are biogeographic puzzles which have not been solved by the better understanding of geographic history brought about by plate tectonics.

Many genera of insects that are now found only in the southern continents (southern Africa, South America, Australia) were once believed to be part of the Gondwana fauna. Surprisingly, some of these genera have since been found as fossils in Oligocene Baltic amber. It is now clear that the southern distributions of these genera are relicts of formerly much wider distributions (Ander 1942). Such cases warn us not to become too assertive in trying to reconstruct the connections between present distribution, the Earth's history, the fossil record, and taxonomic relationship.

THE WEIGHTING OF CHARACTERS

The more characters a taxonomist uses, the more likely it is that the information provided by different characters will be discordant. According to one set of characters, species A and B are more closely related to each other than they are to C, but according to another set, species A and C are more closely related than either is to species B (Figure 11-2). Homoplasy and mosaic evolution are responsible for such seeming contradictions. There once were great hopes of resolving these conflicts with the help of numerical methods (Chapter 11), but these hopes were only partially fulfilled. Unfortunately, the use of different phenetic methods (Presch 1979) often results in different phenograms, and the same problem is encountered with the use of different cladistic methods. Aware of these difficulties, numerical taxonomists are increasingly including weighting in their methods (Funk and Wheeler 1986). Evidently in these cases different characters provide different information.

What the taxonomist must ask is which of the discordant characters

CONCLUSIONS

A taxonomic character is any attribute by which a member of a taxon may differ from the members of other taxa. This attribute may relate to any feature of the dead or living organism that is amenable to comparison.

1 Taxonomic characters that are conservative (i.e., evolve slowly) are most useful in the recognition of higher taxa; those which change rapidly or concern isolating mechanisms are most useful in lower taxa.

2 Taxonomic characters that are subject to parallel evolution, especially those involving loss or reduction, should be used only with great caution.

3 Taxonomic characters are expressions of the biology of their carriers. An understanding of this biology is a prerequisite for the proper evaluation of these characters.

4 The same phenotypic character may vary in value and constancy from taxon to taxon and even within a single phyletic series. The weight given to a character depends largely on its constancy in a given group.

The entire zoological classification is based on the proper evaluation (weighting) of taxonomic characters. This operation, then, is the most important as well as one of the most difficult tasks of the taxonomist.