
INTRAPOPULATIONAL VARIATION AND THE COMPARISON OF POPULATION SAMPLES

The traditional method of classical taxonomy was to group individuals found at a given locality by similarity and call each similarity class a different species. This procedure was legitimate during the period when species status was determined solely by degree of morphological difference. As a consequence, Linnaeus described the brightly colored male mallard as *Anas boschas* and the drab female as *An. platyrhynchos*, and the barred adult goshawk as *Accipiter palumbarius* and the striped immature goshawk as *A. gentilis*. However, as soon as their biological status was recognized, each pair of morphological species was combined into a single biological species.

The male and the female mallard are two different phena, as are the adult and the immature goshawk. Indeed, the populations of most species of animals contain several different phena as a result of sexual dimorphism, age variation, seasonal variation, polymorphism, and other causes. One of the primary tasks of the taxonomist is to unmask such variants and assign them to the species to which they belong. Owing to the great variability of most species, this is by no means an easy task, as proved by the long list of synonyms in many groups of animals, names that were given to phena when they were believed to be different species.

Students of inanimate objects establish classes merely on the basis of similarity. Asked to sort them, they would not hesitate to place objects as different as the caterpillar, chrysalis, and imago stages of a butterfly in

three different classes while also placing the adults of two similar species of butterflies in the same class. Biologists, however, know that they must take into consideration factors other than mere similarity. The continuity of the genotype from the fertilized egg through all the juvenile stages to the adult is one of these factors. *Sexual reproduction*—which results in genetic cohesion among all the individuals belonging to the same local population—is another. All members of a local population are products of the same gene pool and thus belong to a single taxonomic entity.

Knowledge of these biological phenomena permits the taxonomist to assign phena correctly to species. In a species with *sexual dimorphism*, for instance, males and females belong to two different phena. The fact that one phenon consists entirely of males while the other consists entirely of females suggests that these phena are not different species. Additional information should be brought to bear on the situation. For instance, if the two phena are the only ones in a collection made at a given locality that represent a certain genus and were collected simultaneously in the same habitat, the probability is high that they represent males and females of the same species. Breeding tests, the raising of young, and the study of courtship and copulation in nature furnish additional sets of biological information that permit the correct assignment of phena. Powerful evidence is often provided by proteins and other molecules when living material is available. The number of possible inferences that can be drawn from the available information is usually large. Knowledge of the nature and amount of sexual dimorphism found in living (recent) species often permits the correct assignment of fossil phena to species, for instance, among fossil ostracods and vertebrates.

To avoid premature decisions about which forms encountered in nature are genuine species rather than phena and to permit the inclusion of taxa of different rank in a single analysis, numerical pheneticists introduced the term *operational taxonomic unit (OTU)* (Chapter 8). It has ~~turned out, however, that a clear-cut distinction between phena and species is absolutely necessary before a numerical analysis can be undertaken and that after the elimination of phena, the term *taxon* is fully sufficient when one is referring to taxa of different rank. For these reasons the term *OTU* is usually an unnecessary synonym of the term *taxon*.~~

The greater the amount of information available about the phena in question, the easier their classification. This information includes the correct locality, habitat (and other relevant ecological information), and season of capture. The reasons why precise information is needed are twofold:

1 Many aspects of ecology and life history are species-specific.

2 The phenotype of animal populations of the same species often varies according to locality, season, or habitat (see below).

Differences between phena thus may reflect either a species difference or intraspecific variation. A full understanding of intraspecific variation is therefore necessary before we can make the probabilistic statement that phenon *B* belongs to a species different from that of phenon *A*. This is the reason for the immense importance of a thorough understanding of individual and geographic variation.

The taxonomic literature still contains numerous named phena that have not been correctly combined into biological species. These phena include males and females in sexually dimorphic groups of insects, workers and sexual castes in social insects, stages in the life cycle of parasites, and juvenile stages as well as morphs. It is one of the continuing activities of the taxonomist to unmask nominal species that are not genuine biological species.

A distinction must be made between the analysis of phena from a single locality (*sympatric phena*) and that of phena from different localities (*allopatric phena*). Only sympatric phena are considered in this chapter.

When one is sorting specimens from a single locality, it must be remembered that one is potentially dealing with four possibilities (Table 4-1). Two of these (classes 1 and 4) pose no problems. However, difficulties arise when individuals are morphologically different but belong to the same species (class 2) or are morphologically identical (or exceedingly similar) yet belong to different biological species (class 3). Many errors in the taxonomic literature (synonyms) are due to the fact that individuals belonging to class 2 were considered to belong to class 4 or that individuals belonging to class 3 were considered to belong to class 1. Discrimination between classes 1 and 3 is discussed in Chapter 5. The information that must be obtained to permit assignment either to class 2 or to class 4 is discussed in this chapter. Since direct evidence of *reproductive isolation* is usually not available, it must be inferred from the pattern of variation. It is therefore necessary to undertake a detailed analysis of individual variation. Such variation is far greater than the beginner realizes, and it sometimes deceives even the experienced taxonomist.

TABLE 4-1
DISCRIMINATION GRID FOR SYMPATRIC SAMPLES

Morphology	Not reproductively isolated	Reproductively isolated
Identical	1 Same phenon of a single species	3 Sibling species
Different	2 Different phena of the same species	4 Different species

SYMPATRIC SAMPLES

In a study of several phena from the same locality, only two alternatives are possible. Either the phena are individual variants of a single species or they belong to different species. There are three reasons why it may be difficult to make a ready choice between these two possibilities: (1) an extreme difference in phena belonging to a single species (e.g., caterpillar and butterfly); (2) an extreme similarity of good biological species (sibling species); and (3) extreme variability and wide phenotypic overlap of two species. Clues as to whether only a single species is involved in spite of extreme phenotypic difference, or, rather, indications that more than one species is involved in spite of extreme similarity, are usually provided by behavioral, ecological, or distributional data. Molecular or chromosomal data, breeding tests, and other evidence must then be obtained to confirm or refute the earlier supposition.

PHENA (INDIVIDUAL VARIANTS) OR DIFFERENT SPECIES?

Most species contain several phena if not dozens. To add to the complexity of the situation, several other species with a similar assortment of phena may be sympatric. Often a phenon of one species resembles a corresponding phenon of another species much more closely than it does any other phenon of the same species. For instance, the female in some species of many bird and insect genera is more similar to females of closely related species than it is to males of her own species. Nothing in the phenotype of caterpillars permits correct association with imagoes. Only observation of breeding or the careful evaluation of other biological information can do this.

The correct assignment of phena often can be achieved by a correct interpretation of morphological information. If a large sample of a population is available, forms intermediate between the more extreme variants are usually present. Also, certain characters in every group are less subject to individual variation than are others. The genitalic armature in most insects, the palpus in spiders, the radula in snails, and the structure of the hinge in bivalves are examples of such stable characters. When several sympatric phena agree in their genitalic armatures or in one of the other characters mentioned above, it adds to the probability that they are conspecific. However, even here one has to apply balanced judgment. Although in most genera of Diptera there are characteristic differences between the genitalia of related species, there are cases in which forms have identical genitalia even though they are different species by every other criterion (e.g., *Drosophila pseudoobscura* and *D. persimilis*). Similarly, in many other orders of insects closely related species may have

indistinguishable genitalia. Parasitic animals present some rather special problems (Manwell et al. 1957).

The establishment of correlations is often very helpful. If two forms that differ in character *a* can be shown to differ also in the less conspicuous and functionally unrelated characters *b*, *c*, and *d* (principle of covariation), it is very probable that they are different species. Some years ago Mayr found that among birds identified as the southeast Asiatic minivet (*Pericrocotus brevirostris* Vigors), some had innermost secondaries that were all black while others had a narrow red margin on those feathers. A detailed study revealed that birds with red on the innermost secondaries had seven additional minor characters: a more yellowish red of the underparts, a different distribution of black and red on the second innermost tail feather, a narrow whitish margin along the outer web of the first primary, and four other minor characters. Slight though they all were, these characters were well correlated with each other and with geographic and altitudinal distribution. The conclusion that two full species are involved has since been confirmed by several authors.

As a general rule, one finds that the decision of an experienced taxonomist, when based on a careful evaluation of the morphological evidence, is confirmed when a species recognized by that taxonomist is subjected to genetic tests or to an evaluation of molecular and other nonmorphological characters. Various forms of individual variation are listed in Table 4-2. The two most important types are nongenetic and genetic variation.

NONGENETIC VARIATION

It is of course impossible in a preserved museum specimen to determine directly whether a given variant has a genetic basis. Nevertheless, it is important for the taxonomist to understand that many types of variation exist and that in better-known groups it is usually possible to make a valid inference about the status of a given variant on the basis of field observations and available experimental evidence. For a discussion of the evolutionary aspects of individual variation, see Mayr (1963:138-158).

Animals as a whole are developmentally more strongly canalized than are plants and thus are less subject to nongenetic modification. In addition, through their power of locomotion and sensory abilities, they have the capacity for habitat selection. As a result, some well-known exceptions notwithstanding, nongenetic changes of the phenotype are far less of a problem for animal taxonomists than for plant taxonomists. However, every zoologist must be familiar with the types of nongenetic variability that may be encountered in a particular group.

TABLE 4-2
MAJOR TYPES OF VARIATION WITHIN A SINGLE POPULATION

1. Nongenetic variation
 - a. Individual variation in time
 - (1) Age variation
 - (2) Seasonal variation in an individual
 - (3) Seasonal variation in consecutive generations
 - b. Social variation (insect castes)
 - c. Ecological variation
 - (1) Habitat variation (ecophenotypic)
 - (2) Variation induced by temporary climatic conditions
 - (3) Host-determined variation
 - (4) Density-dependent variation
 - (5) Allometric variation
 - (6) Neurogenic or neurohumoral variation
 - d. Traumatic variation
 - (1) Parasite-induced variation
 - (2) Accidental and teratological variation
2. Genetic variation
 - a. Sexual dimorphism
 - (1) Primary sex differences
 - (2) Secondary sex differences
 - (3) Gynandromorphs and intersexes
 - b. Reproductively different generations (sexual and uniparental strains)
 - c. Ordinary genetic variation
 - (1) Discontinuous variation (genetic polymorphism)
 - (2) Continuous variation

Individual Variation in Time

Age Variation Whether they are born more or less developed or hatch from an egg, animals in general pass through a series of juvenile or larval stages in which they may be quite different from their adult forms. The catalogues of any group of animals list numerous synonyms that resulted from the failure of taxonomists to recognize the relationship between various age classes of the same species.

In reptiles, birds, and mammals there are no larval stages, but immature individuals may be rather different from adults, particularly in birds. Several hundred bird synonyms are based on juvenile plumage. Finding specimens that molt from the immature into the adult plumage usually clears up this difficulty.

In many fishes the immature forms are so different that they have been described in different genera or even different families. The immature stages of the eel (*Anguilla*) were originally described as *Leptocephalus brevirostris* Kaup. The unmasking may be especially difficult in neotenic animals, that is, animals that become sexually mature in a larval stage.

The difficulties for the taxonomist are even greater in groups with larval stages so different that they have not the faintest resemblance to the adult (e.g., caterpillar and butterfly). The floating or free-swimming larvae of sessile coelenterates, echinoderms, mollusks, and crustaceans are often extremely different from the adults. The taxonomic status of such larval stages can be settled either by assembling a complete sequence of intermediate stages or by rearing an organism through a complete life cycle.

The taxonomic identification of larval stages of parasites is particularly difficult in groups in which the different stages occur on different hosts. It is customary in helminthology to assign formal taxonomic names to the larval (*Cercaria*) stage of flukes (trematodes) in order to facilitate their identification (Figure 4-1). Such dual nomenclature is dropped as soon as it becomes known to what trematode species a given cercaria belongs. Such a relationship can usually be established only through rearing.

Age variation is not restricted to differences between larval stages and adults but occurs also between "young" and "old" adults. For example, in various species of deer (*Cervus*, etc.) older stags often have antlers with more points than those of younger stags. The shape of the antlers may also change. This age variation must be considered when the antlers of different species or subspecies are compared. There is probably no further addition of points (or only an irregular one) after a certain age has been reached. It would be as futile to try to determine the exact age of a stag by the number of points of its antlers as it would be to attempt to determine the age of a rattlesnake (*Crotalus*) by the number of rings in its rattle.

The taxonomist aims to work with samples that are as homogeneous as possible. It is much easier to achieve this in animals that have a definite adult stage (after the larval ones) than it is in those which show continuous growth, such as snakes and fishes, which may reach maturity after having attained only half their potential size or less. In such forms it is advisable to work with regressions rather than with absolute measurements. In many species, meristic characters (e.g., number of scales or fin rays) do not increase after they are formed in spite of the enormous subsequent growth. These characters are therefore especially useful in herpetology and ichthyology.

Seasonal Variation in an Individual In animals that live as adults through several breeding seasons, the same individual sometimes has a very different appearance in different parts of the year. Many birds have a bright nuptial dress which they exchange for a dull ("eclipse") plumage at the end of the breeding season. (Among North American examples are many ducks, shore birds, warblers, and tanagers. In many species a change of plumage is restricted to the males.)

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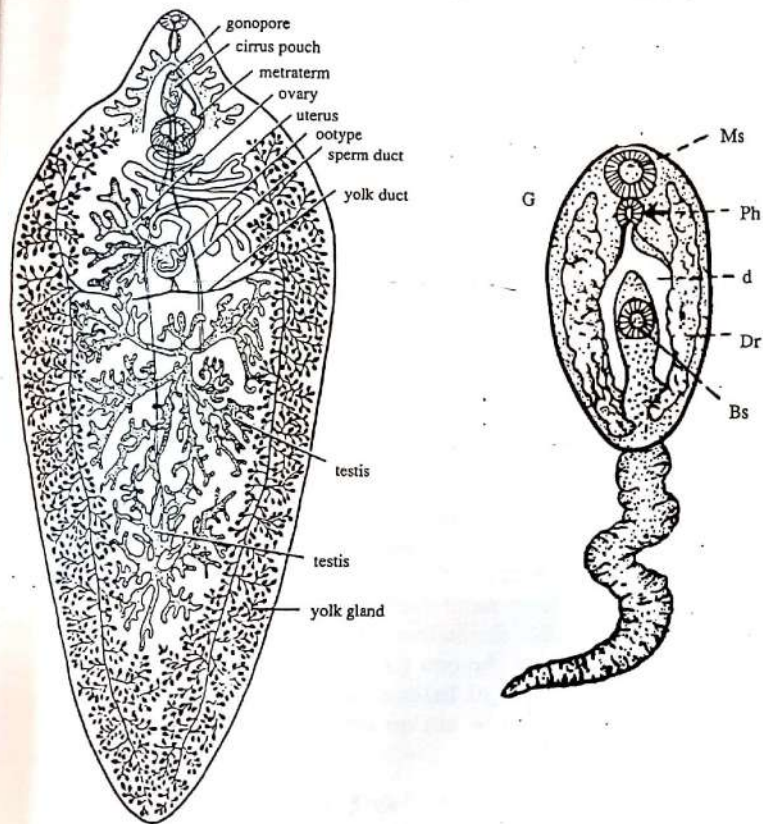


FIGURE 4-1
Difference between the adult liver fluke (*Fasciola hepatica*) and its larval stage (*Cercaria*).
(After Chandler and Read.)

In arctic and subarctic birds and mammals such as ptarmigans (*Lagopus*) and weasels (*Mustela*), there may be a change from a cryptic white winter dress to a "normally" colored summer dress. In other birds the colors of the soft parts change with the seasons. In the common egret (*Ardea alba* Linnaeus) and the European starling (*Sturnus vulgaris* Linnaeus), the bill may change from yellow to black. Plumage changes in birds are usually effected by molting, but wear alone may produce striking changes. In the European starling (*Sturnus vulgaris*), for example, the freshly molted bird of October is covered with white spots and all the feathers show whitish or buffy margins. During the winter the pale edges

Crabs / Mustela

of the feathers wear off, and in the spring, at the beginning of the breeding season, the whole bird is a beautiful glossy black without its having molted a single feather. A similar process of wear brings out the full colors of the nuptial plumage in the males of many other birds. In arid regions, particularly in real deserts, the sun bleaches the pigments. A bird before the molt looks much paler than does one in freshly molted plumage.

In all these cases it is the same individual that looks very different in different parts of the year. Such seasonal variation is particularly common among vertebrates, with their elaborate endocrine systems. Many seasonal variants were described as distinct species before their true nature was recognized.

Seasonal Variation in Consecutive Generations Many species of short-lived invertebrates, particularly insects, produce several generations in the course of a year. In such species it is not uncommon for the individuals that hatch in the cool spring to be quite different from those produced in the summer or for the dry-season individuals to be different (e.g., paler) from the wet-season population. Some tropical butterflies may have very different dry-season and wet-season phena.

Such seasonal forms can usually be recognized not only by the occurrence of intermediates in the intervening season but also through identity of wing venation, genitalia, etc.

Cyclomorphosis A special kind of seasonal variation is found in certain freshwater organisms, particularly rotifers and cladocerans. The populations of a species undergo regular morphological changes through the seasons in connection with changes in the temperature, turbulence, and other properties of the water. Many "species" have been named, particularly in the genus *Daphnia*, that are nothing but seasonal variants. In rotifers, different morphs may also result from different kinds of food. For a recent review, see Kerfoot (1980).

Social Variation (Insect Castes)

In the social insects, such as some bees and wasps, but particularly among ants and termites, castes have developed. These are definite groups of individuals within a colony in addition to the reproductive castes (queens and males or drones); there are workers (sometimes of different types) and soldiers (also sometimes of different types). In the Hymenoptera these castes are most commonly modified females and are genetically identical, but in the Isoptera (termites) both sexes may be involved. The structural types observed may result from different larval food or may be due to hormonal or other controls. Obviously, taxonomic names should not be applied to these intracolony variants, but invalid

species have sometimes been described because it was not realized that there were different types of soldiers or workers in the same colony.

Ecological Variation

Habitat Variation (Ecophenotypic) Populations of a single species that occur in different habitats in the same region are often visibly different. The taxonomic treatment of such local variants has fluctuated between two extremes: Some authors have described them as different species, while others have considered them all to be nongenetic variants. Actually they may be (1) microsubspecies (or ecological races) or (2) nongenetic ecophenotypes. The latter are particularly common in plastic species, such as some mollusks.

Dall (1898) gave a very instructive account of all the variations he observed in a study of the oyster (*Crassostrea virginica* Gmelin). Such habitat forms are particularly common in freshwater snails and mussels. The upper parts of rivers, with cooler temperatures and a more rapid flow of water, have different forms than do the lower reaches, which have warmer and more stagnant waters. In limestone districts the shells are heavy and of a different shape from those which grow in waters low in lime. This dependence of certain taxonomic characters of mussels on environmental factors was, curiously enough, entirely overlooked by some earlier workers, a fact which resulted in absurd systematics. Schnitter (1922:4-5), who largely cleared up the situation, described these absurdities as follows:

The last step in the splitting of the freshwater mussels of Europe was done by the malacozoologists Bouguignat and Locard. According to the shape and the outline of the shell, they split up the few well-known species into countless new ones. Locard lists from France alone no less than 251 species of *Anodonta*. On the other hand, two mussels were given the same name, if they had the same outline of the shell, even though one may have come from Spain and the other from Brittany. It seems incredible to us that it never occurred to these authors to collect a large series at one locality, to examine the specimens, to compare all the individuals and to record the intermediates between all these forms. It is equally incomprehensible that these people did not see the correlation between environment and shape of shell, even though they spent their entire lives in collecting mussels.

All these "species" of *Anodonta* are now considered to be habitat forms of two species, and the other names have sunk into the synonymy of the two valid species.

Whether a given habitat form is an ecophenotype or a microgeographic race is not always evident. It is sometimes necessary to

transplant the organism or raise it in the laboratory to answer this question. Much work of this sort remains to be done.

Variation Induced by Temporary Climatic Conditions Some animals with a highly plastic phenotype may produce year classes that differ visibly from the norm owing to unusual conditions (drought, cold, food supply, etc.) in a given year. Fish of a given year class may be stunted or, on the contrary, may have proportions indicative of particularly rapid growth. Samples of susceptible species must be collected in a way that will compensate for distortions caused by this factor (Harrison 1959; Mayr 1963:145).

Host-Determined Variation Host-determined variation in the parasites of plants and animals provides a potential source of taxonomic error and permits confusion with microgeographic races or sympatric species. This phenomenon is most commonly expressed in size differences but may involve other morphological or physiological characters.

Host-induced variation is not as common as was formerly believed. Many so-called host races in the literature have been found in recent decades to be valid sibling species (Mayr 1963, Chapter 3).

Density-Dependent Variation The effects of crowding are sometimes reflected in morphological variation, especially when crowding leads to a shortage of food materials. However, density-dependent variation need not be related to food supply: Uvarov, Kennedy, and others have shown that gregarious species of locusts exist in various unstable biological phases (Kennedy 1961; Albrecht 1962). These phases differ in anatomy, color, and behavioral characteristics and have often been described as distinct species. When newly hatched nymphs are reared under crowded conditions, they develop into the transitional phase; when they are isolated and reared separately, they develop into the solitary phase. Similar phases have been reported for two species of armyworms (*Lepidoptera*), *Laphygma exigua* (Hübner) and *L. exempta* (Walker).

Allometric Variation Allometric growth may result in the disproportionate size of a structure in relation to the size of the rest of the body. If individuals in a population show allometric growth, animals of different size will show allometric (heterogonic) variability. This phenomenon is particularly marked among insects. It involves such features as the heads of ants (Figure 4-2), the mandibles of stag beetles (*Lucanidae*), the frontal horns and thoraxes of scarabs, and the antennal segments of thrips. Failure to recognize the nature of such variations has resulted in much synonymy.

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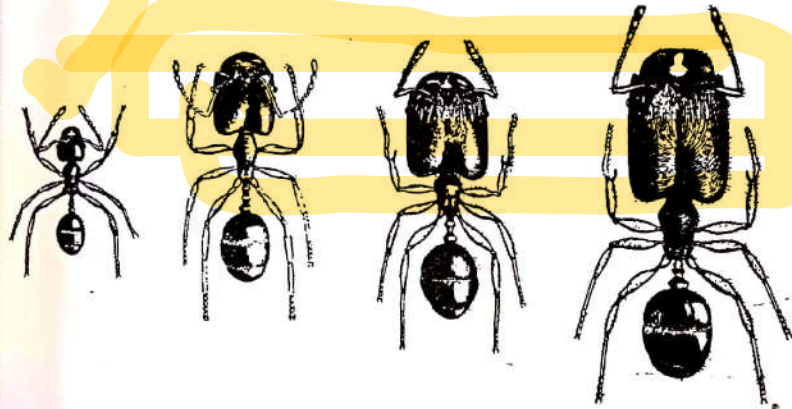


FIGURE 4-2 Allometric variability. Neuters of *Pheidole instabilis*, showing an increase in the relative size of the head with absolute size of the body. (After Wheeler, 1910.)

Neurogenic or Neurohumoral Variation Neurogenic or neurohumoral variation refers to color change in individual animals in response to the environment. These changes are accomplished through the concentration or dispersal of color-bearing bodies known as *chromatophores*. This type of variation was first thoroughly studied in the chameleon. It occurs sporadically in the lower animals but is best developed among crustaceans, cephalopods, and cold-blooded vertebrates (cyclostomes, elasmobranchs, teleost fishes, amphibians, and reptiles). Space does not permit a discussion of this specialized type of variation. The reader is referred to Fingerman (1963), Gersch (1964), and Waring (1963) for details.

Traumatic Variation

Traumatic variation occurs with varying frequency in different groups of animals. The abnormal nature of this type of variation is usually obvious, but in some cases it is subtle and may be misleading.

Parasite-Induced Variation Aside from such familiar effects of parasitism as swelling, distortion, and mechanical injury, parasites may produce conspicuous structural modifications. In the bee genus *Andrena*, for instance, parasitism by *Stylops* frequently results in a reduction in the size of the head, enlargement of the abdomen, and changes in puncturation, pubescence, and wing venation. It also commonly results in intersexes. Since *Andrena* is markedly sexually dimorphic, these

intersexes have been a source of taxonomic confusion and synonymy. However, in one case (Linsley 1937), a stylopized intersex proved to be of value in associating the sexes of a bee that had been described as two different species.

Salt (1927) has conducted the most comprehensive study of the morphological effects of stylopization in *Andrena*. In females he found reduction of the pollen-collecting organs, loss of anal fimbriae, changes in the relative length of antennal segments, reduction of facial foveae, reduction of the sting and accessory organs, paling of ventral abdominal pubescence, acquisition of angular cheeks, and yellow on the normally dark clypeus. In males he reported the development of long hairs resembling those of the female, flocculi, broadening of the posterior basitarsus, changes in proportions of antennal segments, loss of cheek angles and some yellow from the clypeus, indications of facial foveae, and reduction in the size of genitalia.

Some strikingly different termite soldiers from the orient were assigned to a new genus and species, *Gnathotermes aurivillii*. Later it was shown that these modified soldiers are nothing but parasitized individuals from colonies of *Macrotermes malaccensis* (Haviland).

Postmortem Changes

The taxonomist must be aware of one further type of individual variation. In many groups of animals it is impossible to prevent postmortem changes of preserved specimens. Some extreme cases are known in birds. The deep orange-yellow plumes of the twelve-wire bird of paradise (*Seleucidis ignotus* Forster) fade to white in collections. The plumage of the Chinese jay (*Kitta chinensis* Boddaert), which is green in life, turns blue in collections because of the loss of the volatile yellow component in the pigment. Many birds that are clear gray or olive gray when freshly collected become more and more rufous through oxidation of the black pigment ("foxing"). Numerous synonyms have been created in ornithology through the comparison of freshly collected material with old museum specimens.

Other postmortem changes result from the chemical action of preservatives or killing agents. A common color change of this nature takes place when certain yellow insects, especially wasps, are overexposed to cyanide. The specimens turn bright red, and no method has been found for reversing this reaction. When one is preserving specimens with evanescent colors (corals, marine slugs, etc.), it is essential to take full notes and preferably color photographs or make color sketches. These records will allow an accurate description of the living animal.

GENETIC VARIATION

In the cases of variation discussed in the preceding sections, the same individual is actually or potentially subject to a change in appearance. Other kinds of intrapopulation variation are due to differences in genetic constitution. This genetically induced individual variation can somewhat arbitrarily be divided into three classes.

Sexual Dimorphism

Among genetically determined variants within a population, many of the variants are sex-associated. They may be sex-limited (express themselves in one sex only) or be otherwise associated with one sex or the other. Some of these are as follows.

Primary Sex Differences These are differences involving the primary organs utilized in reproduction (gonads, genitalia, etc.). When the two sexes are otherwise quite similar, primary sex differences are rarely a source of taxonomic confusion.

Secondary Sex Differences There is more or less pronounced sexual dimorphism in most groups of animals. The differences between males and females are often very striking, as in birds of paradise, hummingbirds, and ducks. In many cases the different sexes were originally described as different species and retained this status until painstaking work by naturalists established their true relationship. A celebrated case is that of the king parrot, *Eclectus roratus* (Muller), of the Papuan region, in which the male is green with an orange bill and the female is red and blue with a black bill. Described in 1776, the two sexes were considered different species for nearly 100 years, until naturalists proved conclusively in 1873 that they belonged together.

Striking sexual dimorphism is particularly common in the Hymenoptera. The males of the African ant *Dorylus* are so unlike other ants that they were not recognized as ants and were for a long time considered to belong to a different family. In certain families of wasps the small wingless female and the large winged male are so different that some taxonomists use a different nomenclature for the two sexes. Whole "genera" consist entirely of males; others, of females. The best way of determining with which female of genus *B* a given male in genus *A* belongs is to find a pair in copula or to watch a female in the field and catch the males as they are attracted to her. Once it has been established that *B* is the female of *A*, it is sometimes possible to associate several other "species pairs" in the same genus by utilizing additional information on distribution, frequency, color characters, and so on.

Gynandromorphs and Intersexes *Gynandromorphs* are individuals that show male characters in one part of the body and female characters in another part (Figure 4-3). Thus the two halves of the body may be of opposite sexes (this is the most conspicuous example of gynandromorphism), the division may be transverse, or the sex characters may be scattered in a mosaic. In the latter case symmetrical variants may be produced. Usually gynandromorphs are easily recognized as such and rarely provide a source of taxonomic confusion. Gynandromorphism is produced by an unequal somatic distribution of chromosomes, particularly sex chromosomes.

Unlike gynandromorphs, *intersexes* are likely to exhibit a blending of male and female characters. Intersexes are generally thought to result from an upset in the balance between male-tendency and female-tendency genes. This upset may result from irregularities in fertilization or mitosis or from physiological disturbances associated with parasitism. Intersexes are particularly likely to appear in populations of interspecific or intersubspecific hybrids. They have been studied in greatest detail in *Lymantria* (Goldschmidt 1933) but are well known in many other animals.

FIGURE 4-3
Gynandromorph of *Papilio dardanus*; left wing female, right wing male. (From Wells and Huxley.)



Reproductively Different Generations

In many insects there is an alternation of generations that is very confusing to the taxonomist. In the genus *Cynips* (gall wasps), the agamic generation is so different from the bisexual one that it has been customary to apply different scientific names to the two (Kinsey 1930). In the aphids (plant lice) the parthenogenetic wingless females are usually different from the winged females of the sexual generations (Figure 4-4).

Sexual and Uniparental Strains In some species of slugs (*Arion*) several strains are found which differ in their sexuality. The sexually reproducing strains are highly polymorphic in their enzymes, while self-fertilizing hermaphroditic strains are highly homozygous (Foltz et al. 1982).

Ordinary Genetic Variation

Much intrapopulation genetic variation is not sex-limited and does not primarily involve sex characters.

Discontinuous Variation (Polymorphism) The differences between individuals of a population are in general slight and intergrading. In certain species, however, the members of a population can be grouped into very definite classes that are determined by the presence of certain conspicuous characters. Such discontinuous individual variation is called *polymorphism*. Such polymorphism is frequently controlled by a single gene that is subject to simple Mendelian inheritance.

Polymorphism is more pronounced in some groups of animals than it is in others. In many species of Hemiptera and Coleoptera the same population may contain flying and flightless (wingless or short-winged) individuals. It is evidently advantageous to have both residents and dispersers in such populations. The spotting in lady beetles (*Coccinellidae*) is a well-known example of genetic polymorphism, as is industrial melanism in moths. Polymorphism has great biological importance because it proves the existence of selective differences between apparently neutral characters. For a more detailed discussion of this topic, see Ford (1945, 1965) and Mayr (1963). The practical importance of polymorphism to the taxonomist lies in the fact that it has led to the description of many so-called species that are actually polymorphic variants (morphs). In ornithology alone, about 100 species names were given to morphs. The recognition of their true nature has led to a considerable simplification of taxonomy.

Perhaps the most spectacular cases of polymorphism are to be seen in the Lepidoptera, particularly in certain species of butterflies. The com-

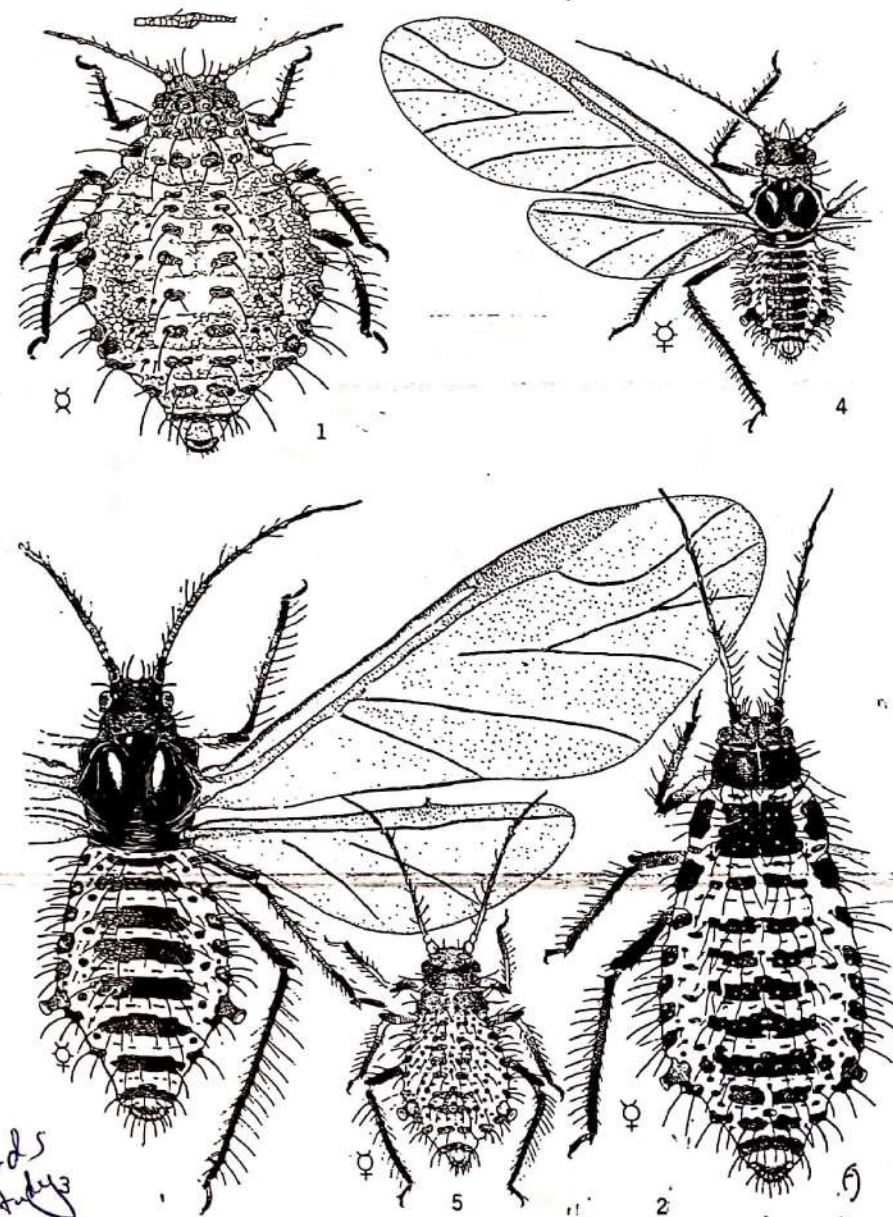


FIGURE 4-4
Periphyllus californiensis (Shinji). 1 = fundatrix or stemmother; 2 = normal apterous parthenogenetic viviparous female; 3 = alate of same; 4 = smallest spring alate viviparous female. (From Essig and Abernathy 1952.)

birds studies

mon alfalfa butterfly, *Colias eurytheme* (Boisduval), for example, has two strikingly different female forms, one largely white and the other resembling the orange-colored male. The most complicated cases of sex-limited polymorphism that have been studied genetically are the examples of mimetic polymorphism in African swallowtail butterflies of the genus *Papilio*. Quite apart from the fact that allopatric populations throughout Africa show distinct subspecific differences that are correlated with differences in the species of the butterflies that they mimic, several distinct female forms may exist within a single population. Thus in west Africa one finds, in the same population of *P. dardanus* Brown, one male form and five female forms, with three of the female forms mimicking different models that belong to the families Danaidae and Nymphalidae (Table 4-3 and Figure 4-5). The most remarkable feature of this polymorphism is that although the various forms are sufficiently distinct to resemble representatives of three different families of Lepidoptera, breeding experiments have shown that the differences are caused by a few Mendelian genes. Other celebrated cases of mimicry are those of the butterfly *Pseudacraea eurytus* Linnaeus (Carpenter 1949) and of the species of *Heliconius* (Turner 1981).

Continuous Variation The most common type of individual variation is due to slight genetic differences among individuals. No two individuals (except monozygotic twins) in a population of sexually reproducing animals are exactly alike genetically or morphologically. One of the outstanding contributions of population genetics has been the establishment of this fact. The differences are in general slight and are often not discovered unless special techniques are employed.

The study of this variation is one of the foremost tasks of the taxonomist. It is now evident that no single individual is "typical" of the char-

TABLE 4-3
MIMETIC POLYMORPHISM IN WEST AFRICAN *PAPILIO DARDANUS* BROWN

Male	Nonmimetic females	Mimetic females	Models
Typical <i>dardanus</i>		<i>hippocoön</i> Fabricius	<i>Amauris niavius</i> Linnaeus
	<i>dionysus</i> Doubleday and Hewitson	<i>trophonissa</i> Aurivillius	<i>Danaus chrysippus</i> Linnaeus
		<i>niobe</i> Aurivillius	<i>Bematistes tellus</i> Aurivillius

Source: From Goldschmidt 1945.

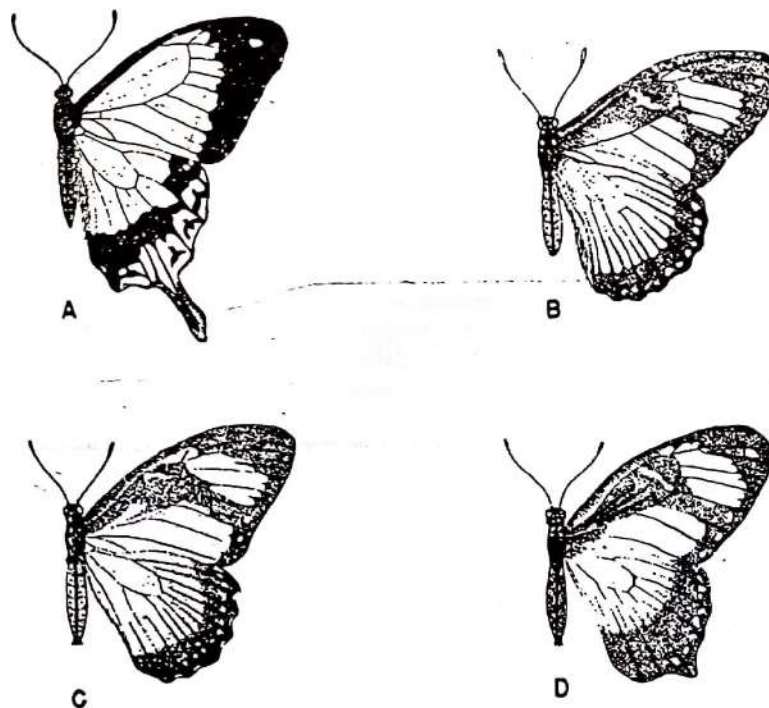


FIGURE 4-5

Mimetic polymorphism in the *Papilio dardanus* complex. (A) Male of *cenea*—also basic type of nonmimetic female, ground color yellow; (B) *dionysus*, nonmimetic female, ground color of forewings white, hind wings yellowish; (C) *trophonissa*, mimetic female, ground color for forewings white, hind wings brownish; (D) *hippocoön*, mimetic female, ground color white. (Redrawn from Eltringham 1910 by Goldschmidt 1945.)

acters of a population. The continuous variation among the members of a population manifests itself most conspicuously in linear measurements and proportions. Mean values, variances, and coefficients of variability for each trait are characteristic of each population and species. A model study of variability based on 2877 skins of the house sparrow (*Passer domesticus*) has been presented by Selander and Johnston (1967).

Each character may show a different degree of variability within a single population. Similarly, there are different degrees of variability among related species. Just why one species should be highly variable while another one is not is not always clear. A taxonomist who has adequate material for one species should not hastily assume that this makes it possible to be certain of the variability of related species.