Lissner (1938) draws a similar picture of the European mackerel, Herald (1941) distinguishes 4 subspecies in the western American pipefish Sygnathus californiensis. The interesting aspect of this case is that one of these subspecies is restricted to the kelp beds and is more or less pelagic, while two intergrading eel-grass forms are strictly coastal. There is complete intergradation in the few localities (for example Elkhorn Slough, Monterey Bay) where the two habitats come into contact. The differences between the races relate to size, number of fin rays (particularly dorsal), number of tail- and body rings, as well as proportions of head, body, and tail. Many additional examples can be found in the ichthyological literature.

**ABSENCE OF GEOGRAPHIC VARIATION**

Some species without noticeable geographic variation (monotypic species) seem to exist in every one of the higher categories of animals. This absence of variability may be due to one of the following factors or to a combination of them: (1) Insufficient analysis, (2) high dispersal facilities leading to a continuous swamping of semi-isolated populations, (3) uniformity of habitat, (4) smallness of range due to lack of other suitable habitat or due to partial extinction, (5) recent expansion of a formerly very localized species, and (6) evolutionary stagnation (reduction of mutability). It will require much more taxonomic, ecological, and genetic research to determine in any given case which one of the above factors is responsible for the absence of geographic variation.

All this evidence may be summarized in the statement that geographic variation seems to be present in at least some species of every major animal group. Every new investigation not only adds more cases of geographic races, but it also leads to simplification of the system by showing that many of the previously recognized “species” are nothing but subspecies of widespread polytypic species. The acceptance of the modern biological species concept, based on the principle of geographical replacement, has resulted in an extraordinary simplification of the system in all those groups in which it has been employed consistently.

**CHAPTER VII**

**THE SPECIES IN EVOLUTION**

Darwin entitled his epoch-making work not The Principles of Evolution, or The Origin and Development of Organisms, or by some other title which would stress the general problems of evolution. Apparently he considered these titles too speculative and therefore chose the more concrete one, On the Origin of Species. To him this was apparently more or less synonymous with these other titles, which is not surprising if we remember that Darwin drew no line between varieties and species. Any pronounced evolutionary change of a group of organisms was, to him, the origin of a new species. He was only mildly interested in the spatial relationships of his incipient species and paid very little attention to the origin of the discontinuities between them. It is thus quite true, as several recent authors have indicated, that Darwin’s book was misnamed, because it is a book on evolutionary changes in general and the factors that control them (selection, and so forth), but not a treatise on the origin of species. Obviously it was impossible to write such a work in 1859, because the whole concept of the species was too vague at that time. This has changed in the intervening years, as we have tried to show in the preceding chapter, and we are now in a much better position to examine the role which the species plays in evolution and how the origin of discontinuities is correlated with evolutionary changes as a whole. The authors who have devoted themselves to a study of these questions during recent decades have come to the conclusion that the problem of the “origin of species” is one of the cardinal problems in the field of evolution.

Somebody might ask at this point if it was not exaggerated to attribute so much importance to the species. This question seems justified when we remember how much the species concept has changed between 1758 and today and how impossible it is to find a completely adequate and satisfactory species definition. There are actually some authors for whom species are merely abstractions and who consider the individual the only unit in nature which possesses any reality. They claim that all organisms form a continuity, which the taxonomist breaks up into species merely for the sake of expedience, to be able to handle them
Frequently during our subsequent discussions, it will be convenient to coin some technical terms for the relationships of species. Such a point of view may have some justification in poorly known groups, but is it true in nature? This question can be tested only by investigating groups which are well known taxonomically and biologically, as, for example, birds. If we ask ourselves whether bird species are objective, that is, whether they are units with a reality in nature, we must ask at once what the criteria are by which the objectivity of a systematic unit can be determined. Thinking this over, we come to the conclusion that such a unit is objective, or real, if it is delimited against other units by fixed borders, by definite gaps.

**GAPS BETWEEN SYMPATRIC AND ALLOPATRIC SPECIES**

Do such gaps exist and how complete are they? Let us look at some common eastern North American birds. The ornithologist unites, for example, all the smaller thrushes of this region in the genus *Hylocichla*. If we examine the variation within the genus in more detail, we find that it clusters very closely around five means, to which we apply the familiar names wood thrush (*Hylocichla mustelina*), veery (*H. fuscescens*), hermit thrush (*H. guttata*), gray-cheeked thrush (*H. minima*), and olive-backed thrush (*H. ustulata*). All five species are similar, but completely separated from one another by biological discontinuities. Every one of the five species is characterized not only morphologically, but also by numerous behavior and ecological traits. Two or three of them may nest in the same woodlot without any signs of intergradation; in fact, not a single hybrid seems to be known between these five common species. I could list genus after genus of familiar North American or European birds and demonstrate exactly the same. Aside from some rare exceptions, which will be treated later (p. 260), there is a clear-cut discontinuity, or to use Goldschmidt's term, a "bridgeless gap" between the species of a given locality. Such clear-cut discontinuity is, however, frequently lacking between species that represent each other geographically. There are thus two ways of delimiting species: (1) against other species that coexist at the same locality, and (2) against species with mutually exclusive geographic ranges. This difference in the geographic relationship of species is of the utmost importance and will be referred to frequently during our subsequent discussions; it will therefore be convenient to coin some technical terms for it. Two forms or species are **sympatric**¹, if they occur together, that is if their areas of distribution overlap or coincide. Two forms (or species) are **allopatric**, if they do not occur together, that is if they exclude each other geographically. The term allopatric is primarily useful in denoting geographic representatives.

The gaps between sympatric species are absolute, otherwise they would not be good species; the gaps between allopatric species are often gradual and relative, as they should be, on the basis of the principle of geographic speciation. The few exceptions to this rule will be discussed subsequently. The failure to recognize the fundamental difference between the two kinds of gaps between species seems to be at the bottom of nearly every controversy between taxonomists on the nature of species and speciation. Goldschmidt (1940) quotes one fact after another in confirmation of the fixity of the "bridgeless gap" between sympatric species, but as soon as this is safely established, he states that "the species limit is characterized by a gap," but meaning, in this case, a gap between allopatric as well as sympatric species.

The delimitation of allopatric species will occupy us during the greater part of this chapter, but first a few more words may be said about the gap between sympatric species.

**THE DELIMITATION OF SYMPATRIC SPECIES**

What difficulties are encountered by the taxonomist when he attempts to delimit sympatric species? The answer is that there are very few difficulties in well-known genera. If a taxonomist of such a group receives a series of specimens from a particular locality, he is almost never in doubt as to whether they belong to one or to several species. "Dans une contrée donnée, il est facile de définir rigoureusement la grande majorité des espèces par leur caractères morphologiques constants, par leur habitat particulier dont elles ne sortent qu'exceptionnellement, par le fait qu'elles ne se croisent pas habituellement entre elles, ce qui est prouvé par leur permanence et l'absence d'intermédiaires," Cuenot (1936:14) with these words very graphically describes the situation which is typical for most animal genera. Unusual cases, such as apomicts or hybrid swarms, found in so many plant genera (*Hieracium*, *Rubus*, *Salix*, and so forth), are exceptional or absent in animals. Nearly all the known hybrid swarms in animals occur at the meeting zone of otherwise allopatric forms. Serious difficulties in delimiting sympatric species are encountered, in general, only in poorly known systematic groups. After such difficulties have been completely analyzed, the final decision usually shows that either (1) several stages or phases (individual variants) of a species are so different that they had been mistaken for different

¹ This term was coined by Poulton (1903).
species, or (2), just the opposite, that several species which occur at the same locality are so similar (sibling species) that they had been considered individual variants of one species.

**Individual variants.**—The striking individual variation of many animals, which we discussed in Chapter II, including the pronounced polymorphism (Chapter IV) typical of many species, have caused the systematicist many difficulties. Among the few species of birds which Linnaeus describes in the *Systema Naturae* are no fewer than 4 or 5 that are nothing but the immature or female plumage of another already described species. Most of these doubtful cases have now been cleared up in the better-known groups; the number of the remaining ones is exceedingly small in birds. Among the 568 species of New Guinea birds, *Meliphaga albonotata* is the only species whose validity is doubtful; it is possibly only an individual color variety of *Meliphaga analoga*. If such color phases are restricted to definite parts of the range of the species, particularly to the exclusion of the “wild” type, the difficulty is still greater. Two well-known pairs of “species” of North American birds seem to fall into this category (only 2 out of about 755). The Great White Heron (*Ardea occidentalis*) of the Florida Keys is currently considered to be specifically distinct from the Great Blue Heron (*Ardea herodias wardi*), and the Lesser Snow Goose (*Chen h. hyperboreus*) from the Blue Goose (*Ch. caerulescens*), but I am confident that in both cases it will eventually be shown that the white partner of the pair is merely a color phase (mutant), which has become the exclusive type of coloration over a smaller or larger part of the range of the species. Two additional doubtful species of North American birds are *Buteo harlanii* and *Dendroica polomac*. The former is either a good species or a color phase of *Buteo jamaicensis krideri*, and the latter (known from only two specimens) seems to be a hybrid between the Yellow-throated Warbler (*Dendroica dominica*) and the Parula Warbler (*Parula americana*). Interspecific hybrids, rare as they are in most families of birds, have been the cause of some confusion. A full discussion of the problems of hybridization will be given later (Chapter IX).

Individual variation affects, in general, invertebrates much more than homoiothermal higher vertebrates. This is primarily due to their greater phenotypical plasticity, but is to some extent also due to the frequency of genetic polymorphism. Individual variation poses many difficulties to the working taxonomist, but these are being overcome steadily, as the available material and our knowledge of the various taxonomic groups increases. However, it seems that a few cases are so difficult that it will be impossible to analyze them satisfactorily, even with help of the finest collections. A study of the ecology and ethology of the doubtful forms or a breeding experiment will usually provide the solution, when the analysis of the morphological characters fails.

**Sibling species.**—Much more troublesome to the taxonomist and more interesting to the student of evolution is another class of difficulties caused by pairs or even larger groups of related species which are so similar that they are considered as belonging to one species until a more satisfactory analysis clears up this mistake. I call such morphologically similar and closely related, but sympatric species, sibling species. This corresponds to the “dual species” of Pryer and of Hering (1935), to the “Doppel”- or “Geschwister”-Arten of some German taxonomists, or the “espèces jumelles” of Cuvéot (1936:236). The category of sibling species does not necessarily include species which are phylogenetically siblings, for example, the members of a superspecies. The term sibling species is arbitrarily limited to species which are as similar as are twins or quintuplets. The term is merely a convenient label for a not-infrequent taxonomic situation and has been adapted from the equivalent German and French terms. It is used only as a practical category, not clearly separable from other groups of similar species. In poorly analyzed groups it happens not infrequently that three, four, or five species are lumped under one species name, because the diagnostic characters of these species have not yet been discovered. An early worker in such a genus might call this group of species sibling species, but subsequent workers might find more and more distinguishing characters showing that these species are no more similar than most related species. In spite of this uncertainty, we recognize and emphasize the existence of sibling species for two reasons. First, because they demonstrate clearly that the reality of a species has nothing to do with the degree of its distinctness. Subspecies show more conspicuous visible differences in many genera than full species in other genera. The second reason for their importance is that many of them were considered “biological races” of one species in the bygone days of a purely morphological species definition. In view of this confusion between sibling species and biological races, it will be best to treat the two subjects jointly in a later chapter (p. 200). At present it may be said only that there is no reason to believe that sibling species evolve in a manner that is in the least different from that of other species.

**THE DELIMITATION OF ALLOPATRIC SPECIES**

The difficulties in delimiting sympatric species, which we have just discussed, are of a technical and temporary nature. They are due to the incompleteness of our knowledge of these species and disappear as soon
as the missing information becomes available. They do not in the least affect the objective reality of these species. In addition to these clear-cut and "bridgeless" gaps between sympatric species, there are, however, the gaps between allopatric forms, and the unbridgeability of these gaps is very often doubtful. Nearly every well-isolated population which has developed some characters of its own may be considered a separate species on the basis of certain criteria. The decision as to whether to call such forms species or subspecies is often entirely arbitrary and subjective. This is only natural, since we cannot accurately measure to what extent reproductive isolation has already evolved. In fact, such cases are logical postulates, if the divergence of isolated populations is one of the important means of species formation. A species evolves if an interbreeding array of forms breaks up into two or more reproductively isolated arrays, to use Dobzhansky's terminology. If we look at a large number of such arrays (that is species), it is only natural that we should find a few that are just going through this process of breaking up. This does not invalidate the reality of these arrays; just as the Paramecium "individual" is a perfectly real and objective concept, we find in most cultures some individuals that are either conjugating or dividing. Such intermediate stages are very troublesome to the taxonomist. We have no way of telling whether the isolated forms that belong to the Monarcha castaneoven·tris group (Fig. 10) or to the Tanysiptera galatea group (Fig. 15), are still members of the nominate species, biologically speaking, or have already acquired reproductive isolation. Morphologically, such forms are often as different as good species and have been regarded as such by the older taxonomists. Reproductive isolation is, however, frequently absent, as is proven by the existence of hybrid populations, such as those found between Pachycephala dahl and bougainvillaei on Whitney Island (Mayr 1932a), Pachycephala torquata and aureoven·tris on Rambi, Fiji (Mayr 1932b), for Megapodus affinis and eremita on Dampier Island (Mayr 1938b), and for many continental species (Meise 1936b).

It is of practical as well as of theoretical interest to learn how common these border-line situations are. We can study this if we examine all the possible gaps between the species of a genus and then segregate the doubtful allopatric gaps. In the North American warbler genus Vermi·sora there are 9 species, which means that there are 36 interspecific gaps n(n-1). Of these only 2 (or 5.6 percent) are possibly incomplete; the other 34 are unquestionably complete. In the related genus Dendroica there are 23 species, with 253 interspecific gaps, of which 2 (or 0.5 percent) are doubtful. A very high number of doubtful gaps exist in the genera in which all the species belong to one superspecies, as, for example, in the genera of birds of paradise Astragaly, Parotia, and so forth. If we were to add the figures of all genera of birds, I believe that the figure of doubtful gaps would be not more than 5 to 7 percent of the total number of intrageneric interspecific gaps.

We may summarize this discussion by saying that the allopatric species borders are not always sharply defined, but that this lack of clear-cut delimitation of some geographic representatives is an inevitable consequence of the continued operation of evolution.

THE DELIMITATION OF ALLOCHRONIC SPECIES

Hitherto we have spoken only of the delimitation of contemporary (synchronic) species. The delimitation of species which do not belong to the same time level (allochronic species) is difficult. In fact, it would be completely impossible if the fossil record were complete. The species of each period are the descendants of the species of the previous period and the ancestors of those of the next period. The change is slight and gradual and should, at least theoretically, not permit the delimitation of definite species. In practice, the fossil record is fragmentary, and the gaps in our knowledge make convenient gaps between the "species." In the few cases, in which an almost complete record of a continuous line is already available, the paleontologist follows the reasoning of the taxonomist who is confronted with an unbroken intergrading series of geo-
graphic populations. He breaks them up for convenience. It is obvious from these remarks that the "species" of the paleontologist is not necessarily always the same as the "species" of the student of living faunas. Breaks in series of intergrading "species" from subsequent geological horizons are not infrequent, even when the complete stratigraphic series from a certain locality is known. It is obvious in such cases, as several authors have pointed out, that the break must be due to a shift in geographic distribution (caused by a climatic or other environmental change), resulting in the replacement of a species or subspecies by a related one which had differentiated in a different region. Such a sudden break in a stratigraphic sequence is by no means proof of the instantaneous evolution of a new species.

THE PROCESS OF GEOGRAPHIC SPECIATION

The term speciation includes two processes: the development of diversity and the establishment of discontinuities between the diverging forms. To be sure, the two processes are correlated and frequently go hand in hand, but nevertheless they represent two rather different aspects of the course of evolution. The development of diversity, which is the more obvious of the two, has been discussed by us in detail in Chapters III and IV, under the heading of geographic variation. But variation and mutation alone do not necessarily produce new species. After all, it is quite thinkable that such variation might lead only to a single, interbreeding, immensely variable community of individuals. But this is not what we find in nature. What we find are groups of individuals that share certain characters, and that are more or less sharply segregated from other groups with different character combinations. These groups of individuals, these populations, races, or subspecies can be combined into species, and the latter into higher categories. This is a rough description of the situation as it occurs in nature. But we are not satisfied with mere description; we are interested in the dynamics of this process of speciation. Therefore, we want the answers to certain questions, such as: (1) Do species originate from individuals or from infraspecific units, and, if the latter, from which units? and (2) Is there any evidence for a broadening of infraspecific gaps, to the extent that they become interspecific gaps?

The answer to the first question is not simple, since it involves indirect proof. Even if no new species had ever developed under domestication or under other conditions of close observation, somebody might still insist that the spontaneous production of individuals representing new species was the usual process of species formation and that this had never been observed, merely because no interested observer had happened to be present when the new species first appeared. When De Vries described his first mutations, it seems that he was convinced that they demonstrated spontaneous species formation, and Lotey insisted on this point even at a much later date. In the meantime the species concept has been clarified by the taxonomist, and we know now that species differ by so many genes that a simple mutation would, except for some cases in plants, never lead to the establishment of a new species. Goldschmidt, therefore, modified the simple De Vriesian concept and replaced it by the hypothesis of speciation through systemic mutations: "Species and the higher categories originate in single macroevolutionary steps as completely new genetic systems." To him a species is like a Roman mosaic, consisting of thousands of bits of marble. A systemic mutation would be like the simultaneous throwing out of all the many thousands of pieces of marble on a flat surface so that they would form a completely new and intelligible picture. To believe that this could actually happen is, as Dobzhansky has said in review of Goldschmidt’s work, equivalent to "a belief in miracles." It seems to me not only that Goldschmidt did not prove his novel ideas, but also that the existing facts fit orthodox ideas on species formation so adequately that no reason exists for giving them up. This statement requires proof and there is perhaps no better way to introduce our arguments than to state briefly how we visualize the course of geographic species formation:

*A new species develops if a population which has become geographically isolated from its parental species acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down.*

This definition contains a number of postulates which we shall now discuss. To begin with, it involves the concept of the "incipient" species. Geographic speciation is thinkable only, if subspecies are incipient species. This, of course, does not mean that every subspecies will eventually develop into a good species. Far from it! All this statement implies is that every species that developed through geographic speciation had to pass through the subspecies stage. There is, naturally, a considerable infant mortality among subspecies and only a limited number reaches adulthood, or the full species stage. We shall see in Chapter IX under what conditions subspecies are most likely to be successful. At this point a few figures may be helpful. There are, in the entire world, approximately 8,500 species of living birds, with probably 35,000 recognizable subspecies. Apparently all the present orders of birds already existed at
the beginning of the Tertiary period, some fifty-five million years ago, and we can think of no reason why the number of species should have increased materially during the last ten or twenty million years. As some became extinct, others took their place. This replacement is apparently a rather slow process, since there is much evidence that most of the present species or the "lines" to which they belong have existed for considerable periods (Miller 1940). Occasionally a species succeeds in entering a previously unoccupied ecological niche. We are forced to the conclusion, on the basis of such considerations, that probably less than 10 or 15 percent of the existing subspecies of birds will both diverge sufficiently and survive long enough in isolation to become good species. The statement that subspecies are incipient species should therefore be emended to read: Some subspecies are incipient species, or subspecies are potentially incipient species. Furthermore, the isolated incipient species may consist of several subspecies or of a subspecifically as yet unmodified population.

We have called the theory of geographic speciation an orthodox theory, and this is correct when we realize how old it is and how widespread its acceptance. It had considerable support among thinking biologists, even long before Darwin. Leopold von Buch, for example, in a description of the fauna and flora of the Canary Islands (1825), writes as follows:

The individuals of a genus spread out over the continents, move to far-distant places, form varieties (on account of differences of the localities, of the food, and the soil), which owing to their segregation [geographical isolation] cannot interbreed with other varieties and thus be returned to the original main type. Finally these varieties become constant and turn into separate species. Later they may reach again the range of other varieties which have changed in a like manner, and the two will now no longer cross and thus they behave as "two very different species."

We can hardly improve on this statement, except for choosing a few different terms. The two points which von Buch makes, namely that geographic isolation was needed to permit the species difference to "become constant" and that proof of the species difference was given by their reproductive isolation, were, curiously enough, not recognized with the same clarity by later authors. Darwin, for example, was primarily interested in the development of the diversity which precedes species formation and hence neglected to explain the development and maintenance of discontinuities. M. Wagner seems to have been the first author to realize this gap in Darwin's argumentation, and it led him to propose in 1869, his "Migrationsgesetz der Organismen," which he later called more correctly the "separation theory" (Wagner 1889). On the basis of his extensive collecting experiences in Asia, Africa, and America, Wagner emphasized the nonexistence of sympatric speciation and stated that "the formation of a real variety which Mr. Darwin considers as 'incipient species,' can succeed in nature only where some individuals can cross the previous borders of their range and segregate themselves for a long period from the other members of their species." Darwin himself, in a letter to Wagner, admitted later that he had overlooked the importance of this point.

The speciation process does not need to be completed during this isolation. Dobzhansky (1940, 1941a) has pointed out that selective mating in a zone of contact of two formerly separated incipient species (zone of secondary intergradation, p. 99) may play an important role. The two incipient species must be sufficiently distinct, so that the hybrid offspring of mixed matings has discordant (unbalanced) gene patterns; in other words, the individuals produced in such matings must have a reduced viability and survival value.

Let it be assumed that two incipient species, A and B, are in contact in a certain territory, and that mutations arise in either or in both species which make their carriers less likely to mate with the representatives of the other species. The nonmutant individuals of the species A which cross to B will produce a progeny which is, by hypothesis, inferior in viability to the pure species; the offspring of the mutant individuals will have, other things being equal, a normal viability. Since the mutants breed only or mostly within the species, their progeny will be more numerous or more vigorous than that of the nonmutants. Consequently, natural selection will favor the spread and establishment of the mutant condition (Dobzhansky 1941a), until only conspecific pairs are formed or, in other words, until complete discontinuity (a bridgeless gap) has developed between the two species. Dobzhansky presents a plausible case, and we agree that such a selective process may help to complete the establishment of discontinuity, in those cases in which some interbreeding has taken place between incipient species.

The question is, however, whether or not this is the only way by which reproductive isolation can be established. Naturalists, from L. von Buch down to our contemporaries, have always believed that good species can complete their development in isolation. They find an abundance of cases in nature which seem to permit no other interpretation. The most conclusive evidence is, of course, presented by the multiple invasion of islands by separate colonizing waves coming from the same parental stock. Let us, for example, take Norfolk Island, 780 miles
from the coast of Australia, and surely never in continental connection with any of the surrounding island areas or continents. Among its scanty bird fauna (about 15 species of land birds) there are 3 species of *Zosterops: norfolkensis, tenuirostris,* and *albogularis,* which in the same order are progressively more different from their only close relative, *Zosterops lateralis,* from the Australian mainland. The island is about 44 square kilometers in area and can easily harbor several thousands of pairs of each species. The following interpretation of this situation is obvious, and there seems no other interpretation nearly so convincing (Stresemann 1931). There were three waves of immigration. The first had already become specifically distinct when the second wave arrived. If the single or the two pairs of *Zosterops* which comprised the second colonization had hybridized with the more-than-thousand-pair population of the first wave, they would have been swamped out of existence within one or two generations. The second wave had developed into a separate species when the colonizing pair of the third wave appeared. The discontinuity between the three species could not have become established through a slow, selective process, as described above by Dobzhansky. The bridgeless gap must have been there already, when the second and third set of colonists arrived; otherwise there would not be three species on the island. The distance of 780 miles between Norfolk and the mainland precludes the possibility of numerous attempts at colonization, by which an isolating mechanism could have been built up gradually through selection. The same explanation applies, *mutatis mutandis,* to all other cases of double or triple invasions (see p. 173). It is also the best interpretation of many other situations in which two related species now have partly overlapping ranges, owing to the breakdown of former barriers (p. 176).

Some geneticists endorse the viewpoint of the naturalist, that the accumulation of small genetic changes in isolated populations can lead in the course of time to a new integrated genetic system, of such difference that it thereby acquires all the characters of a new species, including reproductive isolation. S. Wright (1941c) describes this in the following words:

If isolation of any portion of a species becomes sufficiently complete, the continuity of the fabric is broken. The two populations may differ little if any at the time of separation but will drift ever farther apart, each carrying its subspecies with it. The accumulation of genic, chromosomal and cytoplasmic differences tends to lead in the course of ages to intersterility or hybrid sterility, making irrevocable the initial merely geographic or ecologic isolation.

For a more detailed discussion of the genetic aspects of the establishment of biological discontinuity, we refer to Muller (1940). We maintain, therefore, that the discontinuity between species is due to their divergence (difference), both in regard to their cytogenetics and in regard to their crossability (ecological and ethological). The establishment of discontinuity is closely associated with the process of divergence, and, to make a pun, one might say: "The establishment of discontinuity is a continuous process." In other words, the big gaps which we find between species are preceded by the little gaps which we find between subspecies and by the still lesser gaps which we find between populations. Of course, if these populations are distributed as a complete *continuum,* there are no gaps. But with the least isolation, the first minor gaps will appear.

**Stages of speciation.** — That speciation is not an abrupt, but a gradual and continuous process is proven by the fact that we find in nature every imaginable level of speciation, ranging from an almost uniform species at one extreme to one in which isolated populations have diverged to such a degree that they can be considered equally well as separate, good species at the other extreme. I have tried in a recent paper (Mayr 1940a) to analyze this continuous process and to demonstrate its different phases by subdividing it into various stages. I am well aware that these divisions are somewhat artificial and that a polytypic species may be in different stages in different parts of its range at the same time. Still, this analysis is useful, as we shall see in the subsequent discussion. The classification of my 1940 paper has been somewhat modified, since I now realize that what I then called stage (1) is as much the final as the first stage of speciation. A species may have a small range because it is so new that it has had as yet no time to expand (Willis's age and area concept), or because it is adapted to a unique situation, or because it developed in a particularly isolated location (island, cave), or because it became extinct in the other parts of its range. A widespread species is more likely to represent the first stage of speciation than one with a narrowly restricted range.

There are many cases in nature which cannot be fitted very well into this scheme, but still it will be possible to take the entire number of species of a systematic group (let us say birds or butterflies) from one particular region and classify them according to the stage of speciation to which they belong. The resulting figures of such an analysis shed much light on the degree of speciation and, in particular, on the degree of geographic isolation in the respective region.
Stage 1. A uniform species with a large range

Resulting in:
Stage 2. A geographically variable species with a more or less continuous array of similar subspecies (2a all subspecies are slight, 2b some are pronounced)

Resulting in:
Stage 3. A geographically variable species with many subspecies completely isolated, particularly near the borders of the range, and some of them morphologically as different as good species

Resulting in either
Stage 4. Noncrossing, that is, new species with restricted range or
Stage 5. Interbreeding, that is, the establishment of a hybrid zone (zone of secondary intergradation)

Followed by:
Process 1. Differentiation into subspecies

Followed by:
Process 2. a) Isolating action of geographic barriers between some of the populations; also b) development of isolating mechanisms in the isolated and differentiating subspecies

Followed by:
Process 3. Expansion of range of such isolated populations into the territory of the representative forms

Fig. 16. Stages of speciation.

To demonstrate the value of this method, which is applicable only to well-known groups, I have listed in Table 10 the passerine birds of three geographic regions, including the extraterritorial range of each species. Stage 5 was omitted and in stage 4 every uniform species with small range was included.

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<th>STAGE</th>
<th>MANGCHURIA (CONTINUOUS RANGES)</th>
<th>NEW GUINEA (PARTLY CONTINUOUS RANGES)</th>
<th>SOLOMON ISLANDS (DISCONTINUOUS RANGES)</th>
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<td>1</td>
<td>1.0</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>2</td>
<td>1.9</td>
</tr>
</tbody>
</table>

An analysis of this tabulation shows that stages 3 and 4, which indicate the final stages of evolution, are almost nonexistent when geography and geology favor continuous ranges, while stages 1 and 2a, indicating the early stages of evolution, reach a definite high in such continental areas. In contradistinction, we find that where geographic factors break up the species ranges to a high degree, as, for example, on an old tropical archipelago such as the Solomon Islands, a great number of the species are in the final stages of evolution (3 and 4) and comparatively few in the early stages (1 and 2a). A student of speciation must study regions with continuous ranges as well as those with discontinuous ranges before he can generalize on the dynamics of the speciation process. To base all conclusions on the temperate zones of the large Old World and New World continents leads inevitably into error or to a very one-sided viewpoint, because these two regions are characterized by special conditions. Not only are there very few effective geographic barriers, but most of the populations are also comparatively young, because they occupied their present ranges only after the rather recent retreat of the ice. So far as I know, all workers who minimize the importance of geographic variation for species formation base this opinion...
on work done in the Holarctic region. On the other hand, von Buch, Darwin, Wallace, and others derived their clear ideas on evolution from a study of both continental and insular species. Kiney (1937b) has presented us with a particularly graphic description of the differences between these two types of species.

THE PROOF FOR GEOGRAPHIC SPECIATION

The conclusion of the taxonomist of birds, mammals, butterflies, and other well-known groups that geographic isolation is in most groups of animals one of the necessary conditions of speciation has not remained unchallenged. Rensch (1939a) recently has cited a whole list of books and papers by authors who deny the importance of geographic speciation (allopatric speciation). Goldschmidt (1940) devoted most of the first half of his book (183 pages) to a refutation of this thesis. It may be in order, therefore, to gather additional proof for the existence and importance of geographic speciation. But what is proof? Is it not sufficient to point out, as we have done, that the majority of well-isolated subspecies have all the characters of good species and are indeed considered to be such by the more conservative systematists? Is it not sufficient to show that subspecific characters are of exactly the same kind as specific characters? Is it not sufficient to point out that certain Rassenkreise clearly merge into each other?

All this evidence is highly indicative, but it may not be completely convincing. The fact that Goldschmidt and others, who know this evidence, deny the importance of geographic speciation makes it necessary to present additional proof. The evidence in favor of geographic speciation can be summarized as follows:

**ALL DIFFERENCES BETWEEN SPECIES ARE SUBJECT TO GEOGRAPHIC VARIATION; THERE IS NO DIFFERENCE OF KIND BETWEEN SPECIFIC AND SUBSPECIFIC CHARACTERS.**

The discussion as to what characters are subject to geographic variation (Chapter III), proves this point so conclusively that nothing need be added. If species formation and subspecies formation were two fundamentally different processes, we should find that two different classes of characters were subject to variation in the two categories (geographic race and species). But this is not what we found in our analysis of geographically variable characters. Not a species character is known, be it morphological, physiological, or other, which is not subject to geographic variation. As a general rule it can be said that characters separating full species tend to be more pronounced, and that there are often more differences between species than between subspecies. But this criterion breaks down completely in all the really doubtful cases, and many sub-species are characterized by more striking differences than some "good" species. It is therefore obvious that there is no "gap" between subspecies and species, as far as systematic characters are concerned.

**REDUCED FERTILITY BETWEEN GEOGRAPHIC RACES OF ONE SPECIES**

We have already called attention to a number of mistakes in logic in the discussion of sterility as a species criterion (p. 119). Lack of interbreeding in nature between two forms of animals (in breeding condition) may be due to two different obstacles, sexual isolation and sterility. Even though these two factors are frequently correlated, they actually belong to two entirely different fields: ethology and cytogenetics. It has been proven again and again for birds and many other animals that several species can live side by side in nature without normally hybridizing, even though they are highly or completely fertile with one another in artificial crosses. It is therefore not to be expected that fertility should always be reduced between the geographic races of all the species. Still, the number of cases of partial sterility between geographically distant races of the same species is surprisingly high, particularly among insects. Rensch (1929:93–94, 1933) has listed a number of them and new ones are being discovered and described continually. Very striking are the intersexes or otherwise less viable forms which occur if certain subspecies of Lymantria dispar are hybridized (Goldschmidt 1934). A considerable degree of sterility occurs also between some of the geographic races of many of the "wild" species of Drosophila (excluding melanogaster and other cosmopolitan "domestic" species). These data have been summarized by Spencer (1940) and Dobchansky (1941a). Pictet (1937) found reduced fertility, in certain species of butterflies and moths, between populations that are not even separated into different subspecies. This is true for Nemeophila plantaginias and for the geographic and altitudinal races of Lasiocampa quercus. Neighboring races are highly fertile, but the wider their geographic separation, the more pronounced is the reduction of fertility, some races being almost or completely sterile. It does not require much imagination to picture what would happen, if such races should meet in nature. The presence of even partial sterility would speed up considerably the establishment of biological isolating mechanisms between the two incipient species. The most recent work on Drosophila proves that not only may fertility be reduced in geographic races of the same species, but also the sexual
attraction (Patterson 1942, Stalker 1942). This also proves that reproductive isolation (misogamy) is a by-product of genetic divergence.

THE BORDER-LINE CASES

It is a logical postulate of our thesis (that species originate from geographic races) that we should find certain subspecies which have just about reached the threshold of the species. Such cases are usually called border-line cases, since it is impossible in these situations to decide whether the questionable form is "still" a subspecies or "already" a species; they are in the border zone between the two categories. There are a number of different situations which can be included with the border line cases. For example, a form may be a species on the basis of one species definition and a subspecies on the basis of another definition. Or certain forms may behave like subspecies of a single species in part of their range and like good species in other parts of their range. Border-line cases are by no means exceptional; in fact, we find a surprisingly high proportion of such situations in all the regions in which geographic or ecological conditions promote active speciation. Border-line cases may be classified as follows:

No criteria permit satisfactory distinction between species and isolated subspecies.—The ranges of two allopatric forms are often separated by a geographic gap, a form of distribution which is particularly common among island, mountain, and cave species, where there is, in all cases, a discontinuous distribution of the habitat. The taxonomist who adheres to a strictly morphological species definition is not particularly baffled by such cases. Every isolated form that is separated from its nearest relative by a clear-cut discontinuity of taxonomic characters is regarded by him as a good species. He is, in consequence, forced to admit as good species many isolated forms, which differ by very minute, but constant and unbridged differences. Such a procedure is defensible, as long as we are merely interested in the pigeonholing of specimens in the correct collection cases. It becomes an absurdity when we view the species as a biological unit.

In the Atlantic Ocean, about one hundred miles east of Nova Scotia, there is a small, isolated land mass, Sable Island. On this island, and only on it, lives a sparrow, the Ipswich Sparrow (Passerculus sandwichensis princeps), which is unquestionably derived from the same stock as the Savanna Sparrow (Passerculus sandwichensis) of the mainland of North America. The differences are, however, very striking; the Sable Island bird is much larger (wing, 73.5-79.5, against 66-72 mm.), and of a distinctly different coloration (much more whitish) from the races

of the neighboring mainland. Even in the field the two forms can be told apart at a glance.

Some ornithologists hold that the Ipswich Sparrow is nothing but a subspecies of the Savanna Sparrow, whereas others insist that the morphological gap should be recognized as a species gap. Similar situations are encountered in nearly every well-worked taxonomic group.

It is of interest to find out how common such cases are. I have made an analysis of all the North American birds listed in the A. O. U. Checklist (1937), a work which is rather conservative in its taxonomic point of view. I have omitted only introduced species and the purely marine order Tubinares. In 374 genera there are 755 species with a total of 1,367 species and subspecies. At least 94 of the listed 755 full species of North American birds will be considered by some authors to be merely subspecies of other species. In other words 12.5 per cent of the species of North American birds have reached a very interesting taxonomic stage: They still show by their distribution and general similarity that they had been only recently geographical forms of some other species, but they have, in their isolation, developed morphological characters of such a degree of difference that the majority of authors now prefers to call them good species. Typical examples in the North American bird fauna are: Ipswich and Savanna Sparrow (Passerculus), Red-shafted and Yellow-shafted Flicker (Colaptes), Audubon's and Myrtle Warbler (Dendroica), the various species of the genera Junco and Leucosticte, etc. The majority of these forms are more or less isolated, either on the islands off the California coast or on the various mountain ranges of the Rocky Mountains or in the lowlands east and west of the Rocky Mountains. These "semi-species" comprise 12.5 per cent of the total of species in the rather continental fauna of North America. For a typically insular region, namely the Lesser Sunda Islands, Rensch (1933) thinks that not less than 47 species are intermediate among a total of 160 species. I have analyzed the birds of the Solomons Islands and find that if we employ a narrow species concept there are 174 species of land and fresh-water birds; if we, however, employ a wide species concept (=include within one species all geographical representatives) there are only 125 species. In other words, of 174 species there are 49 of intermediate status, that is 28.2 per cent (Mayr 1940a).

An even clearer impression can be gained if we analyze, in a similar manner, the entire bird fauna of a single island (Table II).

The percentage of border-line cases depends on a number of factors (size, distance from mainland, and so forth) which will be treated in a later chapter. Only one of the birds of the British Islands, the red grouse (Lagopus scoticus), is a border-line case. It is by many authors considered to be a race of the continental Lagopus lagopus.

There is no doubt that similar conditions prevail in other animal groups and even in plants, but the taxonomy of most of these groups has not yet been clarified to the point where we can express the number of
border-line cases in actual percentage figures. Kinsey (1937b) divides species into two classes, continental and insular. A study of his data has convinced me that an ornithologist would call most of his “insular” species either subspecies or border-line cases. Kinsey’s data are therefore of interest to us in this connection. According to him the percentage of insular species in various taxonomic groups is as follows: the gall wasps (Cynipidae) 76 percent, the salamanders of the family Plethodontidae 74 percent, the cave crickets of the genus Ceuthophilus 62 percent, the pond weeds of the genus Potamogeton 15 percent, the spiderworts of the genus Tradescantia 9 percent, and so forth. On the basis of these data, it seems as if animals tended more to the formation of localized, isolated forms than plants, although both Tradescantia and Potamogeton are rather “weedy” plants, and perhaps not typical for all plants.

These isolated forms, or “insular species,” are excellent evidence in support of geographic speciation and, as such, welcome to the student of evolution; but, on the other hand, they are also very troublesome to the modern taxonomist, as far as their practical treatment is concerned. Our species definition included the statement: “A species consists of a group of populations which replace each other geographically which are potentially capable of interbreeding . . . where contact is prevented by geographical . . . barriers.” The question remains, how can we determine which of these isolated forms are “potentially capable of interbreeding”? Unfortunately, there is no way of testing this in most cases, and we may as well admit that a decision is then possible only by inference. We must study other polytypic species of the same genus or of related genera and find out how different the subspecies can be that are connected by intermediates, and, vice versa, how similar good sympatric species can be. This scale of differences is then used as a yardstick in the doubtful situations. And even after all these data have been given due consideration, the decision will often be, to a large extent, as Stresemann would say, “a matter of taste.” Such arbitrary decisions have to be made in all modern taxonomic work. In a revision of the genus Megapodus, I proposed to unite, into one polytypic species, the seven species nicobariensis, tenimberensis, reinwardi, freycinet, eremita, affinis, and layardi, which had been recognized even by such progressive authors as Peters and Stresemann. The reasons were that I found not only that all these species were strictly allopatric, but also because the form (macgillivrayi) from the Louisiade Islands combined the characters of reinwardi and eremita and because members of a hybrid population between affinis and eremita (Dampier Island) were, by convergence, similar to freycinet. On the other hand, it was decided to retain as full species the forms lapérouse (Micronesia) and pritchardi (Niouafu, central Polynesia), which, although strictly allopatric, are separated from all other forms of the genus by very striking morphological as well as geographic gaps (Mayr 1938b). Meinertzhagen (1935:765) lists Alauda arenensis and A. gulgula, Apus apus and A. pallidus, and Riparia obsOLEta and R. rupestris as typical border-line cases among birds.

**Extreme morphological development of terminal subspecies.**—The isolated forms of Megapodus, which are considered separate species, differ only in size, color, and proportions. But sometimes such isolated forms develop such a degree of difference that they might be considered different genera if they were judged only on morphological criteria. As a matter of fact, many of these forms have originally been described as separate genera, and their true systematic position has become clear only recently. That they are nothing but subspecies, or at best allopatric species, is particularly evident in cases in which the widely diverging species are the extreme ends of a long chain of intermediate subspecies.

The distribution map (Fig. 17) of the barking pigeon (Ducula pacifica) of Polynesia well illustrates the geographic conditions under which such extreme morphological development may occur. This species has developed a form (galeata) on the Marquesas Islands which, on account of its peculiarly developed bill, was, until nine years ago, considered a good genus (Serresius).

Other genera that are based on morphologically distinct geographic forms are: in pigeons, Oedirhinus (of Ptinopus izouzus) and Ciroyphna (of Croyphna lutuocirens); in kingfishers, Todirhamphus (of Halcyon chloris); in birds of paradise, Taeniopadiceps and Astrarchia.
(of Astrapia nigra), Schlegelia (of Diphylloides magnificus), Uranornis (of Paradisaea apoda); in drongos, Dicranistes (of Dicrurus bracteatus); in rails, Porphyriornis (of Gallinula chloropus); in Passeres, Galacotides (of Blythropygia), Conopoderas (of Acrocephalus), Pinarolotes (of Clytohynchus), Papxworthonyx (of Orthonyx), Allocotops (of Melanocichla lugubris); and so forth.

I could quote many other similar cases in which subspeciation, that is geographic variation, has actually brought about the formation of unquestionably new species of birds. Unfortunately, the systematics of most other groups of animals is not sufficiently well known to justify our drawing comparable conclusions, but Kinsey reports exactly the same situation in cynipid gall wasps (Kinsey 1930, 1935, 1937a, 1941).

The superspecies, a border-line situation.—Nobody will deny that all the strongly specialised allopatric forms which we have just listed are merely “glorified” geographic races, and it seems possible to combine groups of them into single species if one wanted to carry the principle of geographic representation to an extreme. This is just about what Kleinenschmidt does in his Formenkreise. Rensch (1929, 1934) realizing that two rather different taxonomic concepts were hidden under the term Formenkreis, namely ordinary polytypic species and groups of allopatric species, proposed the term Artenkreis for the latter. I have suggested the replacement of this term, for more convenient international usage, by the term superspecies since it is the superspecific counterpart to the infraspecific unit, the subspecies (Mayr 1931a).

A superspecies consists of a monophyletic group of geographically representative (allopatric) species which are morphologically too distinct to be included in one species. It is inconsequential whether the species of which the superspecies is composed are monotypic or whether some of them break up into geographic races. The principal feature of the superspecies is that it presents, geographically, the picture of an ordinary polytypic species, but that morphologically these allopatric species are different to such a degree that reproductive isolation between them may be suspected. One of the most important aspects of the superspecies is that it is the highest category which can be delimited objectively, as is appar-

*Super*, beyond, is the counterpart of *sub*, below (or within); *supra*, above, is the counterpart of *infra*, below. The term superspecies, used by several recent authors, seems to me to be an unfortunate combination. We can speak of superspecific categories, as we speak of infraspecific factors, but as we use the term subspecies for a specieslike category that is below the species, we must use the term superspecies for a specieslike category that goes beyond the species. This corresponds to a similar usage of these propositions in subgenus and supergenus, in subfamily and superfam-

family, and so forth.
ent from the definition. Rensch has pointed out that the adoption of this concept affects in no way the nomenclature of the species which are involved and that no objections can be raised against it on this basis. On the other hand, it offers a number of considerable advantages in the preparation of faunal lists, in zoogeographic studies, and in discussions on speciation. Some critics (for example Meise 1938:63) have proposed the elimination of the term superspecies by broadening the scope of the polytypic species to the point at which it includes all geographic representatives. If we go back to these Kleinschmidtian views, we shall have to include in one species the red and the yellow birds of paradise; we shall have to call all the Astrapia, all the Parotia, and all the juncos one species, to mention some avian examples. To call all these forms subspecies not only obscures their distinctness, but it violates even our species concept. There is some evidence that many of the species of which the superspecies are composed are reproductively isolated. On the other hand, it may also be called a mistake to list them merely as ordinary species, without combining them into superspecies, because this ignores an important relationship. The superspecies should be employed only in cases of strikingly different allopatric species. It would be an abuse of this concept if an author were to call every polytypic species, composed of insular and thus well-marked subspecies, a superspecies.

The members of a superspecies form a taxonomic and phylogenetic unit, all being descendants of one ancestral population. The recognition of the superspecies helps very materially to reduce the gap between subspecies and species, and, since every superspecies is a border-line case, it calls attention to these intermediate situations. The superspecies has its greatest practical importance in zoogeographic work. It is unwarranted to count the members of superspecies as separate species, if we compare two faunas. For example, it is altogether misleading to say that Polynesia has more species of fruit doves (Philinopidae) than New Guinea. Current check lists record 17 species from Polynesia and 11 species from the mainland of New Guinea, but there are only 3 superspecies in Polynesia as compared to 11 on New Guinea. The comparison of the number of superspecies indicates, therefore, much more accurately how rich the New Guinea fauna is in fruit doves than does a comparison of the number of species.

The ranges of several typical superspecies have been illustrated by me in a recent paper (Mayr 1940, Figs. 2, 3, 4, 7). The superspecies Zoe terops rendova consists of three species: Z. rendova, Z. latirostris, and Z. bellavella; the superspecies Ducula pacifica consists of the species galeata, aurora, pacifica, oceanica, and perhaps myristicivora, and so forth.
it is to be expected that it also has its border cases. The species pairs, *Anthus pusillus* and *euniceps*, *Tanysiptera hydrochares* and *galatea*, *Ptiliopus dubetichouarsi* and *mercieri*, and *Lalage maculosa* and *sharpeti*, which we shall discuss later in this chapter, must be mentioned here. Each of these pairs of species would be considered as belonging to the same superspecies if there was not some overlap of ranges. The superspecies is the stage at which the transition from allopatric to sympatric species is most likely to occur.

The indivisible gradient of the lower systematic categories.—We have stated repeatedly that every one of the lower systematic categories grades without a break into the next one: the local population into the subspecies, the subspecies into the monotypic species, the monotypic species into the polytypic species, the polytypic species into the superspecies, the superspecies into the species group. This does not mean that we find the entire graded series within every species group. It simply means that in the absence of definite criteria it is, in many cases, equally justifiable to consider certain isolated forms as subspecies or as species, to consider a variable species monotypic or to subdivide it into two or more geographic races, to consider well-characterized forms as subspecies of a polytypic species or to call them representative species.

In a revision of the neotropical snake genus *Dryadophis*, Stuart (1941) recognizes 17 forms in 6 monotypic and 3 polytypic species, belonging to 7 species groups. Isolated forms which do not intergrade are considered full species. Many ornithologists would not recognize this criterion and, by considering some of the “species” subspecies, they would reduce the total number of species to 4 or 5 (*bifossatus*, *pulchriceps*, *pleei*, *amarali*, and *boddartii* with *healthii*, *melanolomus*, and *dorsalis* as subspecies). In the bunting genus *Junco* there are about seven or eight possible ways of delimiting the species, and none of the disagreeing authors can prove that his arrangement is more correct than the others. The presence of graded series and the absence of all decisive criteria makes it necessary to rely on subjective judgments. But the fact that so many geographic races stand on the border-line between subspecies and species is further proof of the importance of geographic speciation.

A similar gradient of categories may be observed, if we compare the degree of geographic variation of a number of related species in the same geographic region. Usinger (1941) describes very graphically such a situation among the hemiptera which have colonized the Hawaiian Islands. After arrival on the islands, these species proceeded to diverge, and have now reached varying degrees of differentiation, the extent of which can not be determined without breeding experi-

ments. Thus the various species in the endemic genera fall into a series, ranging from (1) the widespread and variable *Oceansides nimbatus* Kirk, not yet broken up into distinguishable forms on the various islands, through (2) the scarcely differentiated *Nesius saundersianus* Kirk, to (3) the “polytypic species” (Huxley 1938) or “Rassenkreis” (Rensch 1929) *Nesius validus* White, which has structurally distinct but closely allied races on each island, then to (4) the “supra-species” (Huxley 1938) *Nesius hiolens* Perkins, the Oahu form of which was unhesitatingly called a distinct species, until a connecting link was discovered on Molokai, and finally to (5) that which Huxley (1938) has called a “geographical subgenus” and Rensch (1949) has called an “Artenkreis,” namely, the *Nesius maulensis* Blackburn group which has diverged to such an extent that the Oahu and Kauai forms have attained the status of full species and had not even been recognized as belonging to this group previously.

A similar gradient of systematic categories was described by me for some islands and mountains of the Papuan Region (Mayr 1940b:267).

### Double Invasions

Oceanic islands are defined as all those islands that have received their fauna from other islands or from neighboring continents by transoceanic colonization, and not over land bridges (Mayr 1941b). The immigrants soon start to diverge from the original parent population (a process which is speeded up by the small size of most of these island populations) and if, after a sufficient time interval, a second set of immigrants arrives from the same source, the two waves of immigrants will behave like good species.

**Simple cases.—**Cases of double colonization are known from nearly every sufficiently isolated oceanic island, for example among birds, from Tenerife (*Fringilla teydea* and *F. coelebs canariensis*), western Canary Islands (*Columba lauviora* and *C. boliti*), Norfolk Island (*Zosterops albo­gularis*, *Z. tenuirostris*, *Z. lateralis norfolkiensis*), and Samoa (*Lalage maculosa* and *sharpeti*). Double invasions also occur on continental islands, for example Ceylon (*Brachypterus erythromonthus* and *B. benghalensis intermedius*), Luzon (*Pitta kochi* and *P. erythrogaster*), and Celebes (*Dicurus montanus* and *D. hottentottus*). Isolated mountain peaks may present exactly the same phenomenon, since they act as distributional islands. *Dendrobiastes bonthaina* (together with *D. rufula*) on the Pie of Bonthain (S. Celebes) and several of the endemic species of Mount Kina Balu (Borneo) may be explained in this manner. Willis (1949) has listed a number of endemic plant species on the mountains of Ceylon, for which the same manner of origin is probable.

Not a single case of double colonization is known to me from recent continental islands, such as Britain or Ireland, or from any oceanic is-
land (such as Biak or Rennell) which is situated close to a continent. The reason for this is obvious. Two species can develop from immigrant descendants of the same parent species only if the time interval between the first and the second colonization was sufficient to permit the earlier arrivals to develop sexual isolation. The new arrivals are simply absorbed by the earlier ones if this condition is not fulfilled. This is the reason why such twin species are absent from incompletely isolated islands.

Double colonizations of islands are, of course, not restricted to birds; it is only that the advanced condition of avian systematics makes their detection easier. I know of at least one well-analyzed case in butterflies. The common European Swallowtail (Papilio machaon) occurs as a single species in all of the Mediterranean countries. Two species of the machaon group are found only on the islands of Corsica and Sardinia, Papilio machaon subsp. and Papilio hospiton (Eller 1936:79). P. machaon subsp. is closest to the Italian and southern French races of the mediterraneus group, and P. hospiton to the North African races (saharae group) of P. machaon. When the two sets of colonists met on Corsica and Sardinia, they had diverged sufficiently from each other not to interbreed. Some of the species of the hemipteran genus Nysius reported by Usinger (1941) seem also to belong here.

A particularly puzzling case is presented by the Tasmanian thornbill, which reveals how difficult it is to decide, purely on the basis of morphological criteria, whether an island form is a species or a subspecies (Mayr and Serventy 1938). On the island of Tasmania (AE) south of Australia, there are two very closely related species of Acanthiza (thornbill). One of these (A), Acanthiza pusilla diemensis, is very similar to the subspecies Acanthiza pusilla pusilla (B), of the mainland of Australia, opposite. The other species Acanthiza ewingi (E), which lives beside diemensis like a perfectly good species without any signs of interbreeding, is also fairly similar to B (Acanthiza pusilla) and clearly an earlier offshoot of B. However, E is as different from C (western Australia) as is B, but B and C are completely connected by intergradation and interbreeding. E is morphologically closer to B than is C, but since A also occurs on Tasmania, E cannot be considered a subspecies of B. There is no question that we would list E as a member of the species B. C, if the second invasion (A) had not taken place on Tasmania and revealed the specific distinctness of E. This teaches us that analogy is a poor tool in analysing these cases, and that in many of these border-line cases one guess is as good as another.

Archipelago speciation.—The chances for double invasions are particu-

Fig. 18. Double invasion of Tasmania by Acanthiza pusilla. Completion of the speciation process proved by successful second colonization. A = Acanthiza pusilla diemensensis; B = A. pusilla pusilla group; C = A. pusilla apicalis-albovirens group; E = Acanthiza ewingi.

larly favorable in archipelagos consisting of two or three good-sized islands. The representative subspecies which develop in isolation on these islands have a good chance to become in time so different that they can spread to the neighboring island without mixing. This probably explains the presence of two species of related hummingbirds (Eustepha-
taken place on ancient archipelagos, such as Hawaii or the Galápagos Islands. The case of the Geospizidae on the Galápagos Islands has been excellently reviewed by D. Lack (1940a, 1942), while the more ancient and more complicated case of the Drepanididae on Hawaii has, so far, defied adequate analysis. Even richer species swarms than those of the Drepanididae have developed among the Hawaiian invertebrates.

The Proterhinus weevils with one hundred and fifty species, Cerambycidae of the genera Plagithymus and Neoclytarus, Lygaeid bugs of the genera Nysius, Neseis and Oceanides in the tribe Orsillini and a host of other genera in all the principal orders of Hawaiian insects, have developed unique branches of from six to over one hundred species. Each of these is a small phylogenetic world in itself. Here we find geographical replacement, well developed, with distinct forms on each separate island and often on each host [Usinger 1941].

The same is true for the Hawaiian snails and in particular for the genus Achatinella. There is no doubt that archipelago speciation presents some of the most instructive examples of geographic species formation.

**Partial Distributional Overlap**

*Border invasions.*—Another class of border-line situations is presented by cases in which two otherwise allopatric species show a slight overlap of ranges. Particularly interesting are those cases in which the two representative species are so similar that they would probably be considered subspecies, if it was not for the existence of the area of overlap. Even so, the entire distributional picture indicates the former subspecific relationship. Cases of this sort are not frequent, because, aside from some ecological competition, there is no reason why the two species should remain largely allopatric after the biological isolating mechanisms have developed to the point of complete reproductive isolation. As soon as such a species moves back into the range of a sister species (stage 4, p. 160), it is likely to spread so fast that all traces of the original allopatric condition are soon wiped out. This is particularly true for all large genera (with numerous species). Cases of slight overlap, as we shall presently see, therefore indicate generally a rather recently completed establishment of discontinuity between species.

The overlap is usually due to the recent breakdown of a geographic or ecological barrier. Tanysiptera galatea now lives in South New Guinea side by side with Dryadophis, because the arm of the sea that had separated them previously (Fig. 15) recently dried up. T. hydrocharis lived on an island which connected the Aru Islands with the Oriomo River plateau. T. galatea was restricted to the mainland of New Guinea and offshore islands. When the erosion debris of the rapidly rising central range of New Guinea filled the sea, T. galatea was enabled to intrude into the formerly isolated range of hydrocharis, but no interbreeding took place. A similar situation exists in a Venezuelan snake (Stuart 1941). Dryadophis amarali developed apparently from plesi stock during insular isolation on Tobago Island or on the Paria Peninsula. Recent geological events have led to an overlap of its range with that of plesi, but there are no signs of interbreeding. A third situation of the same sort has been described in the case of a Florida dragon fly. The Florida species Progopomphus alachuensis and the Cuban species P. integer developed in insular isolation from the eastern North American species P. obscurus.

The reunion of the central Florida Island (Pleistocene) with the mainland of North America brought the ranges of P. obscurus and P. alachuensis in contact with each other... and P. obscurus invaded north and north-central Florida. In north-central Florida the invading species overlapped the range of the endemic one, but remained ecologically distinct, inhabiting the rivers and streams, leaving the lakes for the species already established [Byers 1940].

More frequent than the joining of an island with the mainland is range expansion due to the breakdown of ecological barriers in connection with climatic changes. The coming and the going of the ice during the Pleistocene age has been responsible for a great many such changes, of which very few have as yet been analyzed. It is not always clear whether the isolation was due to glaciation or occurred at an earlier date. Some authors, notably Salomonsen (1931), list a very high number of European species pairs as being due to Pleistocene separation; other authors hold that this separation was only in exceptional cases long enough to permit the development of interspecific gaps. The final decision cannot be reached until we know more details as to climate and plant distribution during Miocene and Pliocene. Until such time, cases discussed below will have to be treated with some reservation. There is an eastern and a western species in many genera of European birds. Stresemann (1919), who studied the distribution of the western Tree Creeper (Certhia brachydaactyla) and the eastern Tree Creeper (C. familiaris), suggested that this peculiar pattern of distribution was of Pleistocene origin. When, at the height of glaciation, the Scandinavian and the Alpine ice caps approached each other in central Europe to within a distance of about 200 miles, they forced all European animal life into a southwestern (southern France, Spain) and southeastern (Balkans) refuge. During this period of isolation, the parental Certhia population developed specific differences and reproductive isolation and did not inter-
breed when the ranges of the expanding species finally met. (But see Steinbacher 1927.) Today the two creepers occur side by side without interbreeding, in a broad zone which extends from northwestern Germany to the Alps. Salomonsen (1931) explains on the same basis similar species pairs in the avian genera *Hippolais* (polygotta western, icterina eastern), *Luscinia* (megarhyncha western, luscinia eastern), and *Musci­capa* (hypoelca western, and albicollia eastern). A number of parallel situations exist among European amphibia. The western toad, *Bombina variegata*, became a mountain form during the glacial separation, while the eastern toad, *Bombina bombina*, remained a lowland species. Range expansion after the retreat of the ice led to a considerable distributional overlap, but the two species remain effectively isolated, since they occur at different altitudinal levels. At a few localities there is an overlap of the altitudinal ranges, and it is in such places that intermediate (hybrid) individuals have been found. The two species can be hybridized in captivity without difficulty (Mertens 1928a, b). A similar overlap of ranges is shown in the case of two central European frogs, but the ecological factor which keeps the two species separate is, in this case, the breeding season. The western species (*Rana esculenta*) breeds from the end of May well into June, while the eastern species (*Rana ridibunda*) completes its breeding season before the end of May (Mertens 1928a). The two species of newt *Triturus cristatus* and *T. marmoratus* developed apparently during glacial separation. There is now a narrow zone of overlap in central France, in which a few hybrids with reduced fertility have been observed ("T. blasii"). A similar case is presented by *Triturus vulgaris* and *T. helveticus*. The present overlap between these two species is very considerable, comprising the British Isles and the region between eastern France and western Germany. *T. helveticus* prefers the mountains, *T. vulgaris* the lowlands, but both have been found in the same waters, where lack of sexual affinity prevents interbreeding (W. Herre 1936). The glaciers, which at the height of the Pleistocene era advanced into the Po basin from the southern foot of the Alps, separated very effectively a number of snail and insect populations, which lived on southern spurs or foothills of the Alps. These populations expanded when the ice retreated, and, even though they are still largely allopatric, there are now a number of places where two of such "forms" overlap without any signs of interbreeding. Good examples of this can be found in the work of Klemm (1939) on the snail genus *Pagodulina* and of St. Zimmermann (1932) on *Orcula*.

A few similar cases have also been described from North America, although isolation was not as long-continued and effective as in Europe, where the formidable barrier of the Alps has been so important. The geographic ranges of the two mice *Peromyscus leucopus* and *gossypinus* are exclusive except for some areas of overlap in the Dismal Swamp of Virginia, in northern Alabama, and, more widely, in the lower Mississippi Valley. They occupy, in part, the same habitats, where their ranges overlap, but there is no evidence of any interbreeding in nature, except for two presumed hybrids reported from Alabama. The two species are very similar and fully fertile in the laboratory (Dye 1940b). Quite a number of similar cases have been described from North American snakes, of which I shall report only a few.

The polytypic species (or species group) *Crotalus atrox* (diamondback rattler) exhibits very clearly the effects of isolation during the height of the Pleistocene age (Gloyd 1940). The species became separated into three portions, one on the west coast of North America, which developed into *ruber*; a second one in Mexico, which developed into *atrox*; and a third one in Florida, which became *adamanteus*. Additional populations were isolated on the tip of Lower California (*lucasiensis*) and on some islands near Lower California (*eszul* and *tortuagens*). After the retreat of the ice, the populations expanded northward, but the gap between *adamanteus* and *atrox* in the lower Mississippi Valley was never closed. However, *atrox* moved westward until it reached the border of the range of *ruber* in the western part of San Diego County, California. There are no hybrids or intergrades known from this district, but the forms (species?) seem to be ecologically separated. Another interesting case of speciation is presented by the species *Crotalus viridus* and *mit­chelli", which are very similar and the ranges of which are still largely exclusive. In southern California there is, however, a considerable area of overlap, without any signs of intergradation or hybridization. Among the North American bull snakes (*Pituophis*) there is an overlap of the ranges of the species of *catenifer* and *sayi*, which species indicate by their pattern of distribution that they were formerly subspecies of a single polytypic species (together with *melanoleucus*) (Stull 1940). The overlap results occasionally in a limited amount of hybridization without an actual breaking down of the species limits. This happens for example, where the moth *Platyamia cecropia* overlaps the ranges of the closely related species *nokomis*, *columbus*, and *gloveri* (Swedner 1937).

All these cases have one feature in common, namely, that owing to range expansion two formerly allopatric forms begin to overlap and to prove thereby to be good species. If no overlap existed and if we had to classify these forms merely on the basis of their morphological distinctness, we would probably decide, in most cases, that they were sub-
species. But overlap without interbreeding shows that they have attained species rank.

Overlap of the terminal links of the same species.—The perfect demonstration of speciation is presented by the situation in which a chain of intergrading subspecies forms a loop or an overlapping circle, of which

![Diagram](image_url)

**Fig. 19.** Circumpolar projection of the ranges of the forms of the *Larus argentatus* group, showing overlap of the terminal links of a chain of races. A = vegae; B1 = smithsonianus; B2 = argentatus; B3 = omissus; C = californicus; D1 = thayeri; D2 = leucopodus; E1 = hepulina; E2 = antelius; E3 = fuscus; E4 = grattai; F1 = mongolicus; F2 = cachinnans; F3 = michahellis; F4 = atlantis.—*L. fuscus* (with grattai) lives now beside *L. argentatus* (with omissus) like a good species. (From Mayr 1940a.)

the terminal forms no longer interbreed, even though they coexist in the same localities. To be sure, such speciation by force of distance is much rarer than speciation by strict isolation, but at the same time these cases demonstrate species formation by geographic variation in the most perfect manner. One of the reasons why such cases have not been recorded in the literature more frequently is a purely psychological one. The puzzled systematist who comes across such cases is tempted to "simplify" them by making two species out of one ring, without frankly telling the facts. Overlapping rings are disturbing to the orderly mind.
of the cataloguing systematist, but they are welcome to the student of speciation.

In birds such cases are rather frequent, even though the situation is generally more complex than can be indicated in the subsequent discussion. The Great Titmouse (Parus major), for example, was apparently split into at least three groups during the Pleistocene (Rensch 1933). As the three groups came together again after the retreat of the ice, they either formed broad or narrow hybridization zones or they expanded into the same area (upper Amur Valley), behaving like good species. We now have both minor and major in the Amur Region, without signs of intergradation or hybridization, although the two "species" are connected via China-India-Persia through a completely linked chain. Similar cases are those of the Luras argentatus group in northwestern Europe (Fig. 19) and of the Halcyon chloris group in the Palau Islands (Fig. 20). Additional cases are those of Zosterops in the Lesser Sunda Islands, of Lalage in southern Celebes, and of the honey buzzards (Pernis) in the Philippines. A more detailed analysis of the relationship of the babblers Eupetes caerulescens and nigricrus in the Wanggar district of New Guinea may also lead to similar conclusions.

The warbler Phylloscopus trochiloides (Fig. 21) has a wide distribution in Asia. It occurs over most of northern Asia and also on the mountains which surround the arid central-Asianic plateau. Two forms (viridanus and plumbeitarus) meet in the Altai Mountains (western Sayan and Uriankhai) without interbreeding. The two forms are connected by a gapless chain of intergrading subspecies: obscuratus, trochiloides, and ludlowi. The area of overlap is probably rather recent—of post-Pleistocene origin (Ticehurst 1938a).

In the species Phylloscopus collybita there is another possible case of coexistence of two "subspecies" within the same area. The race abietinus, which came from northern Europe, meets in the western Caucasus the subspecies lorenzii, which came from the Himalayas and the western central Asianic mountains. Specimens of both forms have been collected during the breeding season in the same localities, although, in the main, the ranges of the two forms exclude each other. Nothing is known about possible differences of song, habits, and habitat in the area of overlap, but there are some indications that lorenzii is largely an altitudinal representative of abietinus (Ticehurst, op. cit.: 42–52). The ring is closed in the Pamir-Altai region, through the forms tristis and abietinus. The case of the House Sparrow (Passer domesticus) and the Willow Sparrow (P. hispaniolensis) is slightly different (see p. 268), but agrees in one re-

![Figure 21. Overlap of two terminal links in a ring of subspecies of the warbler Phylloscopus trochiloides. The subspecies of this ring are: V = viridanus; L = ludlowi; T = trochiloides; O = obscuratus; and P = plumbeitarus. The overlap between viridanus and plumbeitarus in the districts between the western Sayan Mts. and the Yenisei River is indicated by cross-hatching. (From Ticehurst 1938a.)](image-url)
Forbes 1928). The two colonizing lines met in Cuba, where they now live side by side without interbreeding. Goldschmidt’s question (1940:120): “Would they be able to mate and produce fertile offspring, if brought together?” is beside the point. The point is not what they would do under the artificial conditions of captivity, but what they do in nature. Many good species can be crossed in captivity, but that does not in the least weaken their status as good species. A very interesting overlapping circle of races exists in the mouse *Peromyscus maniculatus*. In Glacier National Park, Montana, a forest-inhabiting subspecies, *P. m. artemisiae*, meets a grassland race, *P. m. ogooodi*, with no evidence of interbreeding (Murie 1933). The failure of the two subspecies to interbreed in the zone of overlap is only partly due to the differences in their ecological requirements, for at some places near the margins of their habitats the two races live together without interbreeding. The two forms would undoubtedly be considered good species if the chain of intergrading races, now connecting them, were broken. (Fig. 22).

The evidence discussed by me on pages 162 to 185 is, it seems to me, conclusive proof for the existence of geographic speciation: If an isolated population of a species remains long enough in this isolation, it may acquire biological isolating mechanisms which permit it, after the breakdown of the isolating barrier, to exist as a separate species within the range of the parental species. The reproductive isolation, which originally was maintained by the extrinsic means of a geographic barrier, is being replaced during this isolation by intrinsic isolating barriers. One species has developed into two.