FIGURE 10–5
Musical rendition of the formation of a calling trio of the Southern Spring Peeper, *Hyla crucifer bartramiana*. [After Goin, *Quart. J. Florida Acad. Sci.*, 1948 (1949).]

have been almost ignored in this research; but the many examples given in this chapter indicate that the principles of behavior formulated for the other groups apply to the herps as well, and that these animals deserve further ethological study.

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SPECIATION AND GEOGRAPHIC DISTRIBUTION

WHEN HUMANS FIRST BEGAN to explore the world, they became aware that different kinds of animals lived in different regions: crocodiles were found in the river Nile, but not in the Thames; many snakes lived in Europe, but there were none in Ireland. As long as the doctrine of Special Creation held sway, it was easy to explain these facts by saying that each region had its own fauna, created especially for it and adapted to it. But this explanation was never really satisfactory. For one thing, there is too much overlap: not all animals are restricted to a single region. Many of the animals the early explorers found in the New World were different from anything they had ever seen, but others were strikingly similar to those they had known at home. It was also observed that animals could adapt well to regions in which they did not naturally occur. Attempts to introduce animals into a new region—for example, the European Edible Frog *(Rana esculenta)* into England—were sometimes successful.

When the true nature of fossils was finally recognized, and their orderly succession became apparent, it was realized that some animals had once lived in regions where they no longer occurred, and that many forms had become extinct. Dinosaurs had once roamed every continent, but they no longer existed. It became necessary to postulate a whole series of special creations, the next to last presumably destroyed by the biblical Flood. The

attempt to maintain the doctrine of Special Creation eventually became absurd.

It was his observations on the distribution and local variation of animals in South America and the nearby Galápagos Islands that led Charles Darwin to his ideas on the origin of species by the gradual change of populations through time. The pattern of distribution of animals is one of the strongest arguments for evolution, and offers many clues to the course evolution has taken. Conversely, to understand the present distribution of animals we must take account of their evolutionary history as well as their ecological requirements. Thus speciation and distribution patterns supplement and reinforce each other.

ORIGIN OF NEW SPECIES

New species arise from preexisting species through the process of evolution. Evolution simply means a change through time, but when we use it to denote a biological process, it means a change in the gene frequency of a population through time. Although old species may be constantly evolving to adapt to changes in their environment, new species are not constantly appearing. If you recall the definition of a species in Chapter 1, you will remember that a species is a group of like organisms that are reproductively isolated from other groups. Thus, for new species to arise, populations of an existing species must evolve separately, and this discontinuity must remain until the difference in gene frequency and composition of the populations results in their inability to produce fertile offspring—that is, until the populations are reproductively isolated.

Since discontinuities may develop in several ways, there are several ways new species may arise:

I. Allopatric speciation—divergence of populations
   in different geographic areas.
II. Sympatric speciation—divergence of populations
   in the same geographic area by
   A. Ecological segregation
   B. Temporal segregation
   C. Polyploidy and parthenogenesis

Allopatric Speciation

No plant or animal species occurs continuously throughout its entire geographic range. A species is broken into a number of small populations, each centered in an area of preferred habitat. Since the environmental conditions differ from area to area, each population is exposed to different selective pressures and evolves to meet them. Although the exchange of genetic material between adjacent populations may be low, immigration and emigration of just a few individuals is enough to maintain the genetic continuity of the species. However, if a population becomes isolated from neighboring populations by a physical barrier, such as a mountain range, the populations begin to diverge genetically, since there is no gene flow. The rate of divergence depends on the nature and intensity of the different selective pressures to which the populations are exposed. If the populations are separated long enough, genetic differences appear that prevent the production of viable or fertile offspring. The isolated population has evolved into a new species, for it is now reproductively isolated from its ancestral species.

Although we have never seen a new species arise, the steps in speciation are visible in extant species. Many of the herp populations of peninsular Florida differ from their mainland relatives. In some instances, the peninsular populations are reproductively isolated from the mainland populations (Florida Black-headed Snake, *Tantilla relicta*); in others, reproductive isolation has not occurred (Florida Mud Turtle, *Kinosternon subrubrum steindachneri*). Whether the differences are specific or subspecific, the change in population characteristics usually occurs in the area of the Suwannee Straits, an ancient seaway that once cut Florida from the mainland.

Sympatric Speciation

In contrast to allopatric speciation, sympatric speciation means the segregation of populations living in the same geographic area. Isolation of populations occurs, not by distance or geographic barriers, but by habitat differences (ecological segregation), different seasons of reproduction (temporal segregation), or instantaneous reproductive isolation (polyploidy and parthenogenesis). Allopatric speciation appears to be the most common mechanism in reptiles and amphibians, as it is in other animals; however, the sympatric speciation mechanisms also appear to have produced new species of herps.

In ecological speciation, an ancestral population occurs in two contiguous habitats that are strikingly different and impose different selective pressures on their inhabitants. Adaptations for survival and successful reproduction in one habitat will be unsuited for the other. Those individuals who breed with members of their own habitat cohort will produce more viable offspring, and if this condition lasts long enough the populations of the two habitats will become reproductively isolated. The Florida Scrub Lizard (*Sceloporus woodi*) and Eastern Fence Lizard (*S. u. undulatus*) live in contiguous but microclimatically distinct habitats, and may be an example of ecological speciation. Such segregation of individuals is also seen in the

Lesser Earless Lizard, *Holbrookia maculata:* the populations living on white sands are lightly colored, those on the adjacent black rock outcrops are dark. These populations are not reproductively isolated, but do show how ecological segregation can evolve.

The potential for temporal speciation exists in herps, but we have no direct evidence that it has in fact occurred. All that is required is for a population to divide its breeding season into two separate periods, with the members of each breeding-period cohort and their offspring confining their reproductive activities to that period. One can imagine a frog species that breeds during the wet season confining its reproduction to the beginning and end of the season and evolving into two species, or sea turtles, with their two- to four-year breeding cycles, segregating into populations breeding in different years, which then evolve into new species through random genetic drift.

New species can arise instantaneously by polyploidy (multiple sets of chromosomes). The Gray Tree Frog, *Hyla versicolor,* of the eastern and central United States is a tetraploid (four chromosome sets), morphologically indistinguishable from the sympatric *H. chrysoscelis,* but reproductively isolated from it. A number of other polyploid frogs are known. Some populations of the South American *Odontophrynus americanus* are tetraploid; *Ceratophrys dorsata* is octoploid (eight chromosome sets). These polyploid frogs are bisexual, and are reproductively isolated from the diploid (two chromosome sets) species from which they evolved.

Speciation by polyploidy can also result from the breeding of two species that do not normally interbreed (hybridization). The salamanders *Ambystoma tremblayi* and *A. platineum* are triploid (three chromosome sets) hybrids of *A. jeffersonianum* and *A. laterale. A. tremblayi* has two sets of *A. laterale* and a single set of *A. jeffersonianum* chromosomes, whereas *A. platineum* has the reverse. The triploids are all females, and reproduce gynogenetically. The eggs are formed by mitosis; development is initiated by penetration of the sperm from either *A. jeffersonianum* or *A. laterale,* but the sperm and egg pronuclei do not fuse, and thus the sperm contributes no genetic material to the offspring. Twenty-six all-female species of lizard are known—some triploid, others diploid. This phenomenon is discussed further under "Parthenogenesis" in Chapter 7.

ISOLATING MECHANISMS

No effort is needed to maintain reproductive isolation if two originally united populations are separated in either time or space. However, such temporal and spatial barriers are often breached, and mating between the

two populations becomes a possibility. If they have not diverged greatly, they will merge back into a single population; if there is sufficient genetic divergence, they will be prevented from successful reproduction by one or more isolating mechanisms:

    I. Premating mechanisms
       A. Differences in breeding behavior
          1. In breeding sites
          2. In breeding season
          3. In courtship behavior
       B. Physical differences
          1. In recognition characters
          2. In body size and form
          3. In form of genitalia and related structures
    II. Postmating mechanisms
       A. Hybrid sterility
       B. Hybrid inviability
       C. Primary sterility

Isolation mechanisms are described briefly in Chapter 1, and many examples are given in Chapters 6 and 7. The point to be made here is that postmating mechanisms are all related to genetic incompatibility. Such incompatibility develops only through genetic divergence arising from the processes of speciation. Postmating isolation mechanisms are usually the ones that operate when two related species first come into contact under breeding conditions. Although such mechanisms maintain the genetic integrity of each species, they are of no benefit to the cross-mating individuals. These individuals essentially waste their gametes, for their offspring cannot survive or are not capable of reproduction. Thus there is a selective pressure for the evolution of premating isolation mechanisms to avoid such loss of gametes. Premating mechanisms dominate in the segregation of sympatric species.

OTHER EVOLUTIONARY PROCESSES

It is frequently assumed that all evolution comprises random mutations and the accumulation of different gene frequencies in different populations. But other processes are also at work: the chromosomes themselves evolve.
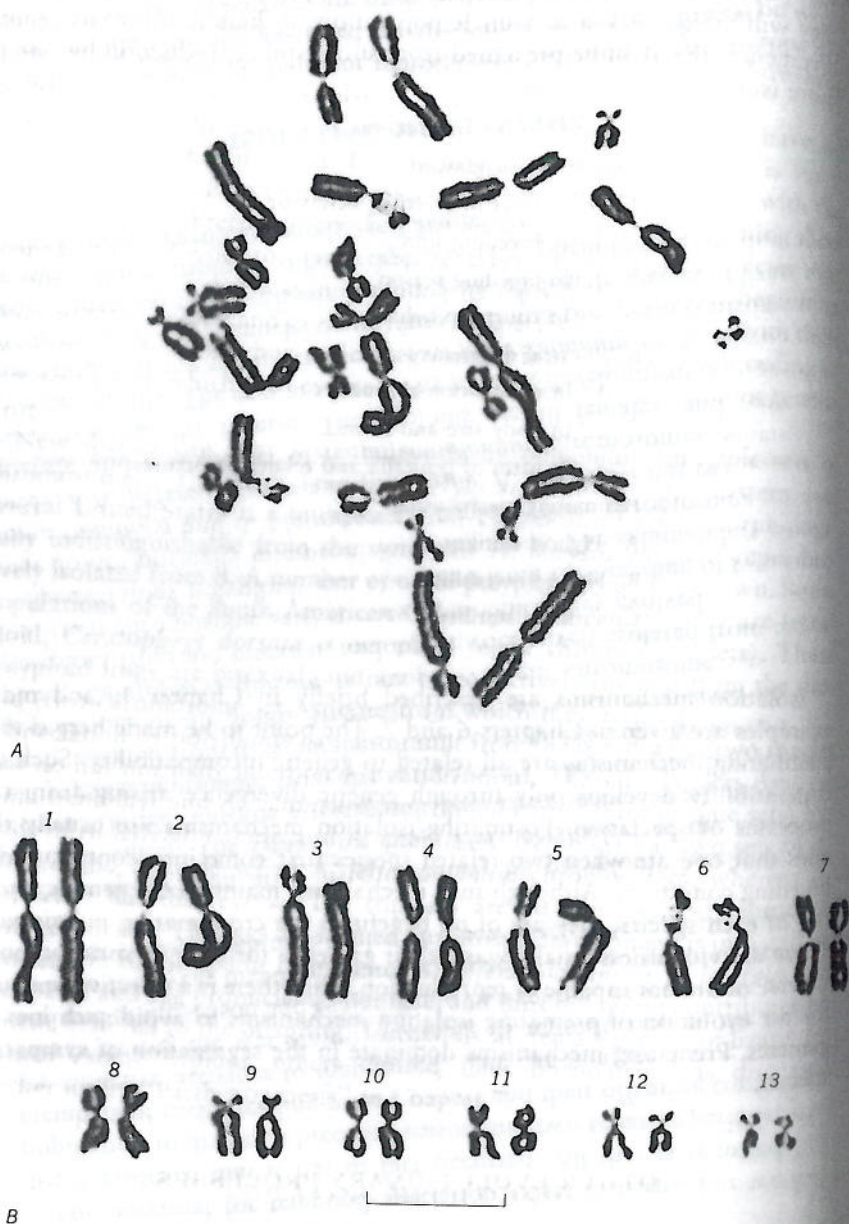
Evolution of Karyotypes

The karyotype of an organism is a description of its chromosome complement. It is usually represented by a photograph or drawing of the metaphase chromosomes, arranged by pairs in order of decreasing length (Figure 11–1). Sometimes the decrease in length is gradual throughout the series, but sometimes the chromosomes are readily divided into two groups, large (macrochromosomes) and small (microchromosomes). The chromosomes differ not only in length, but also in the position of the centromere (the point to which the spindle fibers attach during mitosis). If the centromere is midway between the two ends, the chromosome is said to be metacentric. If it is closer to the midpoint than to one end, the chromosome is submetacentric. If it is closer to the end than to the midpoint, the chromosome is subtelocentric. These chromosome types may be spoken of collectively as bi-armed. If the centromere is at the end, the chromosome is telocentric (or acrocentric or uni-armed) (Figure 11–2). Chromosomes also differ in whether secondary constrictions are present, and in the pattern of banding revealed by special staining techniques.

There are various ways in which a karyotype can be modified. Two telocentric chromosomes can fuse to form a single, larger, bi-armed chromosome, a process known as centric fusion. Centric fission also occurs: a bi-armed chromosome can break in the region of the centromere to form two telocentric ones. The tree frogs *Osteopilus septentrionalis* and *O. brunneus* are closely related. *O. septentrionalis* has a karyotype of $2n = 24$ bi-armed chromosomes, a typical hylid pattern. *O. brunneus* has a karyotype of $2n = 34$ chromosomes, of which 7 pairs are bi-armed and 10 pairs uni-armed. The 20 uni-armed chromosomes correspond to the separate arms of the 5 largest chromosome pairs of *O. septentrionalis*. Apparently the karyotype of *O. brunneus* arose from one like that of *O. septentrionalis* by centric fission (Figure 11–3).

Another process of karyotype modification is pericentric inversion. The part of the chromosome containing the centromere breaks loose and is reinserted upside down. In this way the shape of the chromosome can be changed. For example, a metacentric chromosome can be converted into a subtelocentric one.

Among amphibians, most chromosome evolution has apparently been by centric fusion and the loss of microchromosomes. Primitive forms tend to have a large number of chromosomes, more telocentric ones, and many microchromosomes; advanced forms have fewer chromosomes, most of which are bi-armed, and lack microchromosomes. The hynobiid salamanders have chromosome numbers of $2n = 40–62$ and may have as many as 50 telocentrics, including up to 12 pairs of microchromosomes. The salamandrids have $2n = 22–24$, with no telocentrics or microchromosomes.
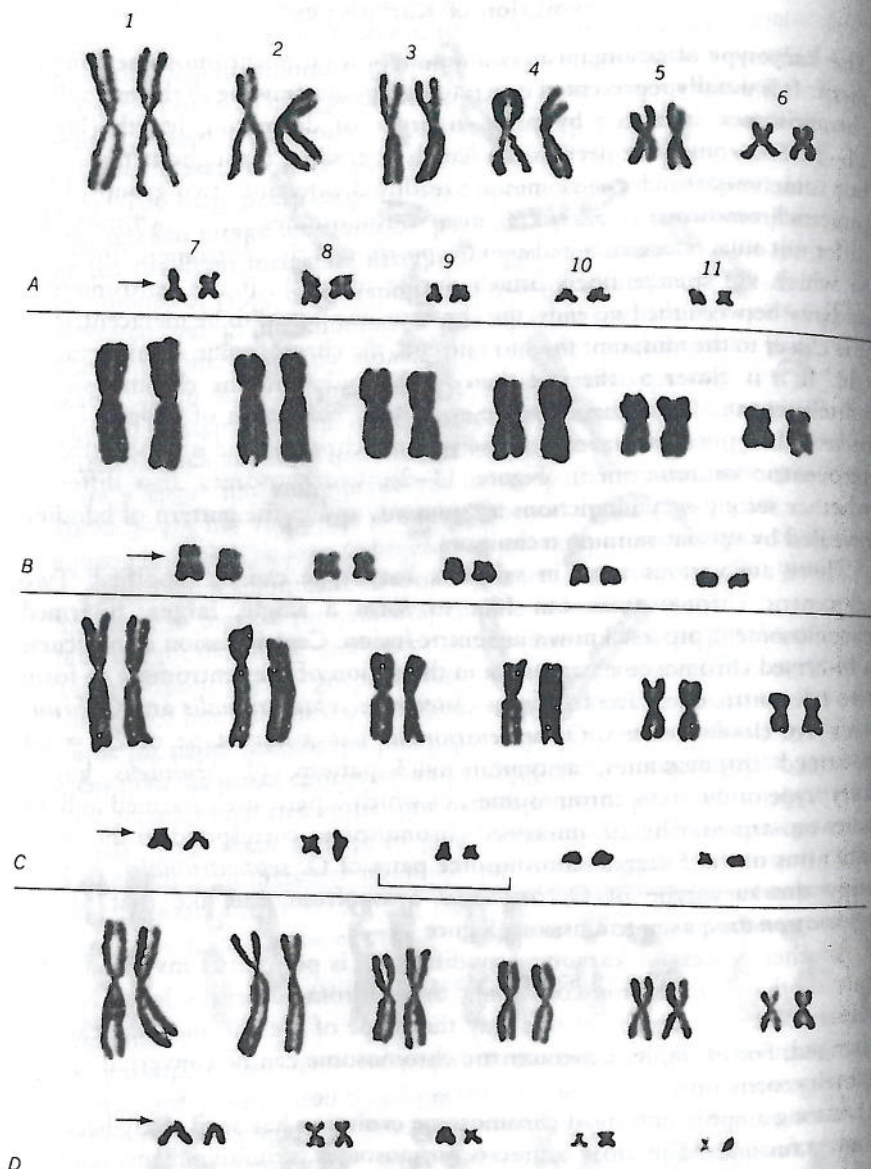

FIGURE 11–1
(A) Metaphase chromosomes of a male *Pachymedusa dacnicolor* as they appear under the microscope. (B) The same, arranged in order of decreasing length. The reference line represents a length of ten microns (10^{-5} m). [Courtesy of Charles J. Cole and *Systematic Zoology*.]

FIGURE 11-2
Karyotypes of four populations of *Sceloporus undulatus*, showing geographic variation in centromere position on chromosome number 7: (A) female *S. u. elongatus*; (B) male *S. u. hyacinthinus*; (C) male *S. u. hyacinthinus*; (D) female *S. u. tristichus*. Reference line = 10 microns. [Courtesy of Charles J. Cole and the American Museum of Natural History.]
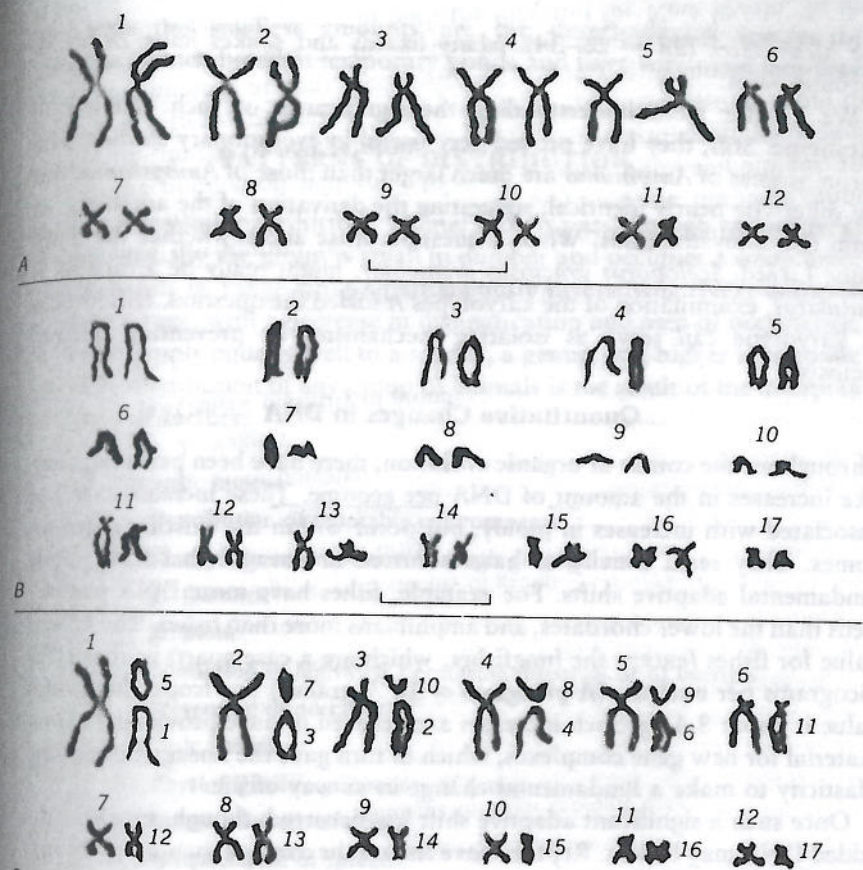
FIGURE 11-3
(A) Karyotype of *Osteopilus septentrionalis*. (B) Karyotype of *Osteopilus brunneus*. (C) The same as B with the chromosomes arranged to show their possible evolution from those in A. Reference lines = 10 microns. [Courtesy of Charles J. Cole and *Herpetological Review*.]

A similar pattern appears in frogs, though chromosome numbers are smaller ($2n = 14$--38) and centric fission appears to occur more frequently. The sirenids have unusual karyotypes: like the primitive hynobiids, they have large numbers of chromosomes ($2n = 46$--64), but they have no microchromosomes and few or no telocentrics. It has been suggested that the ancestor of the sirenids arose as a polyploid of a form that already had an "advanced" amphibian karyotype. Too few caecilians have been studied as yet to permit reliable interpretation.

Similar processes may have occurred in reptiles, but microchromosomes seem usually to have been retained. Among turtles, the cryptodires, usually considered more advanced, have more chromosomes ($2n = 48$--66) than do

the pleurodires ($2n = 26$–34). Many lizards and snakes have $2n = 36$ chromosomes.

We are far from understanding the significance of such changes in karyotype. Still, they have proved very useful in evolutionary studies. The chromosomes of *Amphiuma* are much larger than those of *Ambystoma*, but are otherwise nearly identical, suggesting the derivation of the amphiumids from the ambystomatids. When a question arose about whether the Sand Dune Lizard, *Sceloporus graciosus arenicolor*, might really be a race of *S. undulatus*, examination of the karyotypes resolved the question. Differences in karyotype can serve as isolating mechanisms by preventing normal meiosis.

Quantitative Changes in DNA

Throughout the course of organic evolution, there have been periodic, step-like increases in the amount of DNA per genome. These increases are not associated with increases in ploidy, but occur within the existing chromosomes. They seem usually to have occurred in lineages that have made fundamental adaptive shifts. For example, fishes have more DNA per nucleus than the lower chordates, and amphibians more than fishes. The modal value for fishes (except the lungfishes, which are a case apart) is about 1.7 picograms per nucleus. (A picogram $= 10^{-12}$ grams.) For frogs, the modal value is about 8.4 pg. Such increases are believed to have provided the raw material for new gene complexes, which in turn gave the lineage the genetic plasticity to make a fundamental change in its way of life.

Once such a significant adaptive shift has occurred, though, much of the added DNA may be lost. Reptiles have less on the average than amphibians, about 3–5.7 pg, and birds less than reptiles, about 1.5–3.5 pg.

As a class, the amphibians are unusual in the enormous interspecific variation they show in the amount of DNA per nucleus. The quantity of DNA is correlated with several other characters. The correlation is not exact, but in general, the more DNA, the larger the cell, the lower the metabolic rate, and the slower the rate of development. It has been suggested that, in the amphibians, it is selection for precisely these effects of the amount of DNA on metabolic and developmental rates that is responsible for the great intraclass variability. The salamanders, with their inefficient oxygen intake mechanisms, have very large to enormous amounts of DNA. The primitive hynobiids have about 33–43 pg/nucleus. The forms with the highest amounts, 90–165 pg, are all paedomorphic (*Andrias, Necturus, Proteus, Amphiuma*). The paedomorphic sirenids also have DNA amounts of over 90 pg. The more advanced salamandrids and plethodontids have intermediate amounts. Evolution in the salamanders and sirens seems to have entailed large increases in the amount of DNA per nucleus. Frogs, with their better-developed lungs, have less DNA (3–30 pg/nucleus). The

forms with the smallest amounts are the desert-adapted species of *Scaphiopus*, which breed in temporary ponds and have very rapid development rates.

PATTERNS OF DISTRIBUTION

During their evolutionary history, animal groups pass through certain typical stages. Initially the group is small in number and occupies a small area. It then expands its range while simultaneously diversifying. Next comes a contraction stage, with a decrease in diversification and area of occurrence. These stages apply equally well to a species, a genus, or a higher taxonomic group. The distribution of any group of animals is the result of the interplay of two sets of factors:

I. Extrinsic factors
   A. Distribution of favorable environments
   B. Changes in environments through geologic time
      1. Climatic
      2. Biotic
   C. Formation of highways permitting dispersal or of barriers preventing dispersal
II. Intrinsic factors
   A. Physiological requirements of group
   B. Time and place of origin
   C. Potential rate of spread
      1. Biotic potential
      2. Vagility
   D. Genetic plasticity of group

Extrinsic Factors

An animal's distribution reflects an area of favorable environment. The environment must be favorable for all life stages, for if one life stage cannot survive, the population will soon become extinct. Both amphibians and reptiles are limited by temperature, because their ectothermic physiology requires heat from an external source. Proceeding north or south from the tropics, the number of herp species declines rapidly with the annual mean temperature. Amphibians are more cold-tolerant than reptiles, and the true frogs (*Rana*) reach the Arctic in both the Old and the New World. In the Old World, a salamander (*Hynobius keyserlingi*), a lizard (*Lacerta vivip-*

ara), and a snake *(Vipera berus)* extend into the Arctic in areas where the temperature is moderated by warm currents. The reptilian osmoregulatory system is more resistant to water loss than that of amphibians, so that reptiles are able to live in drier areas and cross extensive salt-water barriers. A favorable environment implies not only favorable physical conditions, but favorable biotic ones as well. There must be a balance between predators and prey, hosts and parasites, competitors and food.

Most environments are stable only over relatively short periods of time by geologic standards. One of the best-known changes that has taken place is the warming of the northern hemisphere over the last ten thousand years. This trend is demonstrated by the retreat of the glaciers since the close of the Ice Age. The process appears to be continuing to the present day, and many groups of animals are still extending their ranges northward. Further back in geologic time, the coal beds in Pennsylvania show that semitropical swamps once flourished in what is now a hilly, well-drained, temperate region.

Climatic aspects of the environment are not the only ones that change: biotic factors are also constantly shifting, since the forces of evolution are continually at work on all forms of life. New sources of food become available to animals able to take advantage of them; new enemies appear that must be evaded. Perhaps most important of all, new and better-adapted competitors for food and breeding sites either move into the area or evolve within it.

Although the main continental land masses have probably remained relatively constant, at least since the Cenozoic, there have been many changes in the connections between them. South America was cut off from North America by an arm of the sea for the greater part of the Cenozoic era. During this time, distinct faunas evolved in the two regions. When the land connection was reestablished during the Pliocene, it became possible for North American forms to invade South America and vice versa. The mingling has been very incomplete, and the two faunas are still essentially different. For example, only one group of salamanders *(Bolitoglossa* and its allies of the family Plethodontidae) has invaded South America.

Of course, the same topographic feature may serve as a highway of dispersal for some forms and as a barrier to others, depending on the physiological requirements of the groups in question. Broad lowland valleys are barriers to salamanders adapted to dwelling on mountaintops, but may serve as highways to other forms, such as toads.

Intrinsic Factors

Even closely related forms often show differences in their physiological requirements. Furthermore, some animals have broad ecological tolerance and are able to adapt to conditions over a wide area, whereas others are

limited in ecological tolerance and hence are restricted to a narrow range. This sort of difference is probably reflected in the distribution of two of the North American Rat Snakes: the ecologically adaptable *Elaphe o. obsoleta* ranges from Ontario and northern New England south to Georgia and west to Minnesota and Texas, whereas *E. subocularis* is limited to the arid region of trans-Pecos Texas, southern New Mexico, and adjacent Coahuila.

Besides physiological requirements, which determine which environments a group can occupy and what highways of dispersal are available to it, the group's time and place of origin play an important part in determining its geographic distribution. If a group arises in a region that is blocked from an adjacent region by some barrier, it will not be able to spread into that region—even though there may be environments there that are well suited to its needs. The frog family Leptodactylidae is very widespread in South America and contains many genera, but only three of these are present in the United States; this is probably because it was only recently, in the geologic sense, that a passageway was opened.

If a group is of very recent origin, it may not have had time to spread very far from its center of origin. How fast a group will spread depends in part on its biotic potential. Animals capable of producing large numbers of offspring in a relatively short time will, other things being equal, be able to occupy new areas more rapidly than forms with a low rate of reproduction. The vagility (inherent power of movement) of the species may also affect the rate of dispersal. Both of these factors are probably relatively minor, since many forms with low biotic potentials and limited vagility have been able to occupy large areas of the earth's surface.

Finally, the genetic plasticity of the group will determine whether it will be able to occupy new environments, whether it can adapt itself to changes in the environment *in situ,* or whether it must follow receding belts of its old environment or become extinct.

MOVEMENT OF SPECIES

The movement of a species is a populational phenomenon. An entire species does not emigrate *en masse,* abandoning its old range and establishing a new one. Instead, a few individuals move into new regions and establish new populations; populations elsewhere become extinct. The species moves slowly over decades or centuries like a huge amoeba, withdrawing from unfavorable areas (local extinction) and expanding into favorable ones (colonization). The net result may be nothing more than a continual adjustment in the edge of the species' range, or it may be an actual shift in the species' distribution, its adaptation to a different environment, or the generation of a new species from a population that has become isolated.

Expanding Populations

Most animals produce more offspring than can survive within the distributional confines of the parent population. Thus overcrowding is an ever-recurring phenomenon in any but a dying population. Individuals near the periphery of the range are constantly being pushed into new and unfavorable environments. Undoubtedly, most of them perish; however, occasionally such colonists find a favorable area and establish a new population, or adapt to an area unfavorable to their parents.

Relict Populations

Under favorable conditions, a species will thus increase its range by founding new populations along the periphery of the range. Eventually, conditions will change, and the species must retract its range if its populations are unable to adapt to the changing environment. Populations often become isolated in small pockets of favorable environment as the main range of the species retracts from them. The survival of such relict populations depends on the stability of these pockets of the original environment. The existence of relict populations does not necessarily indicate that a species is becoming extinct, but simply that the range of suitable habitat is not as great as it was. The cluster of prairie species (*Kinosternon flavescens, Heterodon nasicus, Pseudacris streckeri*) in Illinois shows that the prairie once extended that far east. The relict populations of *Salamandra salamandra* in northern Africa indicate the past existence of a continuous humid land connection to Europe. Other relict distributions, such as the confinement of *Sphenodon* to a few small islets in New Zealand, do indicate that a species is becoming extinct.

Waif Populations

A waif population is one whose ancestors reached an area (usually an island) as strays or castaways rather than through the normal dispersal of an expanding population. In times of flood, an uprooted tree or a fragment of riverbank may be swept downstream and carried out to sea. It may be caught by ocean currents and eventually stranded on the shores of a distant island. Such a natural raft may harbor a clutch of eggs, a pregnant female, or a pair of individuals of the same species. If they survive the hazards of the journey, they may be able to establish a population on the island.

It is not always easy to tell whether a population is waif or whether it reached the island at a time when the island was still connected to the mainland. In either case, speciation may have occurred, so that the population differs from any now found on the mainland. Islands that have been formed entirely by volcanic action, or that have been completely submerged

since their last previous connection with another land mass, must *ipso facto* be populated by waifs.

In the past few thousand years, man has, either accidentally or intentionally, carried many animals from one part of the globe to another. It is customary, though, to speak of populations arising from animals transported by human agency as introduced rather than waif species.

The island of Bermuda is inhabited by a species of lizard, *Eumeces longirostris*, that differs greatly from all other species of its genus and is found in no other place; it is undoubtedly waif. All the other herps of the island seem to have been introduced by man.

DISTRIBUTION OF FAUNAS

Animal and plant species naturally occur where they can survive and reproduce. A species' distribution indicates its ecological and physiological requirements and limits. The edge of its range shows the presence of a barrier. Where the barrier is common to most species of a fauna, it is likely to be a geographic barrier of long standing, and nearly impossible to cross. The areas on either side represent centers of speciation and dispersal for unique faunas. The world was recognized to comprise six of these faunal regions, or zoogeographic realms, by P. L. Sclater in 1858. Although the names of these zoogeographic realms have changed somewhat, their delineation remains basically the same (Figure 11–4).
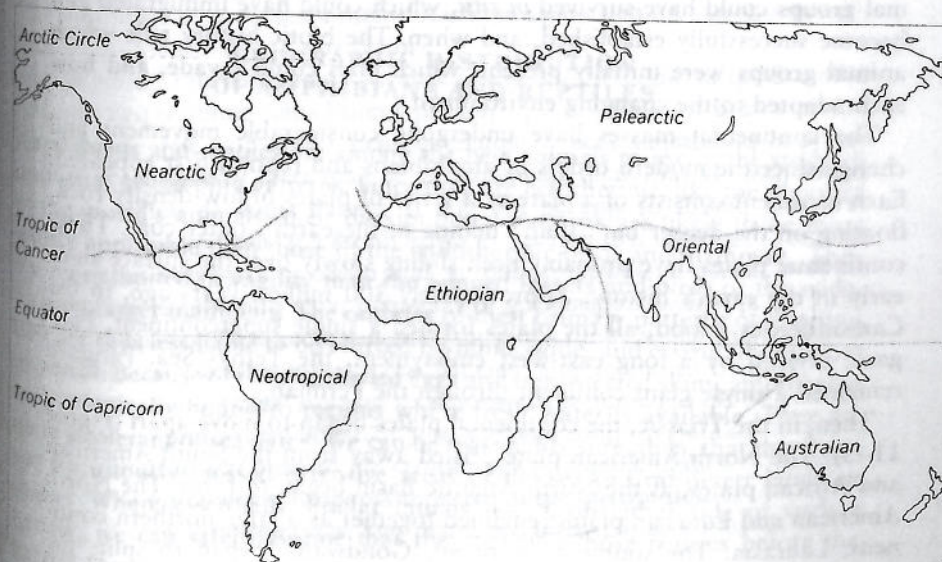

FIGURE 11–4
Zoogeographic regions of the world.

The New World is divided into the Nearctic region (North America, including the Mexican Plateau) and the Neotropic region (Central and South America). All of Europe, Africa north of the Sahara, and Asia north of the Himalayas constitute the Palearctic region. Since there is a high degree of faunal similarity between the Nearctic and Palearctic, Sclater combined them as the Holarctic region. Africa south of the Sahara, the Arabian Peninsula, and Madagascar form the Ethiopian region. The Oriental region includes all of Asia south of the Himalayas and extends southeastward through the Malay Archipelago to Celebes and the Philippines. The Australian region comprises Australia, New Guinea, New Zealand, and adjacent islands. The scattered islands of the Pacific are sometimes recognized as the Oceanic Islands region.

Although it is best not to try to define these regions too sharply, they are useful to describe gross distributional patterns and are, furthermore, deeply entrenched in the zoological literature.

CONTINENTAL DRIFT

The faunal composition of any area is a product of the area's biotic, climatic, and geologic history. The geologic history delimits the area's boundaries: when, for how long, and to what other areas it was connected, its longitudinal and latitudinal movement, and the topography of the land. The climatic history determines the past living conditions, and thus which animal groups could have survived *in situ,* which could have immigrated and become successfully established, and when. The biotic history tells which animal groups were initially present, which ones could invade, and how each adapted to the changing environment.

The continental masses have undergone considerable movement and change since the modern orders of amphibians and reptiles first appeared. Each continent consists of a plate or a series of plates of low-density rock, floating on the denser but "fluid" mantle of the earth's outer core. These continental plates have probably been sliding slowly over the surface since early in the earth's history. Approximately 300 million years ago, in the Carboniferous period, all the plates formed a single supercontinent, Pangaea, divided by a long east-west embayment, the Tethys Sea. Pangaea remained a single giant continent through the Permian.

Then, in the Triassic, the continental plates began to move apart (Figure 11–5). The North American plate drifted away from the South American and African plates, as the North Atlantic Basin began to form. The North American and Eurasian plates remained together as a large northern continent, Laurasia. The southern continent, Gondwana, began to split: the South Atlantic appeared as a narrow rift developing from the south, though

South America and Africa were still broadly connected to each other and to the Indian plate. These three combined plates began to move northward, while the combined Antarctic and Australian plates rotated eastward. Rifting continued throughout the Jurassic and the Cretaceous. The Indian plate, containing the future India and southwest Asia, separated from Africa and moved northward. Madagascar drifted away from Africa, and later, near the end of the Cretaceous, Africa and South America completed their separation.

Early in the Tertiary, the North Atlantic rift split North America from Eurasia, Australia began to drift away from Antarctica, and South America joined with North America. Later the Indian plate collided with the main Asiatic land mass and slid partly under it, thrusting up the Himalayas. The world was beginning to assume its present appearance. The classic zoogeographic realms described so many years ago correspond remarkably well to the continental plates delimited by modern geologists.

Climatic conditions on the early continents differed considerably because of the differences in continent sizes and ocean currents. Even more important were the positions of the continents on the globe. Initially, much of Laurasia was tropical and much of Gondwana was either temperate or subtropical. (During the Permian, a massive ice sheet covered much of Gondwana.) The general movement of all the plates except the Antarctic has been northward, so that the Gondwanan components have become warmer and the Laurasian ones cooler.

GEOGRAPHIC DISTRIBUTION
## OF AMPHIBIANS AND REPTILES

Amphibians and reptiles are among the best animals to use in the study of terrestrial geographic patterns. Since they are ectothermic, like the majority of the world's animals, their distributional patterns are likely to be more widely applicable than those of the endothermic birds and mammals. They are more limited in vagility than the winged insects and birds or the wide-ranging larger mammals. The outlines of their primary patterns of distribution are thus less liable to be blurred by rapid, wide, and essentially random dispersal. Because of their unshelled eggs and unprotected skins, amphibians are ecologically bound to regions where fresh water is available. They are quite intolerant of seawater. We can be reasonably sure, then, that they have not fortuitously crossed extensive areas of the sea or arid desert lands *en masse.* Where essentially similar faunas occur, on either side of such a barrier, we can safely assume that they reached those regions before the barrier formed.
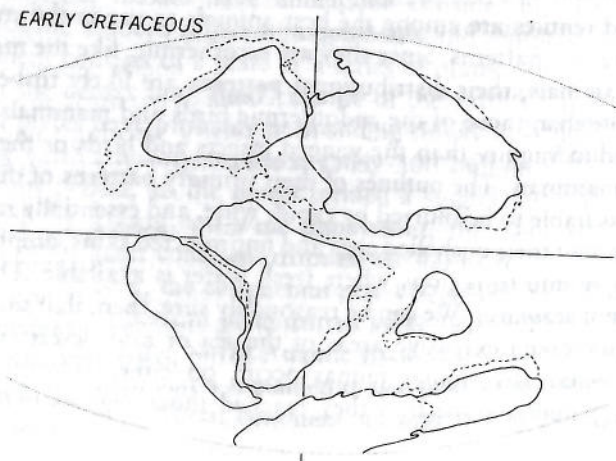
EARLY TRIASSIC

Tethys sea

EARLY JURASSIC

L a u r a s i a

G o n d w a n a
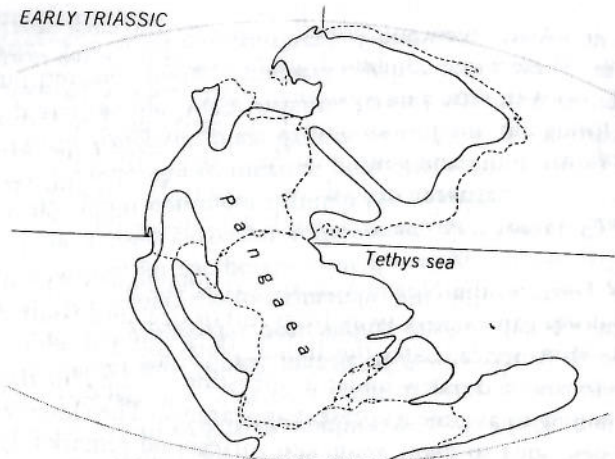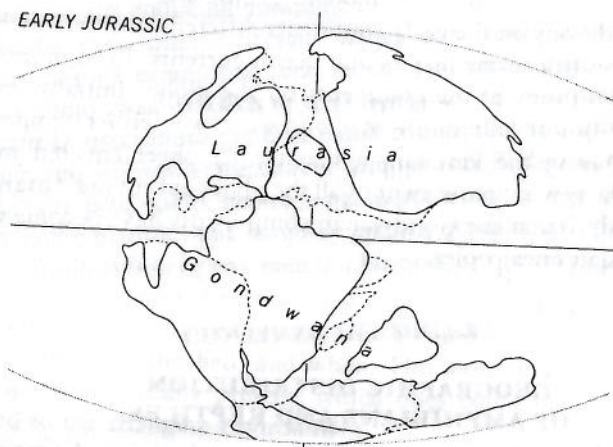
EARLY CRETACEOUS

Geographic distributions may be analyzed at different levels, and each level will yield a different historical picture. Familial distributions indicate the center of origin of a family and its probable dispersal routes. Specific patterns of geographic variation yield data on the evolution of a species and the effect of relatively recent climatic and geologic events on its movements. No matter what level is analyzed, it is essential that the true relationships of the group be known; otherwise the geographic interpretation will be incorrect.

Distribution of Amphibian Families

The caecilians are tropical animals, and probably have always been so. Their greatest diversity and most continuous distribution occurs in Africa and South America; they also occur discontinuously in the Oriental region, from the Seychelles Islands, India, and Ceylon to Java, Borneo, and the southern Philippines. An early Tertiary fossil has been found in South America, and a Pleistocene one in Europe. Caecilians probably arose in the tropics of Gondwana, and moved into Central America and the Oriental region in the early Tertiary.

The salamanders are predominantly Holarctic in distribution, and presumably originated and diversified in Laurasia. Only one subgroup of plethodontid salamanders has invaded the tropics, and this appears to have been a recent (late Tertiary and Pleistocene) radiation. The general pattern of salamander distribution today is discontinuous and relict: cryptobranchids in eastern North America and eastern Asia, proteids in eastern North America and Adriatic Europe, plethodontids in the New World and the eastern Mediterranean. These families must have enjoyed widespread distribution throughout the Holarctic at one time, perhaps comparable to the present Holarctic distribution of salamandrids. The Asian hynobiids and the North American ambystomatids may have risen from a cryptobranchid stock. The amphiumids may in turn have been derived from an ambystomatid stock, and today share a relict distribution in the southeastern United States with the sirens.

In contrast to the salamanders, the frogs probably arose in Gondwana. The xenoanurans (pipids and rhinophrynids) are Gondwanan derivatives:

FIGURE 11–5

The continents at three stages during the Mesozoic era. Solid lines indicate the shorelines of the ancient continents, broken lines the present continental shorelines. Vertical and horizontal lines represent 0° longitude and 0° latitude, respectively. Even though the continental plates were abutting, the continents may have been separated by shallow continental seas. These seas appeared and disappeared with great regularity in the past. [Composite after Dietz and Holden, Sci. Amer., 1970, and Tarling and Tarling, Continental Drift, Doubleday, 1975.]

their present and fossil occurrence is associated with the South American and African plates. The scoptanurans (microhylids) are also Gondwanan derivatives. In view of their diversity and wide distribution in the Neotropic, Ethiopian, and Oriental regions, they may originally have been residents of the warm temperate and subtropical areas of Gondwana, exclusive of the Antarctic and Australian plates. Although they occur in the Australian region today, their greatest diversity there is in New Guinea, and they have very limited distribution in Australia proper—which suggests that they penetrated into the Australian region by invasion from the East Indies.

The lemnanurans (ascaphids, discoglossids) are Holarctic forms, and probably originated from an early penetration of primitive anurans into temperate Laurasia. Although *Leiopelma* is often considered a member of this group, its New Zealand distribution and derived characters suggest that it represents another lineage of primitive frogs from temperate Gondwana. The acosmanurans (bufonids, ranids, hylids, leptodactylids) are largely southern-hemisphere groups, but their supposed ancestral group, the pelobatids, are Holarctic—suggesting a Laurasian origin for this family, which must have expanded into tropical Gondwana and there given rise to the modern frogs. The ranids and their relatives (hyperoliids, rhacophorids) are primarily Ethiopian and Oriental. They may have arisen in Africa and dispersed several times, the older dispersals giving rise to new families, such as the rhacophorids, the more recent to the genus *Rana,* with sufficient time for high speciation, but with no great specialization of any species group. The bufonids show a predominantly Neotropic and African radiation pattern. The hylids, including pelodryadids, and the leptodactyloids (leptodactylids, heleophrynids, and myobatrachids) appear to be of temperate or subtropic Gondwanan origin. The remaining small families probably all arose *in situ*—the sooglossids on the Seychelles Islands and the others in South America—and have never spread to other areas.

Distribution of Reptile Families

The rhynchocephalians are a declining group. The single surviving member, the Tuatara, shows a relict distribution restricted to New Zealand; fossil forms are found in Africa, Eurasia, and North America. Although the crocodilians are more widespread, their present distribution, compared with that in the late Cretaceous and early Tertiary, is relictual. Fossil evidence suggests that the modern subgroups of crocodilians originated in subtropical and tropical Laurasia and spread into South America and Africa, where they underwent a secondary radiation.

Modern and fossil turtle distributions indicate a Gondwanan origin and radiation for the pleurodires and a Laurasian origin for the cryptodires, with radiations occurring in both the northern and southern continents. Many of

the early pleurodires appear to have been marine, and although a few penetrated into the northern hemisphere, their major radiation occurred in the southern. Today, South America is the center of their distribution, since both living families occur there. The history of the cryptodires is somewhat more complex: their fossil forms are predominantly from the northern hemisphere, yet some have had successful radiations in the Oriental, Ethiopian, and Neotropic regions. The trionychids and testudinids have their greatest diversity in Africa, the kinosternids in Central America, and the batagurines in Southeast Asia. The emydines and chelydrids are largely Nearctic. The sea turtles (cheloniids and dermochelyids) are tropical, and may have had their origin in the ancient Tethys Sea or the early Atlantic Ocean.

The squamates, with their great diversity and relatively poorly known fossil record, present an even more complex history. Today, the amphisbaenians are tropical or subtropical animals; but they have a strong fossil record in North America, and may have risen there under tropical conditions. The gekkonids and scincids occur throughout the tropics, and both have primary centers of radiation in Africa and the Indoaustralian area. The iguanids are mainly a Nearctic group, yet have isolated members in Madagascar and the South Pacific; they probably once had worldwide distribution and have been replaced in the Old World tropics by their relatives, the agamids. The anguinids are probably Laurasian derivatives that have expanded into the southern-hemisphere tropics and undergone a secondary adaptive radiation. The teiids are strictly a New World group, the lacertids Palearctic, and the cordylids Ethiopian. The chamaeleonids are now centered in Africa, but have been reported from the upper Cretaceous of eastern Asia. The varanids are widespread in southern Asia, Africa, the East Indies, and Australia, and are known as fossils from North America and Europe. The xantusiids and helodermatids are North American, but fossils of both are reported from Europe. If all these fossils are correctly allocated, these families must once have been more widely distributed. The dibamids and xenosaurids clearly have relict distributions, the former in eastern Asia, the East Indies, and Mexico, the latter in Mexico and China. No fossils of *Lanthanotus* of the East Indies or the pygopodids of Australia have ever been found, so there is no evidence they ever were more widespread.

The fossil record of snakes is very poor. All three scolecophidian families are clearly southern-hemisphere groups, and their primitiveness suggests that they arose when Gondwana was a single continent. The henophidians are also presumably Gondwanan. The acrochordids are Australian, the uropeltids Indian, and the xenopeltids southwestern Asian. The boids are widespread in the tropics and subtropics, reaching the temperate zone in North America, and have a fossil record in North America and Europe. The aniliids have a relict distribution in Mexico, Central America, and Southeast

Asia. They have been reported from the Miocene of North America. Like the anguinids, the viperids are probably Laurasian derivatives that underwent a secondary adaptive radiation in the southern-hemisphere tropics. Since the relationships of the colubrids remain unknown, no sensible distribution pattern can be discerned, except that the Holarctic was one center of adaptive radiation and each of the other zoogeographic regions except Australia was a radiation center. The elapids either replaced the early Australian colubrids or evolved earlier and did not permit the colubrids' establishment and radiation. The Australian and Oriental regions are centers of distribution and radiation for the elapids and their sea-snake derivatives. It is strange that the New World elapids have been so adaptively conservative. Are they really elapids, or are they separately derived from the colubrids? Such questions are one of the reasons for studying distributional patterns, for patterns that do not fit the known dispersal routes may indicate errors in the accepted classification.

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