Speciation

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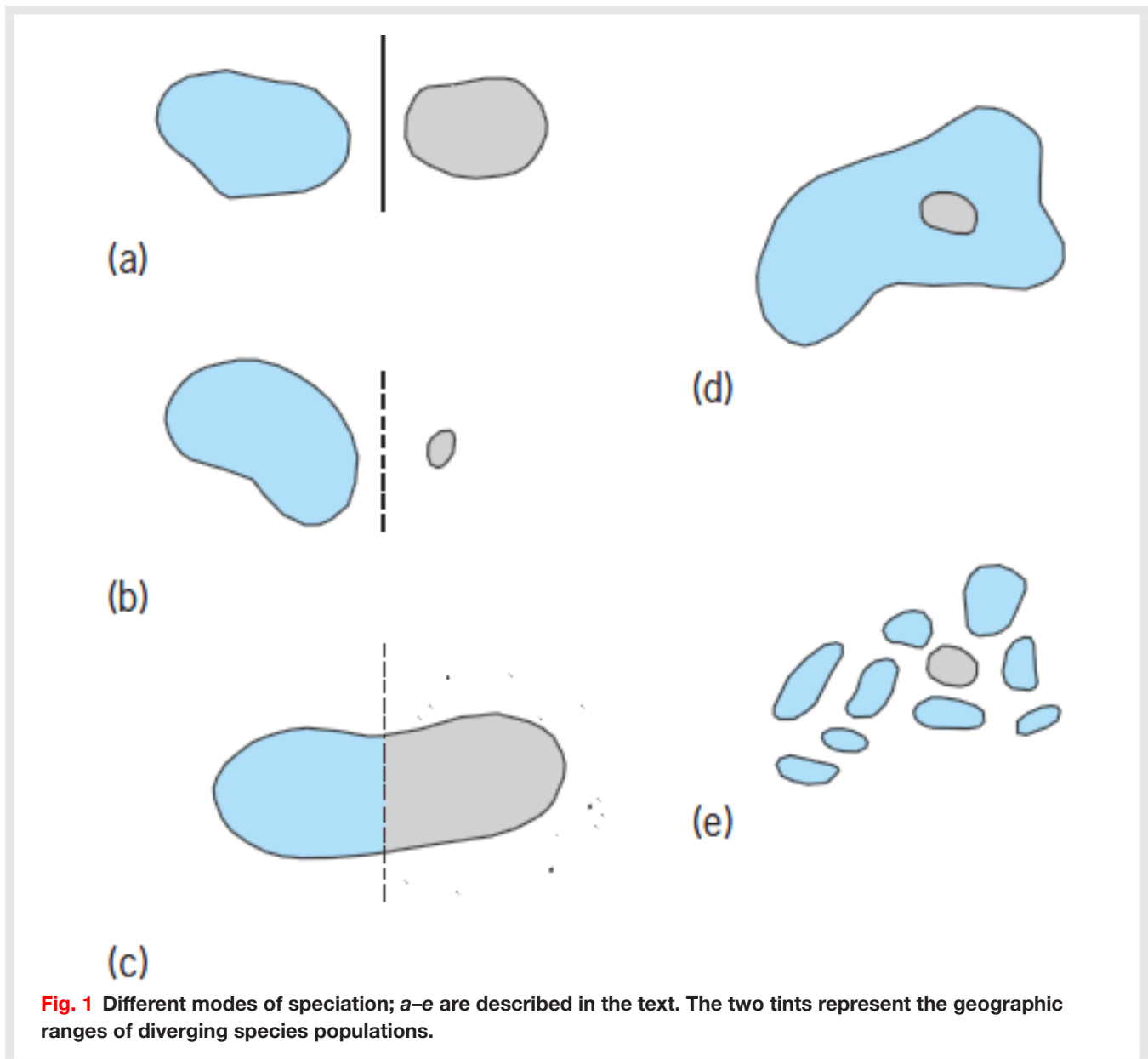
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The process by which new species of organisms evolve from preexisting species. It is part of the whole process of organic evolution. The modern period of its study began with the publication of Charles Darwin's and Alfred Russell Wallace's theory of evolution by natural selection in 1858, and Darwin's *On the Origin of Species* in 1859.

There was no problem of speciation during the period when it was believed that species were divinely created and immutable. Belief in the fixity of species was almost universal before the middle of the nineteenth century. Then it was gradually realized that all species continuously change, or evolve; however, the causative mechanism remained to be discovered.

Darwin proposed a mechanism. He argued that (1) within any species population there is always some heritable variation; the individuals differ among themselves in structure, physiology, and behavior; and (2) natural selection acts upon this variation by eliminating the less fit. Thus, if two members of an animal population differ from each other in their ability to find a mate, obtain food, escape from predators, resist the ravages of parasites and pathogens, or survive the rigors of the climate, the more successful will be more likely than the less successful to leave descendants. The more successful is said to have greater fitness, to be better adapted, or to be selectively favored. Likewise among plants: one plant individual is fitter than another if its heritable characteristics make it more successful than the other in obtaining light, water, and nutrients, in protecting itself from herbivores and disease organisms, or in surviving adverse climatic conditions. Over the course of time, as the fitter members of a population leave more descendants than the less fit, their characteristics become more common.

This is the process of natural selection, which tends to preserve the well adapted at the expense of the ill adapted in a variable population. The genetic variability that must exist if natural selection is to act is generated by genetic mutations in the broad sense, including chromosomal rearrangements together with point mutations. *See also:* GENETICS; MUTATION.

If two separate populations of a species live in separate regions, exposed to different environments, natural selection will cause each population to accumulate characters adapting it to its own environment. The two populations will thus diverge from each other and, given time, will become so different that they are no longer interfertile. At this point, speciation has occurred: two species have come into existence in the place of one. This

Fig. 1 Different modes of speciation; *a–e* are described in the text. The two tints represent the geographic ranges of diverging species populations.

mode of speciation, speciation by splitting, is probably the most common mode. Two other modes are hybrid speciation and phyletic speciation; many biologists do not regard the latter as true speciation.

Splitting

There are four ways in which a species population can become separated into two (or more) parts that can undergo genetic divergence and evolve into separate species (**Fig. 1**). G. L. Bush has named them types Ia, Ib, II, and III.

In type Ia, an extensive population becomes split into comparatively large parts (Fig. 1*a*). In terrestrial species, this may happen because movement of the Earth's crustal plates rafts the parts away from each other; or else a barrier such as a mountain range or a tract of desert may form and split a once-continuous population. A marine population is split if a land bridge forms which cuts through it; for example, the fall in sea level that accompanied the Pleistocene glaciations created a land bridge between Alaska and Siberia.

A type Ib split occurs if a small, outlying segment of a population becomes detached from the rest (Fig. 1*b*). Such a peripheral isolate is usually a colony founded by a few emigrants from the main body of the species population. The colony can evolve into a new species even if it is not totally isolated from the parent population, provided its necessarily small gene pool chances to be well adapted to the habitat in which it finds itself. The "preadapted" possessors of these genes will be selectively favored within their small local habitat, and will quickly proliferate.

Population splits of both types Ia and Ib cause the diverging populations to be geographically separated, or allopatric. The resultant genetic separation is known as allopatric speciation.

In type II, a population becomes split into geographically contiguous parts between which there is a limited amount of gene exchange. The environments of the daughter populations are assumed to differ sufficiently for natural selection to override the effects of the restricted gene flow, and speciation can therefore occur. This is parapatric speciation (Fig. 1*c*).

A type III split occurs if, within a single geographic region, parts of a population in some way become so isolated from each other that gene exchange between them falls below the level needed to maintain the integrity of the original population. The result is known as sympatric speciation (Fig. 1*d*). It is probably common among parasites and parasitoids, but is thought to be rare or nonexistent in free-living organisms. Even though closely related species adapted to different habitats, or with different modes of life, or with different resource requirements, often co-occur in the same geographic area, their co-occurrence should not be ascribed to sympatric speciation unless a mechanism can be found that could have initiated their divergence in the first place. A more likely explanation for such co-occurrences is that the species evolved allopatrically or parapatrically, that ecological divergence accompanied speciation, and that the new species then became secondarily sympatric by migrating into each other's areas after the geographic barrier that formerly separated them disappeared. *See also:* ISLAND BIOGEOGRAPHY.

Descriptions of allopatric, parapatric, and sympatric speciation often tacitly assume that, in the absence of clear, unmistakable barriers, gene exchange occurs freely throughout very extensive populations; often an entire species is treated as a single breeding population. However, P. R. Ehrlich and P. H. Raven have argued that usually the total population of a whole species is broken into a large number of small breeding populations (demes) that are fairly isolated from each other and among which gene exchange is comparatively rare. Thus, a deme rather than a species population is the unit of evolution. As a result, sympatric speciation will sometimes seem to have occurred if a deme near the center of a species' range chances to diverge from the surrounding

demes; the process may be called quasisympatric speciation (Fig. 1*e*). The fact that all demes do not diverge from one another, giving as many species as there are demes, presumably results from stabilizing selection. Stabilizing selection causes groups of demes to persist in their resemblance to each other, and such groups are the "populations" constituting the visible units of evolution. *See also:* POPULATION GENETICS.

Isolating mechanisms

Two genetically diverging populations are not separate species so long as it remains possible for them to lose their distinctness, by interbreeding, if they chance to become sympatric. For speciation to be complete, the populations must evolve isolating mechanisms that prevent gene exchange between them; this allows them to maintain their genetic integrity.

There are many kinds of isolating mechanisms. The diverging populations may become genetically incompatible, so that hybrids either are never produced or are sterile. Even when the diverging populations can be shown to be infertile, they may be effectively isolated by a variety of mechanisms; they may breed at different times or in different habitats; they may have evolved different patterns of mating behavior, different mating calls, or different sex attractants (pheromones), so that individuals of the two populations never attempt to copulate; copulation may be mechanically impossible because of the structure of the genitalia (this occurs in some insects); and in insect-pollinated plants, diverging populations sometimes become adapted to different species of insect pollinators.

Hybrid speciation

In plants, new species are sometimes formed abruptly by the following mechanism. The accidental crossing of two diploid plants of different, though related, species yields a healthy but sterile diploid hybrid. The hybrid is sterile because the chromosomes it has received from its parents cannot form normal bivalent pairs; meiosis is upset, and functional gametes cannot be produced. But now chromosome doubling occurs in the sterile hybrid, making it tetraploid; normal meiosis becomes possible; fertile gametes are produced; and a new species has appeared.

In symbols, let the genomic constitution of the parents be *AA* and *BB*, respectively. That of their sterile hybrid is *AB*, in which none of the chromosomes has a homologous partner to pair with at meiosis. After chromosome doubling, however, the hybrid, now tetraploid, has the constitution *AABB*; meiosis can proceed normally, and the gametes are fertile. The new species is called an amphidiploid (or allotetraploid).

A whole range of similar, but more elaborate, variants of this process occur as well, yielding hybrids with different numbers of chromosome sets. The general name for the process, with numbers unspecified, is amphiploidy (or allopolyploidy or alloploidy).

The process happens because chromosome doubling is a common occurrence in plants; doubling results either from somatic doubling at mitosis (the paired chromosomes fail to separate) or from non-reduction at meiosis. Amphiploids may be produced repeatedly, with new lineages being added in a succession of outcrossings, backcrossings, and chromosome doublings. The result is a polyploid complex, an array of interrelated diploid and polyploid species. *See also:* MEIOSIS.

Speciation in uniparental organisms

Many plants reproduce uniparentally for long periods of time. Uniparental reproduction occurs in two ways: by autogamy (self-fertilization) and by apomixis (asexual reproduction); the latter term includes both vegetative multiplication and agamospermy (the asexual formation of viable seeds). A uniparental plant is not a member of a "biological species" as the term is usually defined, namely, a reproductively isolated collection of interbreeding individuals. This has led to the definition, by G. G. Simpson, of the "evolutionary species," a more inclusive category, defined so as to apply to both uniparental and biparental organisms. An evolutionary species is a collection of genotypically similar individuals of common ancestry whose similarity is maintained by stabilizing selection in a given environment.

In describing speciation in uniparental organisms, one must consider how a new uniparental lineage arises in the first place, and how its members can subsequently speciate. A uniparental lineage arises when two sexual species hybridize and the hybrids, though sexually sterile, reproduce uniparentally. If many crossings occur between the two sexual species, the result is a collection of hybrid individuals that are similar, but not identical, genetically. The collection constitutes an evolutionary species. Suppose now that each individual becomes the ancestor of a succession of uniparentally produced descendants. If the progenitors of these lineages begin growth in a number of slightly different habitats, natural selection will lead to differentiation among them: the survivors in each habitat will be adapted to that habitat. Thus, the plants in any one habitat are likely to differ slightly from those in other habitats. The differences are genetic, and they persist. Each distinguishable group of plants is called a microspecies. An array of microspecies, descended from the same ancestral pair of sexual species, is an agamic complex.

Microspecies that reproduce asexually (apomictically) are usually highly heterozygous; but autogamous microspecies lose the heterozygosity of their hybrid origin after several generations of self-fertilization and become complete, or nearly complete, homozygotes.

Phyletic evolution and chronospecies

Consider a series of fossils spanning a long interval of time (long in the geological sense) and believed to represent the successive forms of a single lineage. If there has been appreciable evolution within the lineage, the change is described as phyletic evolution or anagenesis.
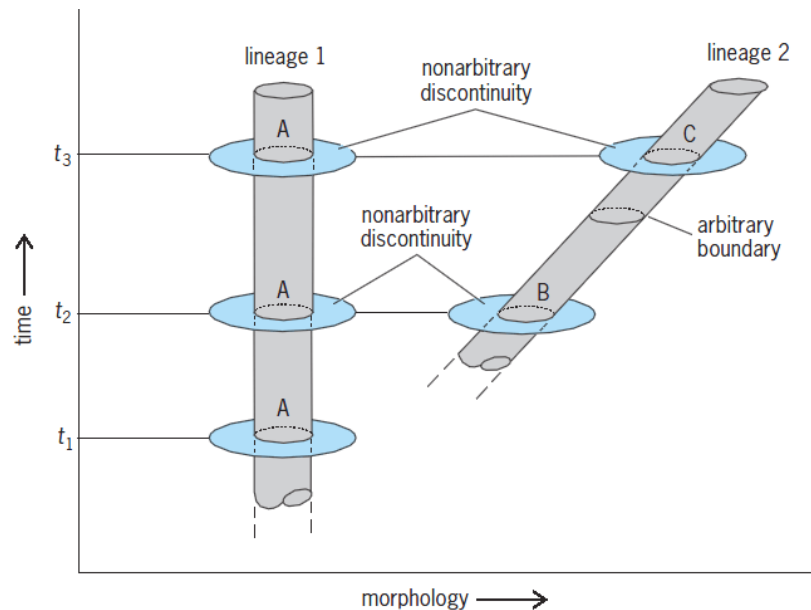
Fig. 2 Evolution of two lineages. Lineage 1 (species A) persists unchanged. Lineage 2 changes with time and has been divided, at an arbitrary boundary, into two chronospecies, B and C. (*After P. D. Gingerich, Univ. Mich. Pap. Paleontol., 15:1–140, 1976*)

Fossils from a single lineage but of different ages may differ from each other so conspicuously that, even though the younger is directly descended from the older, paleontologists find it convenient to treat them as taxonomically different species. Such species are called chronospecies (or successional species, paleospecies, or evolutionary species). They are not species in the usual sense; questions as to whether or not they can interbreed do not arise, since they are never alive at the same time. In a lineage evolving gradually, decisions on where to put the dividing line between each chronospecies and its successor are arbitrary. A "vanished" chronospecies, one that has disappeared and been replaced by a successor chronospecies of the same lineage, is said to have undergone pseudoextinction.

Figure 2 contrasts the behavior of a lineage evolving phyletically (lineage 2) with one persisting unchanged (lineage 1). The "species" labeled B and C in lineage 2 are chronospecies. At an arbitrary point on the time scale, B becomes pseudoextinct and is succeeded by C.

The transition from a chronospecies to its successor is not usually regarded as speciation in the strict sense. Speciation as usually defined entails the splitting of lineages.
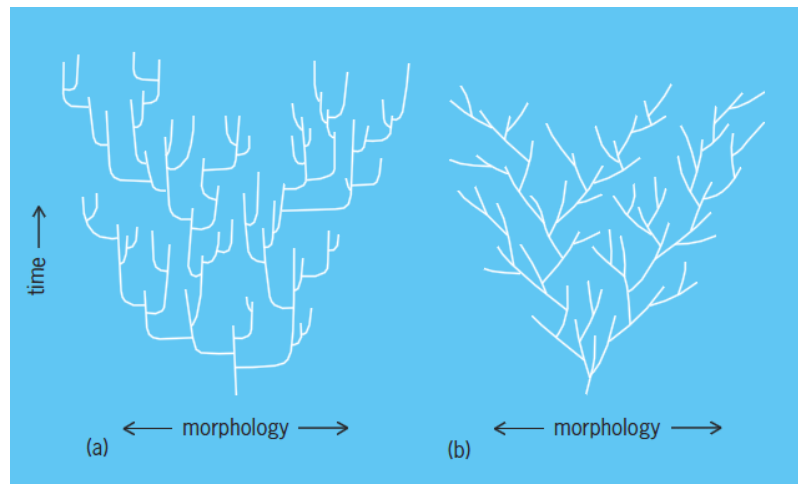
Fig. 3 Two contrasted modes of species evolution: (*a*) punctuated equilibrium model and (*b*) phyletic gradualism model. (*After S. M. Stanley, Macroevolution: Pattern and Process, W. H. Freeman, 1979*)

Quantum speciation versus phyletic gradualism

When a lineage splits, the two descendant lineages may diverge slowly or rapidly. There has been much debate on whether one or other of these modes has dominated the course of evolution and, if so, which. The two modes to be contrasted are shown diagrammatically in Fig. 3.

The tree on the right in the figure represents evolution and speciation according to the model known as phyletic gradualism. It supposes that all lineages undergo continuous gradual change (that is, phyletic evolution as described above) at a fairly constant rate. When splits occur, the descendant lineages diverge gradually from each other. There is no appreciable change in evolutionary rate at the time a split takes place. While the separated lineages are still capable of interbreeding to a limited extent, though with reduced fertility, they are known as semispecies. Their morphological divergence may sometimes be so slow that they remain practically indistinguishable even after they have lost the capacity to interbreed and have therefore reached specific rank; if so, they are known as cryptic species.

In Fig. 3*a*, the tree represents the punctuated equilibrium model of evolution and speciation, so called by N. Eldredge and S. J. Gould. It supposes that the splitting of a parent species population is always (or nearly always) accompanied by quantum speciation, the extremely rapid (in the geological sense) and pronounced divergence of one of the descendant lineages from the ancestral form. It is assumed that the divergent species originates most often by the chance splitting off of a small peripheral isolate from an extensive parental population; this is allopatric speciation of type Ib (Fig. 1). If the isolate is small, its small gene pool may not be at all representative of the parent gene pool from which it is drawn. It may, simply by chance, deviate markedly. Further, because of

its peripheral location, the environment of the isolate is likely to differ from that of the main body of the species population, and natural selection will then tend to magnify the deviation.

Evolutionary changes associated with the appearance of new species are thus, according to this model, concentrated in speciation events of very short duration; they are represented by the horizontal segments of the tree's branches (Fig. 3*a*). During the long time intervals between successive speciation events, a species remains almost unchanged, as shown by the vertical segments of the branches. While a species is in this static condition, phyletic evolution may bring about minor adjustments; this within-species evolution is known as microevolution. But the magnitude of these phyletic changes is negligible compared with that accompanying macroevolution, the formation of new species. Ernst Mayr introduced the terms maintenance evolution and switch evolution to describe these two evolutionary modes.

Many students of evolution are of the opinion that most groups of organisms evolve in accordance with the punctuated equilibrium model rather than by phyletic gradualism. There are two chief arguments for this view. First, it is clear from the fossil record that many species persist without perceptible change over long stretches of time and then suddenly make large quantum jumps to radically new forms. Second, phyletic gradualism seems to be too slow a process to account for the tremendous proliferation of species needed to supply the vast array of living forms that have come into existence since life first appeared on Earth. *See also:* ANIMAL EVOLUTION; SPECIES CONCEPT.

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