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Evolution, Coevolution, and Biodiversity

The theory of biological evolution is of one of the most important, central theories of biology. Many evolution-theoretical theses can be proven, owing to the enormous scientific progress recently made in many biological fields (e.g., paleontology, biogeography, and molecular biology). The most important evolutionary factors are mutation, recombination, and selection. Of particular relevance is speciation, which is usually due to the geographic separation of populations and genetic isolation, in combination with an adaptation process induced by selection pressures, for example, of a special environment (allopatric speciation). However, speciation may also occur within an area and population, for example, by polyploidization (sympatric speciation).

Coevolution is defined as a process in the course of which two partners or entire partner systems (animals, plants, bacteria, or fungi) depend on one another in their evolution. Both acquire specific adaptations as a consequence of mutual selection pressure. Examples for a gene–gene coevolution, for a close coevolution between species (specific coevolution), as well as for a coevolution between species groups (diffuse or guild coevolution) will be presented. These examples concern flower–pollinator systems, the dispersal of plant species by animals, protection of plants by animal species, and coevolution between plant species and phytophagous insects.

Evolutive processes bring about biological diversity (biodiversity). The concept biodiversity will be defined, and the hierarchical levels of various biological organization forms will be differentiated. The different elements of diversity (taxonomic diversity, diversity of life-forms, diversity of spatial patterns, etc.), the diversity of organismic interactions, evolution-biological and ecological factors causing diversity, and functional processes of diversity will be discussed. Special attention will be given to intra- and interbiocoenotic diversity, the many and diverse phenomena occurring within and between biocoenoses. It will be shown that the preservation of biodiversity is of paramount importance; it is an essential prerequisite for the survival of man on Earth and has thus been incorporated into the concept of sustainable development.

Basic Principles

The theory of biological evolution influenced man's conception of the world — also on humanistic, social, and religious levels — in a radical and far-reaching way. Man's anthropocentric conception was first shaken in the sixteenth century by Nicolaus Copernicus, whose Copernican system moved the earth — and thus man — out of the center of the universe. The selection theory of the English naturalist Charles Darwin (1809–1882) upset it even further: The species *Homo sapiens* is related to all other organisms.

Biological evolution, coevolution between species, and the phenomenon of biodiversity (which is the result of evolutive processes) are causally closely connected. The factors discussed in the following sections are essential prerequisites for evolutive processes.

Energy

Without the sun as an extraterrestrial energy source, life would not be possible. The development of higher molecular chemical compounds due to photosynthesis, the primary production of autotrophic organisms (producers) — without which the consumers and decomposers (animals, bacteria, and fungi) could not have evolved — and temperatures favorable for the metabolism processes of living organisms are an essential prerequisite for organismic life. However, the ordered variety of different life-forms (biodiversity) within biocoenoses and ecosystems, reflected by numerous plant and animal species, is also based on a constant energy supply. The thermodynamic laws (basic principles of thermodynamics) apply both to inorganic matter and to organismic life. Order (neg entropy) within a system (in this case, a biosystem) is only possible when energy is available (supply of free enthalpy). Without energy supply, the components of a system (compartments) cannot ensure any transfer of matter or information. Such a transfer, however, is necessary for the functioning of the entire system, which is maintained by system-inherent characteristics — that is, the interactions of its compartments. Energy failure, on the other hand, leads to entropy (disorder) and breakdown in the system.

Organisms and Their Genetic Information

The genetic code (DNA and RNA) of organisms contains information regarding the preservation of the species- and organism-specific life processes and the organization of the constructive and the energy metabolism. Moreover, it ensures that the organism is able to respond to environmental influences and that the genetic information is passed on to the next generation.

Organisms and Their Structures and Functions

Organisms have structures: To survive in a specific abiotic and biotic environment, they have acquired morphological, physiological, and biochemical adaptations, and animals have also acquired ethological adaptations. The many and diverse environments (habitats as well as habitat complexes) bring about a diversity of structures. As a rule, structures of organisms (adaptations) are linked to certain functions and vice versa.

Mutation

Mutations are the basis of evolution. A mutation is a change in the genotype, either spontaneous and natural or induced by certain mutagenes (substances provoking mutations, high temperatures, and UV rays). The variation of genetic information within populations and between them (genetic variability) is due to mutations.

Selection

Mutation provides a wide variety of possible forms and phenomena; selection then "chooses" from the existing organisms those reaction types which are best suited, for example, to the prevailing environmental conditions. These types reproduce best ("high fitness") and thus pass on many their genes and alleles to the next generation.

Time

The historicity of the taxonomic systems is one of the fundamental characteristics of biology. Biodiversity is the product of evolution and thus the result of phylogenesis effective over millions of years. Dollo's law on the irreversibility of evolution-historical processes implies that a species can only originate once. Intricate structures lost in the course of evolution can never be regained in their original form since combinations of random mutations and directional selection, as a rule, are not reproducible and evolution takes a linear course. However, there are examples showing, for instance, that some metabolic pathways which occur in different related groups have obviously been acquired by more simple mutation and selection steps (e.g., the Crassulaceae acid metabolism in plants).

In the following section, some basic principles of the biological evolution are explained. The evolution process may be considerably accelerated and the degree of coordinated adaptations may be especially pronounced when species or species groups exercise a significant selection pressure on each other (coevolution). Some particularly spectacular phenomena are due to coevolution. The forms of diversity will be described on the different hierarchy levels of biological systems (species, biocoenosis, ecosystem, and landscape).

Evolution

The Evolution Theory

The theory of the phylogenetic development of organisms, first outlined in Charles Darwin's epochal work *The Origin of Species by Means of Natural Selection* (1859), is essentially still valid today and has been substantiated by data from nearly all fields of biology.

The theory is based on two central principles: (i) All organisms are phylogenetically related to each other, and (ii) evolution is due to undirectional changes in the genetic material (mutation), leading to transformations of shape, function, and mode of life of organisms (species) and to directional selection by the abiotic and biotic environment.

Darwin's selection theory (with regard to phylogenesis designated as *theory of evolution* or *theory of descent*) contradicts the thesis of the French zoologist Jean-Baptiste de Lamarck (1744–1829). According to Lamarck's thesis (developed in 1809), there is no genealogical relationship between the organisms. Evolution is caused by a change in the genotype, provoked by altered environmental conditions. The newly acquired characteristics are passed on to the next generations (Lamarckism) due to an organism-inherent impulse of perfection (psycho-Lamarckism). The selection theory, however, implies that only the phenotype, and not the genotype, can be changed, via modifications, by environmental influences, but environmental influences determine the selection processes and favor specific genotypes.

At the same time, but independent of Charles Darwin, the biogeographer Alfred Russel Wallace (1823–1913) ascertained the same main mechanisms of evolution. He did not work out a detailed theory, however.

Modern genetic (especially population-genetic) data have contributed to a better understanding of mutation processes and genetic variation and have thus confirmed and further substantiated the evolution theory. Disciplines such as ecology, ethology, developmental biology, systematics, special botany and special zoology, and paleontology have made considerable progress, and differentiated mathematical procedures have been developed. Consequently, evolutionary biology could be established as synthetic science (synthetic evolution theory; Huxley, 1974).

The course of phylogenesis and the factors which induced it are a topic of current research.

Evidence for Evolution

Important tasks of evolution research are the analysis of the change in species (anagenesis), reconstruction of the phylogenetic development ("phylogenetic tree" research), and demonstration of evolution factors (causal evolution research).

The following evidence for evolution has been gathered.

Data of Homology Research. Organisms can be distinguished from each other by certain organs and structures. Organs and structures of organisms whose similarities are due to the same hereditary information are homologous. As homologous organs change in the course of evolution, they have to be investigated with regard to certain criteria. The following homology criteria apply (Osche, 1966):

Criterion of position: Organs and structures are homologous when they occupy the same position within an organism (*homotopic organs*); for example, the position of labium, labrum, mandible, and maxilla of the mouthparts of insects (Fig. 1).

Criterion of continuity or steadiness: Organs and structures which are neither similar to each other nor occupy the same position within an organism (*heteromorphous* or *heterotopic organs*) can be recognized as homologous by transitions and intermediate forms. Examples can be given

(i) from the embryonic development — conversion of the serially and segmentally arranged, homologous appendices within the insect embryo into mouthparts and extremities (see Fig. 1);

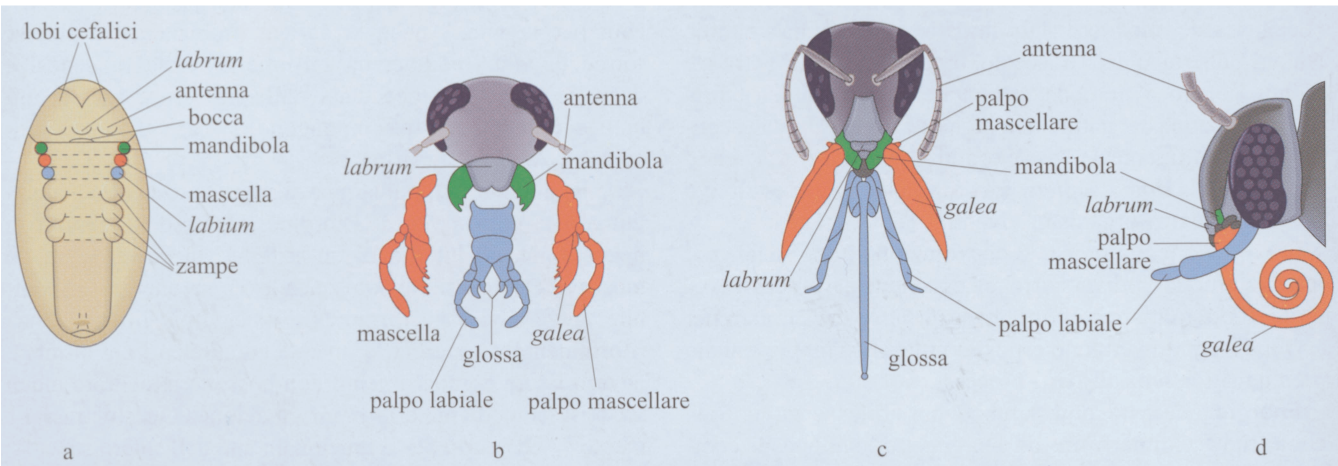

FIGURE 1 Homology of the mouthparts in different orders of insects. Dark blue, mandible; red, maxilla; light blue, labium. (a) Ventral view of the embryo of an insect, with the segmental rudiments of the extremity buds which in the head develop into mouthparts and in the thorax into the extremities. (b) Cockroach (genus *Blatta*); the mouthparts (shown separately) have the typical original chewing form. (c) Honeybee (genus *Apis*); maxilla and labium parts have been converted into a sucker and the mandibles are fully developed. (d) Butterfly (order Lepidoptera); parts of the galea are stretched into a proboscis, whereas the mandibles are reduced (adapted from Czihak *et al.,* 1976).

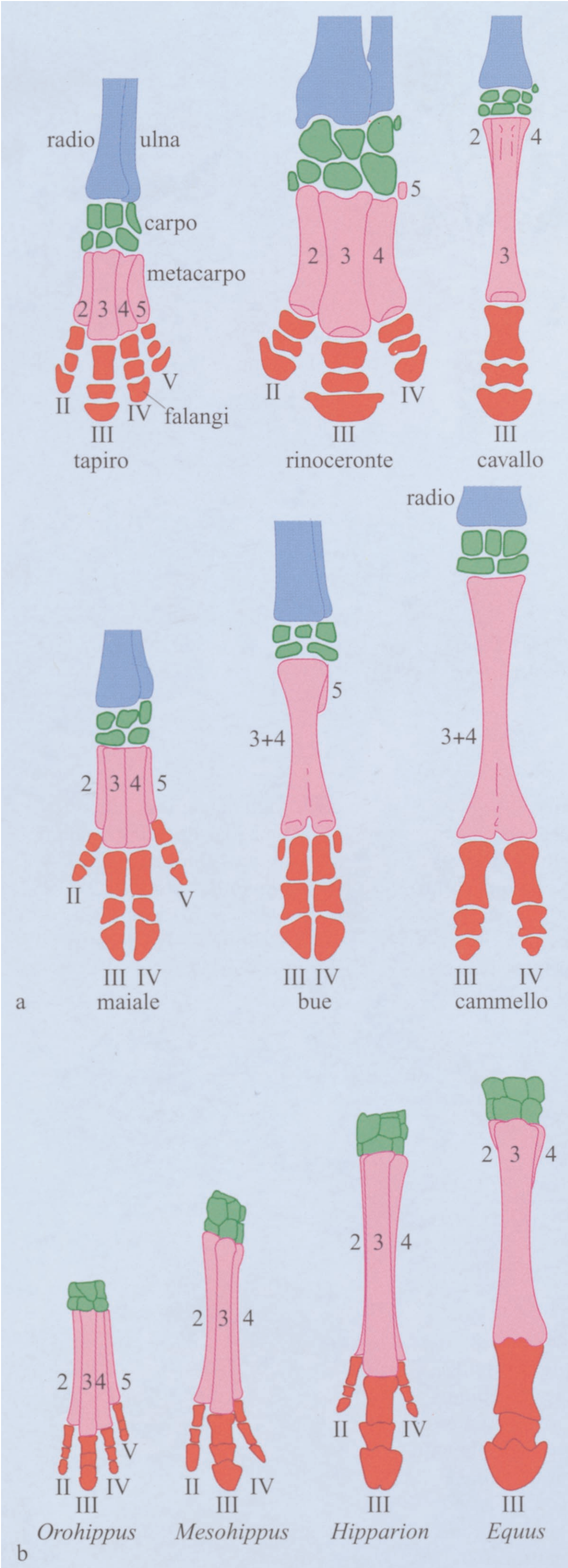

FIGURE 2 (a) Examples of the skeletal structure of the fore-extremities of extant hoofed animals. Perissodactyla: tapir (genus *Tapirus*), rhinoceros (genus *Rhinoceros*), and horse (genus *Equus*). Artiodactyla: pig (genus *Sus*), ox (genus *Bos*), and camel (genus *Camelus*). (b) Skeletal structure of the fore-extremities of a series of fossils showing the transformation of the horse from a slow woodland animal into a quickly running steppe animal. In *Orohippus* (Eocene), the first digit disappears; in *Mesohippus* (Oligocene), the fifth digit disappears and a more pronounced development of the third digit is observable, whereas *Hipparion* (Pliocene) is already a functional perissodactyl. Lastly, in the genus *Equus* (extant) the limb is typically one-toed. The numbers from 2 to 5 and from II to IV indicate respectively the metacarpals and the phalanges (adapted from Wehner and Gehring, 1990).

(ii) from the comparison of closely related living or fossil forms — reduction of the toes (phalanges) of hoofed animals (Fig. 2);

and (iii) from the comparison of serially recurring organs at the same individual of an organism — transition from normal leafs to sepals by progressive reduction of the upper leaf and transitions from petals to stamens (Fig. 3).

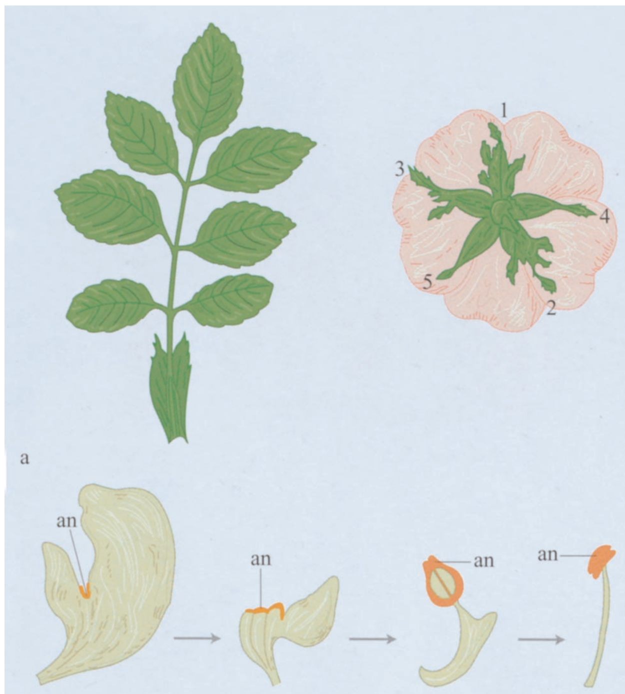

FIGURE 3 Metamorphosis of the leaves of a rose. (a) Normal leaf (left) and flower (right, seen from below), characterized by five sepals in a ⅖ divergence, with progressing reduction of the upper leaf. (b) Transitions from petals to stamens. An, anthers or their rudiments (adapted from Stocker, 1952).

Criterion of specific quality: Independent of their position within the organism, complex structures can be recognized as homologous when they have numerous similar individual structures (*homomorphous organs*); for example, teeth of vertebrates.

In addition to the determination of morphological characteristics, a homologization may also cover biochemical (comparison of enzymes, hormones, DNA, etc.) and ethological aspects (e.g., comparisons of inborn articulations of animal species).

Paleontological Data. Fossils constitute important evidence for the evolution of certain organism groups. In some cases, it is possible to precisely trace the sequence of adaptations and speciation — for example, for the evolution of horse-like mammals (Equidae) in the Tertiary and Quaternary Periods (Fig. 4).

Transition forms (connecting links) also play an especially important role between higher organization types. Examples include Ichthyostega from the Devonian, with characteristics of fish and amphibians (Fig. 5), and Archaeopteryx from the Jurassic, with characteristics of reptiles and birds (Fig. 6).

Biogeographic Data. Many organism groups are restricted to certain geographic areas. They probably originated in their current distribution area, and (natural) barriers (oceans, mountains, etc.) prevented a further dispersal. This would explain the fact that they are absent in other regions.

Species which only occur in a restricted area are called *endemics.* Continental islands are particularly rich in endemics; for example, Australia with its marsupials (Marsupialia). The same applies to old islands, frequently of volcanic origin; for example, the Galapagos Islands with their

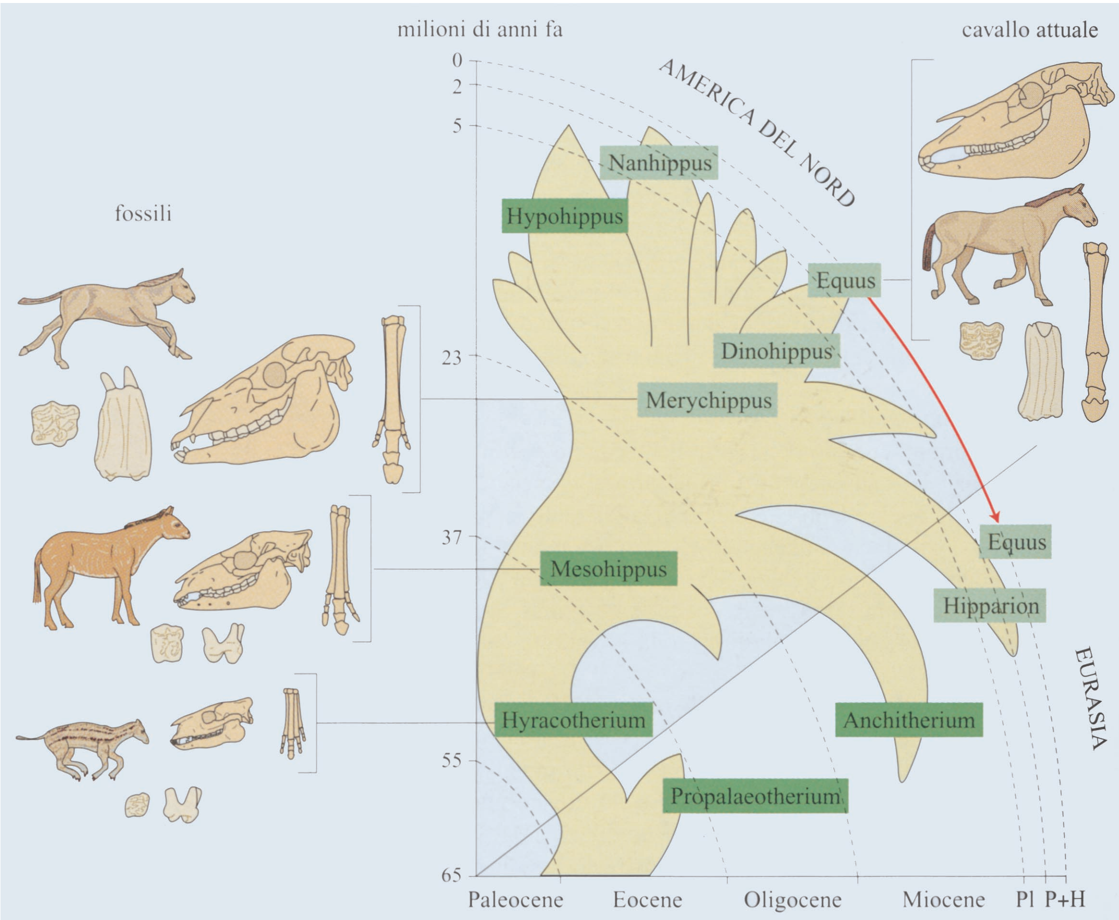

FIGURE 4 Phylogenetic tree of the horse (Equidae), with a selection of skeletal characteristics (skull, forearm, and molar teeth seen laterally and from above) of the important fossil genera. The species that ate leaves are shown in dark green; the grass eaters are shown in light green. The red arrow indicates the migration of *Equus,* which became extinct in northern America after the Pleistocene. Pl, Pliocene; P, Pleistocene; H, Holocene (adapted from Wehner and Gehring, 1990).

FIGURE 5 The fossil vertebrate *Ichthyostega* (top, in reconstruction; bottom, the skeleton) represents a transition form between a crossopterygian fish (Crossopterygii) and a typical amphibian. It is the oldest known quadruped land vertebrate and appeared more than 350 million years ago. All fossils of specimens of this genus were found in lacustrine water deposits of Mount Celsius on Ymer Island in Greenland. The relationship with fish is evident in the structure of the skull, dentition, and the typical fishtail, whereas the relationship with amphibians is evident in the extremities and in the fact that the pelvis is connected to the vertebral column (adapted from Carrol, 1988).

FIGURE 6 The best preserved fossil of *Archaeopteryx lithographica* found to date was excavated near Eichstätt (Altmühltal, southern Germany) in 1877. It is now conserved in the museum of Humboldt University, Berlin. *Archaeopteryx* represents the connecting link between reptiles and birds. The structure of the skull, toothed jaws, free fingers with claws, a missing carina, and the long reptile's tail composed of free vertebrae are all characteristic of reptiles, whereas the presence of feathers, a furcula, one toe directed backwards, and pneumatized bones are typical of birds. *Archaeopteryx lithographica* is a species that lived about 150 million years ago (photo courtesy of H. Jaeger).

Darwin's finches (Geospizinae; Lack, 1947) (Fig. 7) and Hawaii with its honeycreepers (Drepanididae; Mayr, 1943).

A distinction is made between origin endemism (the center of origin and current distribution are identical; e.g., Darwin's finches) and relict endemism (the current distribution represents only the remnants of a formerly much larger distribution area).

Rudiments. The continuous modifications of organs and structures in the course of evolution has frequently led to a change in function. The auditory ossicles of mammals, for example, evolved out of bones of the jaw hinges of original amphibians, reptiles, and birds. In individual cases, certain organs no longer have a function: They represent reduced organs (rudiments). Rudiments are "adaptations of the past."

The following are examples in the fauna:

Retrogression of the extremities in reptiles with a winding mode of locomotion: A python still has rudiments of a pelvis and of the hind extremities. Toothless whales (Mysticeti) completely lack external parts of the hind extremities; in their bodies, however, rudiments of the femur and of the pelvis can be found (Fig. 8).

Rudimentary eyes of cave animals (among the fishes the characine *Anoptichthys jordani;* Characidae) or of animals living in the soil (among the rodents the mole rat *Spalax typhlus;* Spalacidae).

Examples of rudiments in the flora include the retrogression of the five upper stamens in species of the genus *Scrophularia* (Scrophulariaceae), the occurrence of stamen remnants

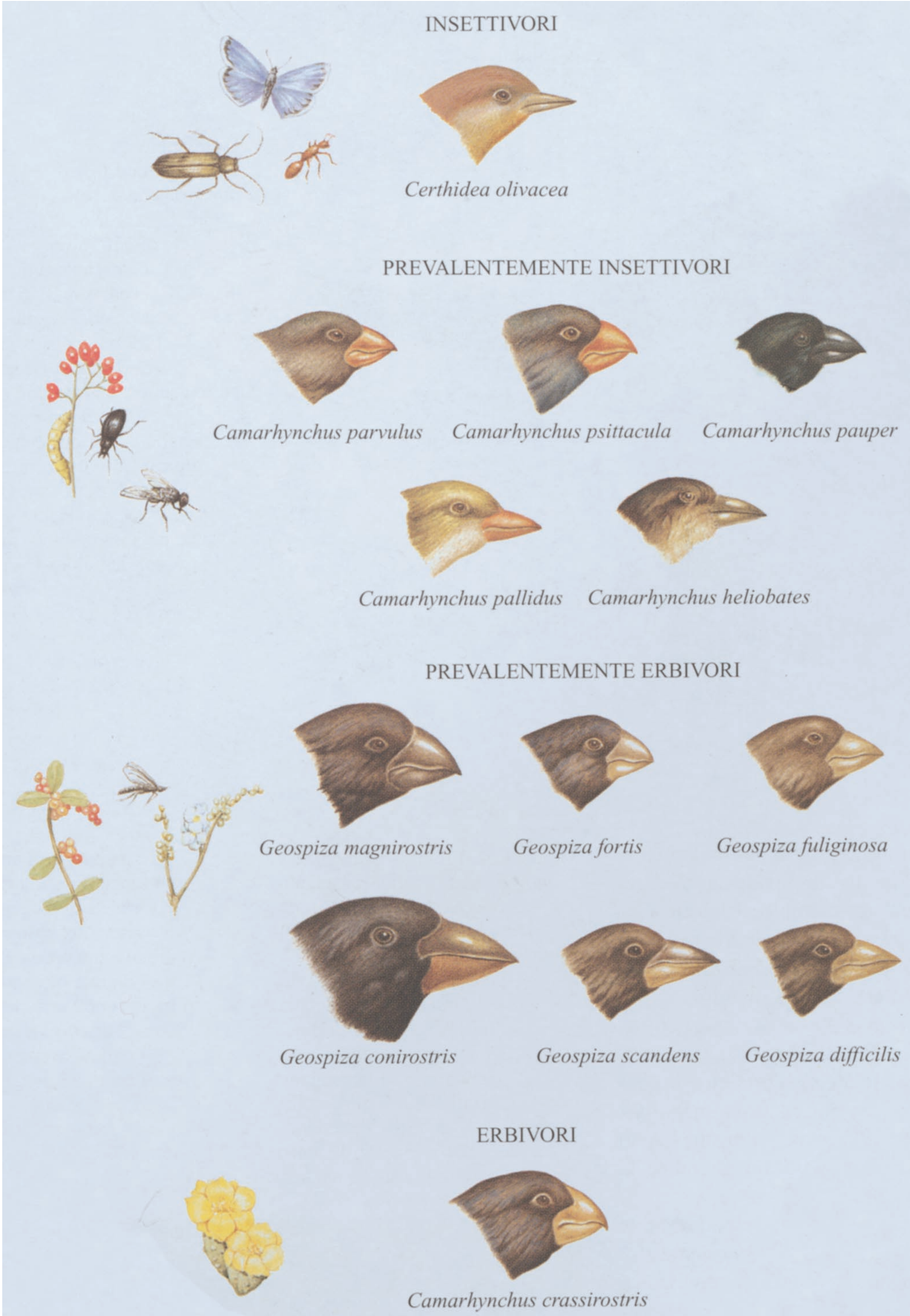

FIGURE 7 A classic example for origin endemism is provided by Darwin's finches (*Geospizinae*) on the Galapagos Islands. At the end of the Tertiary Period, nearly 1000 km of land was colonized by a few individuals of the original *taxon.* Over the course of time, by food specialization the 13 current species could differentiate. They are shown grouped according to their alimentary preferences, which are strictly related to the morphology of the beak.

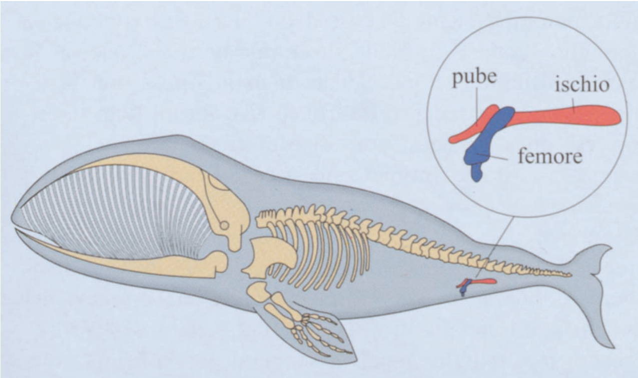

FIGURE 8 The toothless whales (Mysticeti family) completely lack external parts of the hindlimbs but, in their bodies, rudiments of the thigh bone (femur, in blue) and of the pelvis (pubis and ischium, in red) can be found (adapted from Czihak *et al.,* 1976).

in diclinous flowers (which evolved out of originally complete flowers), and the occurrence of no longer needed stomata in some aquatic plants.

Evidence Supplied by the Development of Individuals. In the course of their individual development (ontogenesis), numerous organisms form organs and structures which again regress completely (*circuitous development*). Many of these correspond to organs and structures typical of the organisms' phylogenetic ancestors. For example, as freshly hatched fish larvae, flat fish (Pleuronectifomes such as Scophthalmus and Scophthalmidae or Pleuronectidae such as Pleuronectes) are bilaterally symmetrical; only at this stage do they develop an asymmetry (Fig. 9).

Toothless whales (also called whalebone whales; Mysticeti) absorb their food (tiny crustaceans) with a trap device, the baleen. In the embryonic stage, however, they develop rudimentary teeth, which then regress again. Their phylogenetic ancestors had teeth, like today's toothed whales (Odontoceti), such as the dolphins (Delphinidae). The arbor vitae (Thuja, Cupressaceae) has short, scale-shaped leaves; in its adolescent stage, it first develops long needles typical of original specimens of the conifers (Coniferophytina).

Adaptations to the Environment

Evolution documents the variety of possible organismic adaptations to certain environmental factors in space and time. Adaptations are essential for an organism to survive and reproduce in a specific environment; in this way, the preservation of the species is ensured.

In this context, the environment is understood as a complex of external factors (ecofactors) which affect an organism directly and indirectly. This includes the factors essential for its survival (minimum environment) and the additional environmental influences (ecological environment). The environment of an organism thus comprises all abiotic and biotic factors affecting it in a positive or a negative way within the colonized habitat.

FIGURE 9 Four stages of the larval development of the plaice (Pleuronectes family), showing the shift of eye and mouth opening from the original bilaterally symmetrical arrangement (top) to one side of the body (bottom).

Abiotic (Physiographic) Environmental Factors. The abiotic (physiographic) environment is characterized by climatic factors (warmth, light, humidity, precipitation, wind, current, etc.), edaphic factors (physical and chemical properties of the soil), and orographic factors (geomorphology of a landscape), including exposition (position in relation to the compass point) and inclination (slope).

Biotic Environmental Factors. The biotic environment of an organism is determined by the interactions between the organisms: mutualism (symbiosis in the broader sense), predation, parasitism, intraspecific competition (competition within a species) and interspecific competition (competition between species), herbivory (absorption of plants), etc.

The Ecological Niche. The ecological niche of a species characterizes the relationship between a species and its specific environment. It is not understood as a spatial unit but as the dynamic relation system of a species' abilities and the habitat in which these abilities can develop (Hutchinson, 1965). The ecological niche is thus composed of an autophytic/autozooic dimension and an environmental dimension. The autophytic/autozooic dimension comprises the phylogenetically acquired morphological and physiological (for animals, also ethological) characteristics of the species, whereas the environmental dimension comprises the sum of all ecological factors effective within a specific habitat. Where both dimensions overlap, the ecological niche of a species is realized (Schmitt, 1987).

Evolutionary Factors: Mutation, Recombination, and Selection

The most important evolutionary factors are mutation, recombination, and selection.

Mutation. The genes located on the chromosomes determine the hereditary characteristics of organisms; their entirety is called *genome.* Depending on the degree of ploidy of its carrier, a gene may have several alleles. In a diploid set of chromosomes, two alleles determine a quality. A characteristic of an organism may be due to the combined action of several genes (polygeny), but it is also possible that one gene influences the development of several characteristics (polypheny).

Changes in the genotype can be caused by mutations, which may either be spontaneous (random mutations) or provoked by mutagenes (high temperatures, short-wave radiation, or certain chemical compounds such as colchicine). Mutations can cytologically be divided into four groups: genome, chromosome, gene, and point mutation. Point mutation is the mutation of one base. The phenomenon whereby genes are changeable by mutations is called *mutability.* Owing to the large number of all genes of an organism (100,000 to more than 1 million) there is a quite high mutation probability, even at a very low average spontaneous mutation rate of 10^{-4}–10^{-6} per gene and generation. Two or 3% of the individuals of every generation of the fruit fly *Drosophila* are mutated forms. In human beings, one mutation occurs per 100,000–200,000 gene replications. This means that every human being has on average one or two mutated alleles.

Mutations are responsible for the maintenance of a certain genetic variability within a population (*gene pool*). A population is defined as a group of individuals from the same species which form, at the same time (synchronously) and in the same spatial unit (syntopically), a potential reproductive community. Mutations provide the "raw material" for evolution (Fig. 10).

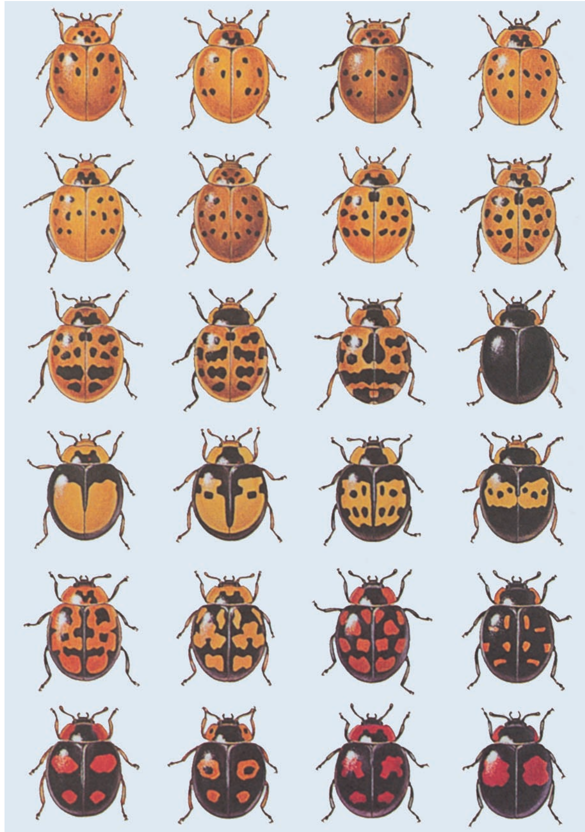

FIGURE 10 Variations in the color patterns of the elytra of the Asian lady beetle *Harmonia axyridis,* common in Siberia, Japan, Korea, and China (reproduced with permission from Ayala, 1978).

Recombination. By *recombination,* the recombination of alleles in the course of sexual reproduction (meiosis and fusion of gametes = syngamy) is understood. The developing new genotypes significantly extend the genetic variability of a population. Recombination is also a random process.

Selection. Selection "assesses" the genotype carriers: Those not adapted are eliminated. Only the adapted genotypes can pass on a high percentage of their alleles and genes to the next generation (high fitness). Selection stabilizes or alters the frequency of certain genes within a population (stabilizing and dynamic selection).

Selecting factors may be the weather (cold and dryness), competition for food, spatial competition, enemies and parasites, and for plants certain nutrients (e.g., nitrogen). Selection is always intraspecific (between the individuals of a species); it works opportunistically and not at random.

An example concerns industrial melanism. In its normal form, the light-colored peppered moth *Biston betularia* (Geometridae) can hardly be detected when it sits with spread wings on tree trunks overgrown with lichens. By mimesis (camouflage by similarity of the physiognomy to the underground) it largely escapes its enemies. Due to pollution of the air by sulfur compounds in industrial regions, lichen vegetation increasingly disappeared. In addition, the tree trunks were covered with soot. In 1848, a dark-colored (melanistic) form of the peppered moth (*B. betularius carbonarius*) was discovered for the first time in Manchester, England. The selection advantage (better protection on dark underground) led to a distinct increase in the number of these specimens: Fifty years later, 95% of the entire population, and from 1952 to 1956 even 98%, consisted of carbonarius forms (Kettlewell, 1972) (Fig. 11). Recent improvements in the field of technical environmental protection have resulted in a regeneration of the lichen vegetation and thus a selective advantage of the light-colored form.

Analogies Due to Adaptations. Organs and structures of organism groups not closely related may have to fulfill the same function and accordingly develop similar adaptations (analogies). The phenomenon in which these originally different structures and organs become increasingly more similar in the course of evolution is called *convergence.* An example of convergence in plants is the stem succulence (formation of a water reservoir to survive in dry habitats) in Asclepidiaceae, Compositae, Euphorbiaceae, Cactaceae, and Didiereaceae.

An example of convergence in animals is the streamlined shape of the body of different vertebrates: elasmobranch (shark), osseous fish (swordfish), fossil reptile (ichthyosaur), bird (penguin), and mammal (dolphin) (Fig. 12).

Especially remarkable are the convergences between the placental mammals and the marsupials (Marsupialia), the distribution of which is limited to Australia.

Speciation by Separation and Isolation

There are different definitions of a biological species:

Morphological–physiological species concept (morphospecies): A species is defined as all individuals (including their descendants) the essential characteristics of which (morphological, physiological, and also ethological, etc.) are identical. This definition is the only one applicable to fossil material.

Genetic species concept (biospecies): A species consists of actually or potentially crossing populations which are reproductively isolated from others, i.e., no genes are exchanged (species concept of the reproduction community).

Ecological species concept (ecospecies): Species make ecological demands on their environment; these demands are in part reflected by their ecological niche. Species living

a

b

c

FIGURE 11 Cryptic mimetization of the light and melanistic varieties of the moth *Biston betularia* in relationship to environmental pollution. (a) On the lichen-free bark (darkened by industrial fumes) of an oak tree near Liverpool, England, the melanistic black *carbonarius* form is better protected from its enemies than the light-colored one. (b) On a beech trunk covered with algae and the lichen *Lecanora conizaeoides,* which tolerates a slight pollution of the air, both forms of *B. betularia* are conspicuous. (c) On the lichen-overgrown bark of an oak tree in Wales the light-colored form can hardly be detected, giving it a considerable advantage with respect to predators (photo courtesy of L. Cook).

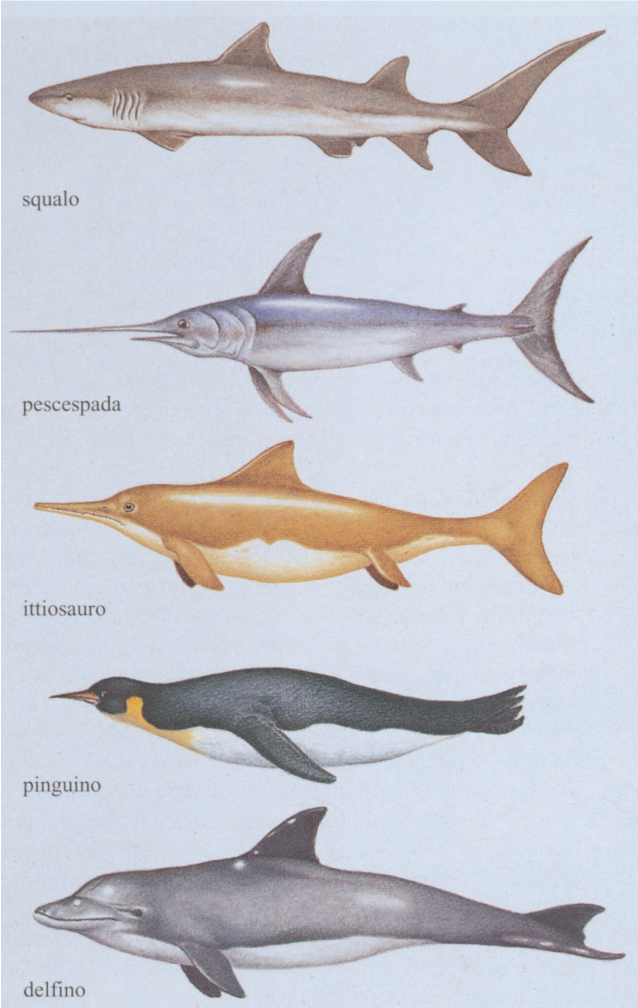

FIGURE 12 The streamlined bodies of elasmobranch (shark), osseous fish (swordfish), fossil reptile (ichthyosaur), bird (penguin), and mammal (dolphin) are perfect examples of convergence (as similarity of form) as a consequence of evolutionary adaptation to the same function (in this case, swimming).

syntopically and synchronously cannot form the same ecological niche.

Speciation. Apart from the allochronous speciation by historical species transformation over many generations (and consequently spanning long geological periods), there is a synchronous species formation, i.e., the segregation of a species into two sister species (cladogenesis).

Allopatric Speciation Step 1: Separation. The first step in an allopatric species formation is the (geographic) separation of originally genetically linked populations which may occur for several reasons: A few individuals overcome certain geographic barriers (mountains, deserts, and seas), macroclimatic changes in geological periods (ice ages) force the species to escape to different refugia, and increases in the sea level entail the separation of continental land parts (continental island formation). The lower variation in genotypes, new mutations, and differing environmental conditions (selective factors) may then bring about a speciation. The importance of separation is substantiated by the fact that species with a very large distribution area form geographic subspecies. Subspecies slightly differ with regard to their genetics and phenotype; each inhabits a certain geographic subregion within the area of the corresponding species (e.g., subspecies of the steppe zebra) (Fig. 13).

Allopatric Speciation Step 2: Development of Isolation Mechanisms. After a (geographic) separation of a continuously distributed population into two or more populations, mechanisms evolve against hybridization in a secondary contact zone, which would occur after a reintrogression. Possible mechanisms include metagamous isolation mechanisms (incompatibility of the genomes after mating) and progamous isolation mechanisms (prevention of mating).

Progamous isolation mechanisms include seasonal or cyclic isolation, i.e., different reproduction times (e.g., of butterflies) and different flowering times of plants; mechanical isolation, i.e., differences in the structure of copulation organs (e.g., of spiders); and ethological isolation, i.e., changes of optical, acoustic, and olfactory species characteristics by which animals recognize their mating partner (e.g., monkeys, birds, locusts, and butterflies) and by which plants "choose" their animal pollinators in the case of zoogamy.

Sympatric Speciation. Sympatric species formation occurs among the individuals of a species in the same distribution area. It is particularly frequent among plants. The chromosome set is duplicated (autopolyploidy), and the originating polyploid individuals are isolated from diploid ones (e.g., various ferns). About one-third of all plant species developed by polyploidy. Closely related polyploid species, however, may cross in certain cases and accordingly form new species by allopolyploidy that, in turn, are genetically isolated from the original species. Many of our cultivated plants (cotton and Gossypium, our cereals) were developed by allo- or autopolyploidy. Among animals, polyploidy is rare.

Macroevolution

Evolution processes in populations of species are called microevolution (changes of the allele frequencies in populations); macroevolution denotes the formation of new species, families, orders, classes, or phyla in flora and fauna.

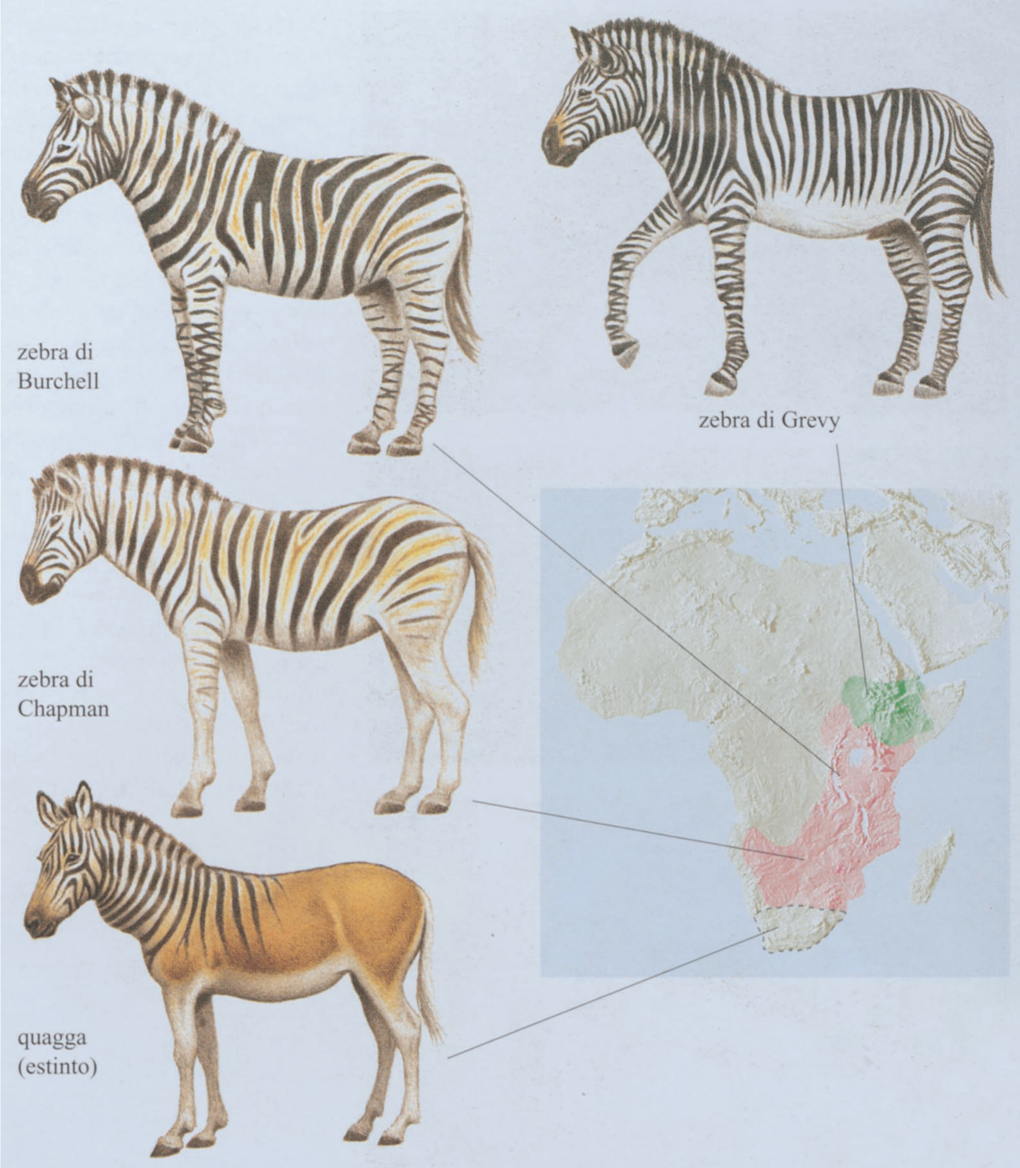

FIGURE 13 Several geographic breeds of the steppe zebra *Equus* can be distinguished by the varying stripe patterns of the coat and by the striping of the legs, which reduces increasingly toward the southern part of the territory. Grevy's zebra, *Equus (Dolicohippus) grevy,* lives in the northern regions of the territory (Kenya, Ethiopia, and Somalia); Burchell's zebra, *E. (Hippotigris) burchelli,* is diffuse in eastern and southern regions, together with the subspecies *chapmani* (Chapman's zebra) in the more southern part; and the quagga, *E. (H.) quagga,* now extinct, occupied the savanna of South Africa (adapted from *Wissen im Überblick. Das Leben. Die Welt der Modernen Wissenschaft: Zelle, Pflanze, Tier, Entwicklung, Evolution, Informationsverarbeitung, Verhalten,* Focus International/Verlag Herder, Stockholm/Freiburg, 1972).

The evolution of such higher organization forms does not occur rapidly but in small steps (additive typogenesis). Evolution processes (speciation) may be accelerated when organisms are able to realize a large ecological niche. Examples of this in phylogenesis are the conquest of the land by the fish group Crossopterygia, the conquest of airspace by birds, and the first terrestrial plants in the Devonian. Such a realization of a large ecological niche often entails a rapid splitting into numerous species (adaptive radiation); examples are Darwin's finches (Geospizinae) on the Gala-

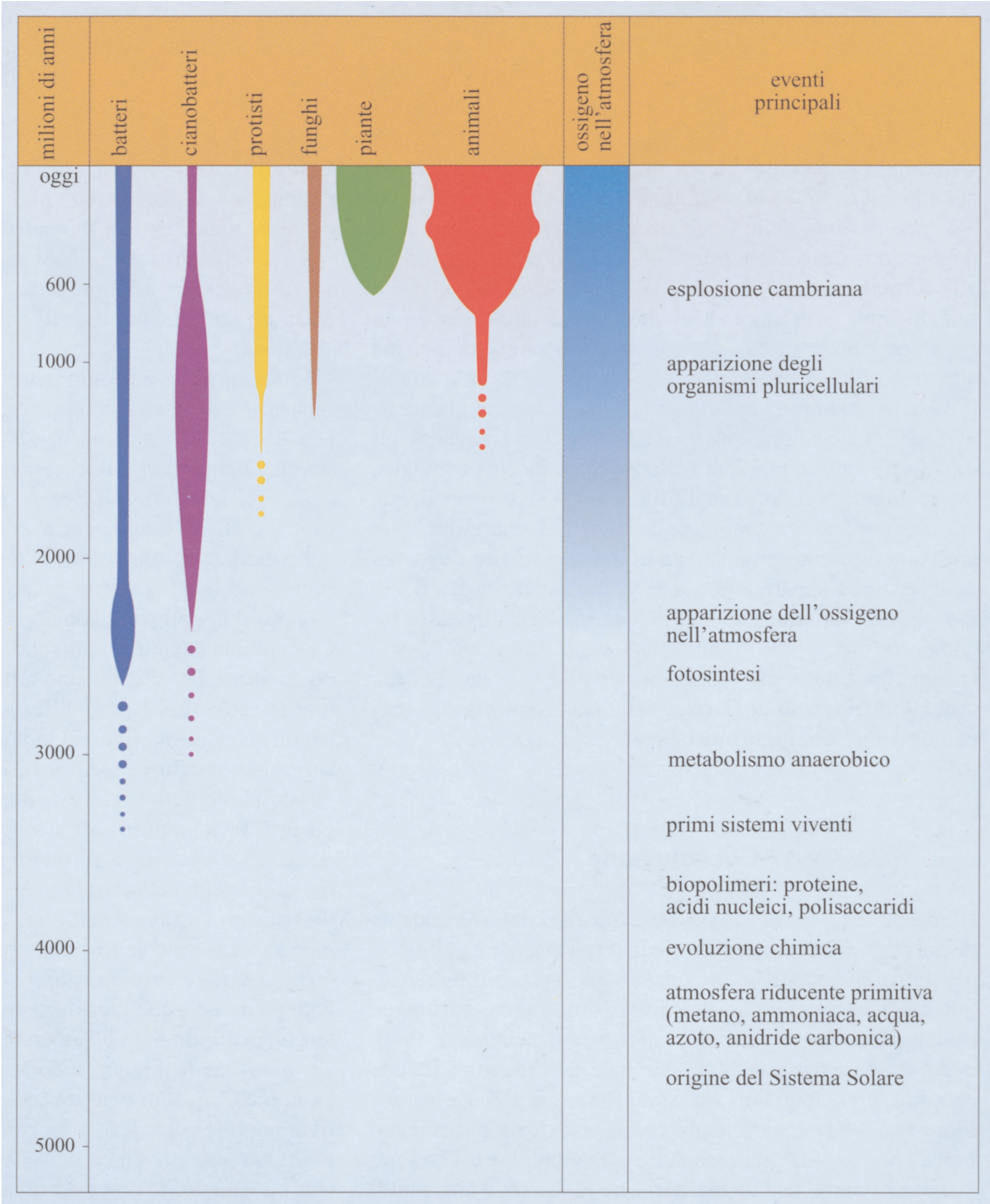

FIGURE 14 The geological timescale in relationship to the principal events which characterized the origin and evolution of life on Earth (adapted from Hickman *et al.,* 1997).

pagos Islands, honeycreepers (Drepanididae) on Hawaii, and marsupials (Marsupialia) in Australia.

The earth originated about 5 billion years ago and the first life-forms about 3.5–3.8 billion years ago. The development of prokaryotes (bacteria and cyanobacteria) began about 3.5 billion years ago. The first sponges occurred about 570 million years ago, fishes about 450 million years ago, reptiles about 280 million years ago, mammals about 200 million years ago, birds about 150 million years ago, and primates about 60–70 million years ago (Fig. 14).

Coevolution

Coevolution means that two partners or partner systems (plants, animals, fungi, or bacteria) depend on one another in their evolution and that both acquire specific adaptations as a consequence of mutual selection pressure. As a rule, it is distinguished between a *pairwise coevolution* (Janzen, 1980), in which in a more or less close relationship between two species the partners exert a continuous selection pressure on each other (*reciprocal coevolution*), and a *diffuse* or *network coevolution* (Gilbert, 1975), in which several species on both sides participate(d), e.g., a flowering plant that is visited and pollinated by several insect species and which develops, in adaptation to its pollinators, certain characteristics (shape, color, and scent) in the course of evolution.

The degree of dependence of the partners may vary significantly. In extreme cases, the successful reproduction of one species completely depends on another species (e.g., pollination of the fig by the fig wasp).

There are three different forms of coevolutive interactions: gene-by-gene coevolution, coevolution between species (specific coevolution), and coevolution between species groups (diffuse coevolution). In the following sections, these types are characterized.

Gene-by-Gene Coevolution

If a certain gene of a parasite, which codes for virulence, is complemented by a gene of its host, which codes for resistance to the parasite, this is called gene-by-gene coevolution. This kind of interaction especially occurs between plants and pathogenic fungi.

In a population of *Glycine canescens* (Fabaceae), 11 different phenotypic resistance patterns, based on at least 12 genetic resistance factors, could be identified as response to nine genotypes of the rust fungus *Phakopsora pachyrhizi* (Burdon, 1987).

Coevolution between Two Species (Specific Coevolution)

A close coevolution can be particularly shown for certain mutualistic or symbiotic systems. Examples for the systems flower–pollinator and plant species–animal disperser are given.

Flower–Pollinator Systems. The pollination of figs (Ficus and Moraceae) is very complicated (Wiebes, 1979). The urn-shaped inflorescences (syconia) of a fig tree, in which the extremely reduced flowers line the inner cavity, attract thousands of fig wasps of only a few millimeters in length (Agaonidae: genera *Ceratosoles, Blastophaga,* and *Sycophaga*). Each fig species (worldwide there are more than 1000) is pollinated by its "own" wasp species. The female wasp, transporting the pollen in two thorax bags, crawls through the very narrow, scale-covered opening of the inflorescence (ostiole) into the cavity. The stigmata are covered with pollen. Then the wasp jabs its ovipositor into the style of a flower and places an egg there. At this spot, as a consequence of the puncture and certain substances secreted by the fig wasp, a cell growth (gall) develops. The larva lives in this gall and feeds on the cell tissue. During this time, the carbon dioxide content within the syconium increases; at the end of the larval development it amounts to about 10%. At this concentration, only the male fig wasps are active. They fertilize the females in the gall, then leave it and bore a hole into the wall of the syconium. With decreasing carbon dioxide concentration, the female wasps become active. They leave the galls, fill both thorax bags with pollen, which has meanwhile been secreted by the carpellate (male) flowers, and leave the syconium. The process then starts anew. In order to avoid eggs being placed on all flowers, there are two different female flower types: short styled and long styled. Eggs are only placed in short-styled flowers; the ovipositor does not reach far enough into the long-styled ones (Fig. 15).

Dispersal of Plant Species by Animals (Zoochory). There is a very close relationship between the nutcracker *Nucifraga caryocatactes caryocatactes* and the arolla pine *Pinus cembra* (Mattes, 1978). In Europe, the nutcracker is found in mountainous habitats with fir- and larch-arolla forests. It mainly feeds on the nuts of the arolla cone which it pecks open with its chisel-shaped peak. For the winter, the nutcracker hides cedar nuts (2–11 nuts per hiding-place; average, 3.5). One individual may have more than 10,000 hiding places. The "forgotten" hiding places (about 20%) are essential for the young growth of arolla pines. The nutcracker also selects hiding places at the timberline, thus promoting the growth of trees there. Similar relationships have been shown, for example, for the Japanese nutcracker *N. caryocatactes japonicus* and *P. pumila* in Japan (Fig. 16).

On the island of Mauritius, today there remain only a few specimens of the endemic tree species *Calvaria major* (Sapotaceae). All the *Calvaria* trees are about 300 years old, although every year plenty of fruits and seeds are formed; thus, a rejuvenation should be possible. That it does not occur is due to the bisystem of *C. major* and an indigenous bird species, the dodo *Raphus cucullatus* (family Raphidae; columbaceous birds), which became, as it can be proven, extinct in the Year 1681. The dodo ate the approximately 5-cm-long fruits of *C. major.* In its muscular stomach, with the help of stones contained therein, it filed off part of the 1.5-cm-thick seed coat; therefore, the seeds could germinate. Since extinction of the dodo, artificially filing off the seeds of *Calvaria* has been attempted to achieve germination (Temple, 1977).

Coevolution of Species Groups (Diffuse Coevolution)

Examples of a coevolution between species groups can be found particularly where certain guilds are involved in

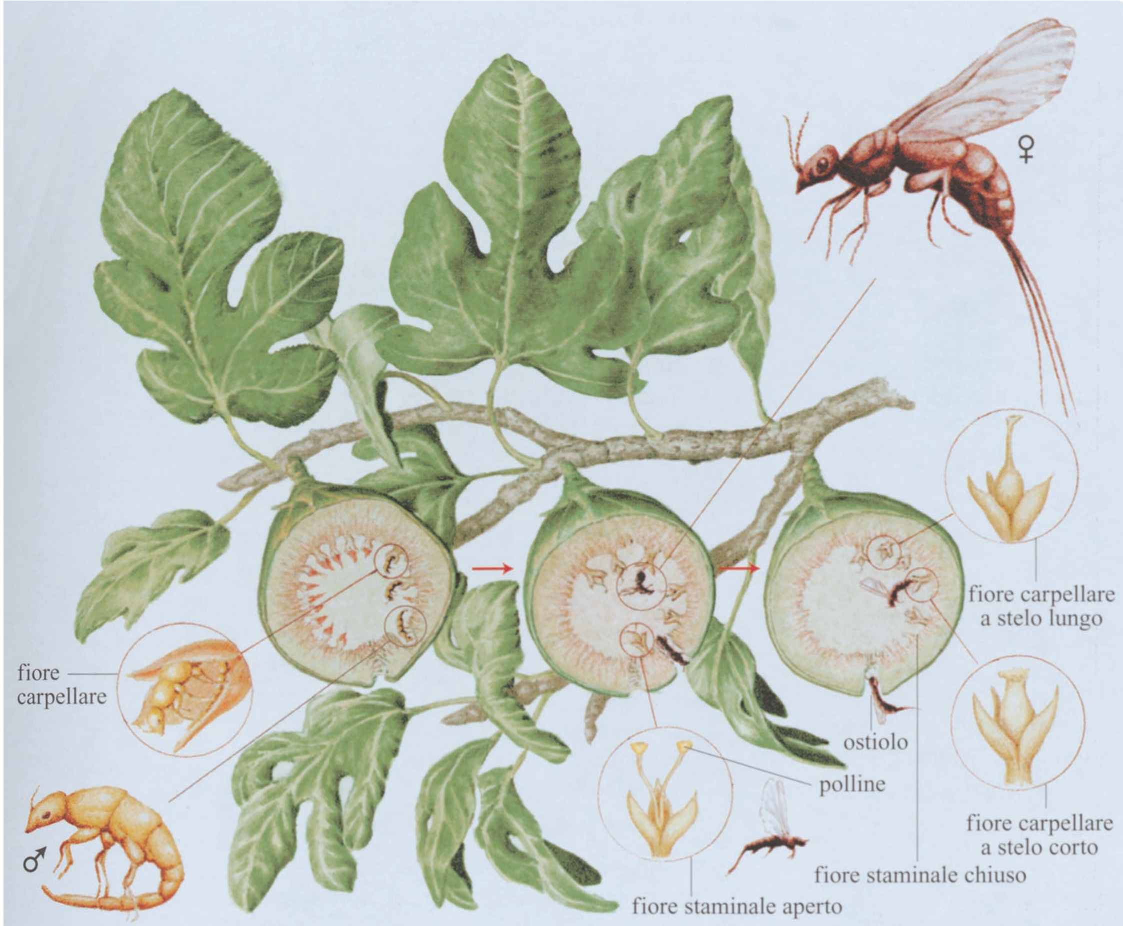

FIGURE 15 Symbiosis between the fig and the fig wasp (genus *Blastophaga,* family Agaonidae). (Left) The female fig wasp oviposits her eggs into the carpellate flowers, causing the formation of a gall in which the insect larvae develop. The male fig wasps hatch first within the gall, insert their abdomens into the gall flowers inhabited by the unhatched females, fertilize them, and leave the fig by a hole that they bore in the fruit. (Center) The fertilized female fig wasps leave the fig flower hours later. At the same time, the staminate flowers secrete pollen. The females fill their thorax bags with the pollen and then leave the fig through the holes bored by the males. (Right) After arriving at a young fig, in which the staminate flowers are still closed, the female squeezes through the ostiole. The pollen is put on the carpellate long-styled flowers, whereas the eggs are only oviposited into the short-styled flowers (adapted from Hickman *et al.,* 1997).

the ecological structure (guild coevolution). A *guild* is defined as a group of species using the same class of environmental resources in a similar manner — for instance, phloem feeders (greenfly: Aphidina), pollinators, and predators. In this context, it is important that several different species may be evolutionary vectors.

In mutualism, there are numerous examples of this form of coevolution: the many interactions between plants and their animal pollinators, between plants and their animal dispersers, and between plants and their animal "protectors."

Plants and Their Animal Pollinators. Many plant species have developed strategies to make use of the mobility of animals to attain a cross-pollination (*borrowed mobility*). By zoophily, the pollen is in a purposeful manner transferred in such a way that an exchange of genes is ensured. In the temperate zones, insects transport the pollen (entomophily); in the tropics and subtropics, this is additionally done by birds (ornithophily), bats (chiropterophily), and reptiles (saurophily), and in Australia it is also done by phalangers (Marsupialia; Faegri and van der Pijl, 1979). The flower visitors are "rewarded" by nectar and/or pollen, oil, and partly also by plant tissue.

The margin of flower visitors ranges from generalists (euryanthic flower visitors) such as bumblebees (Bombus) to specialists (stenanthic flower visitors) that can only use

FIGURE 16 A nutcracker (*Nucifraga caryocatactes*) on an arolla (*Pinus cembra*) (photo courtesy of R. Oggiani/Panda Photo).

the flowers of certain plant species, genera, or families. Examples are the silker bee *Colletes cunicularius,* which exclusively visits willows (*Salix* and Salicaceae), and the andrenid *Andrena florea,* which is only found at the bryony species *Bryonia alba* and *B. dioica* (Cucurbitaceae).

Many and diverse coadaptations have evolved between flower visitors and plant species. Thus, the development of some primary attractants in plants (pollen grain types, nectar, and oil) correlates with the evolution of the structure of the mouthparts and of the pollen-gathering and -transport devices in animals (Table 1).

Pollen grains have specific surface structures which correlate with the structures of the pollen-gathering device of a bee. The bee *Lasioglossum lineare* (Halictidae), one of the main pollinators of the pasque flower *Pulsatilla vulgaris* (Ranunculaceae), has a specific gathering device at its hindlegs composed of particularly fine hairs. These hairs exactly fit into the sutures of the pollen grains of *P. vulgaris* (Kratochwil, 1988) (Fig. 17).

The entire flower morphology of zoophilous plant species is adapted to the morphology of the respective pollinator, its sensory physiological abilities (recognition of colors and scents, etc.), and its behavior ("handling" of the flower).

Certain adaptive syndromes have evolved between different animal groups (insects and birds) and the plant species pollinated by them. The syndrome of ornithophily (pollination by birds) is compared to that of chiropterophily (pollination by bats) in Figs. 18 and 19.

Plants and Their Animal Dispersers: Myrmecochory. The phenomenon by which ants disperse the seeds of plants

TABLE 1

FLOWERS	ANIMALS
Bird flowers	**Flower birds**
Flowering during the daytime	Active during the daytime
Garish colors, usually red	High spectral sensitivity to red
No landing surface	Too heavy for landing on a flower
Thick flower tissue	Hard beaks
Scentless	Poor ability to smell
Much nectar	Great need of nectar
Mechanism to retain nectar	Great need of nectar
Nectar hidden deep within the corollae	Long beaks and tongues
Hardly any flower characteristics	Great ability to learn
Bat flowers	**Bats**
Flowering during the nighttime	Active during the nighttime
White or creamy colors, often also greenish or purple	Color-blind, good sight in the immediate area, echolocation by ultrasound
Musty smell	Good ability to smell for distance orientation
Large bowl- or bell-shaped single flowers or larger inflorescences	Large pollinators with claws at the extermities to hold on to the flower
Much nectar	Great need of nectar
Large pollen amounts, large or many anthers	Pollen is the only protein source
The flowers/inflorescences are located outside the foliage, often directly at the stems (cauliflory); long corollae	Size, lower maneuverability in flight

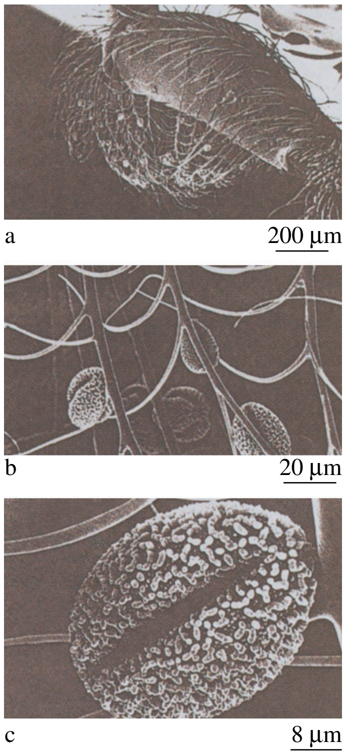

FIGURE 17 (a) Micrograph of the pollen-gathering device on the hind leg (femur) of a worker bee *Lasioglossum lineare.* (b) Micrograph of the pinnate hairs of the pollen-gathering device with pollen from the pasque flower (*Pulsatilla vulgaris*). (c) Micrograph of a pollen grain of *Pulsatilla vulgaris.*

and may in turn use the yellow to yellow-white lipoid appendage of the diaspore (elaiosome of the seed) for feeding is called *myrmecochory.* Myrmecochorous plant species include the ramson *Allium ursinum* (Liliaceae), violet species (*Viola* and Violaceae), the common celandine *Chelidonium majus,* and the holewort *Corydalis cava* (Papaveraceae and Fumariaceae). Worldwide, there are 70 plant families in which myrmecochory occurs (Beattie, 1983). Both in woodland regions and in dry open-land areas, myrmecochory may be important: Notably, many myrmecochores can be found in the fynbosch of Cape Province (South Africa), a sclerophyllous vegetation similar to the maquis in the Mediterranean region (Fig. 20).

FIGURE 18 The flower visit of a bat of the *Glossophaga* genus (photo courtesy of M. D. Tuttle/Panda Photo).

FIGURE 19 The flower visit of a hummingbird (*Cynanthus latirostris*) to an ocotillo flower (*Fouquiera splendens,* Fouquieriaceae) (reproduced with permission from Reichholf and Weidensaul, 1990).

Plants and Their Animal Protectors. The so-called ant plant (myrmecophyte) provides a comfortable habitat for ants, which in turn protect the plant from phytophages and contribute to its feeding (myrmecotrophy).

Especially interesting are some ant plants of the subtropics and tropics, which also provide a living space for the ants (myrmecodomatia) and in turn use (via a transport of ions) the waste material of the ant colony as nutrients or are even freed from lianas by the ants (Fig. 21).

Coevolution between Plants and Phytophagous Insects. Closely related herbivorous animal species often eat closely related plant species. Within butterflies, the cat-

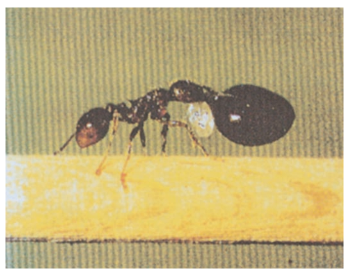

FIGURE 20 A worker ant of the genus *Myrmica* transports a diaspore of *Corydalis cava* (*Papaveraceae*) into its nest. The white appendix is the elaiosome, whereas the seed is black (reproduced with permission from Zizka, 1990).

FIGURE 21 The ant plants of the genus *Myrmecodia* (madders, Rubiaceae) grow as epiphytes on other plant species. Therefore, they have to rely on ants to supply them with mineral salts. The thickened parts of their stems are traversed by passages and chambers which serve ants of the genus *Iridomyrmex* as living space (adapted from *Geheimnisse der Natur-Entdecken, Entschlüsseln, Erklären.* Bertelsmann Lexikon Verlag/Beazley, Munich/London, 1992).

erpillars of the whites (Pieridae) prefer crucifers. These possess as secondary plant matter mustard oil glycosides, by which the pierids recognize the larval plant. On bacteria, fungi, other insects, and mammals, these substances have a toxic or repulsive effect (Feeny, 1977).

Many plant species contain certain secondary substances (vegetoalkaloids, furanocumarine, and others) to protect themselves from being eaten (chemical defense).

Phenomena of coevolution also occur in predator–prey relationships and between hosts and parasites.

Biodiversity

In its original sense, diversity means variation, differentiation, and diversification, in contrast to uniformity. Diversity may be understood as something static: Heterogeneity, then, denotes irregularities and variety denotes differences. Variability covers dynamic aspects. Diverse systems may be simple, but they also may be very complicated. As a rule, complexity is a sure sign of diverse systems: It is defined as something very intricate or complicated. Complexity covers the profundity of system structures and diversity their width. When assessing biological systems, diversity may also be seen as richness.

By biodiversity, biological diversity is understood: the total differentiation, variation, variability, complexity, and richness of life on Earth. Article 2 of the Convention on Biological Diversity of the IUCN, Rio de Janeiro, 1992 (as quoted in Bisby, 1995) states that

> 'Biological diversity' means diversity (according to differentiation, variation, variability, complexity, and richness) among living organisms from all sources, including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part, this includes diversity within species, between species and of ecosystems.

Ranges of Validity of Biodiversity

Diversity is a fundamental quality, manifesting itself in the different organization levels of matter and energy. It is a characteristic feature of all levels of the nonbiological and the biological hierarchy (hierarchical diversities); there is diversity on every single level (Fig. 22).

The levels of life are particularly diverse; here, we generally distinguish between structural diversities and functional diversities. Data on diversity may be studied at each level of the hierarchical structure using two different approaches (Solbrig, 1991): a descriptive approach (e.g., identification, determination, description, and differentiation of elements and their components) and a functional approach (e.g., a causal analysis of the combination of the elements and their components as well as of absorption, transformation, and processing of energy and matter).

The subject of this analysis is the level of ecosystems in the broader sense: their biotic components (biocoenoses) and their habitats (biotopes). Also, the level of ecosystem complexes (landscape units) will be dealt discussed. Such complexes are formed by several ecosystems, the correlations of which follow certain rules. Since the Neolithic Period and increasingly in the past 150 years, man has considerably influenced ecosystems and ecosystem complexes in many parts of the world. A study of biodiversity therefore must include man–environment systems. An increase in and also a reduction of biodiversity may be anthropogenically caused.

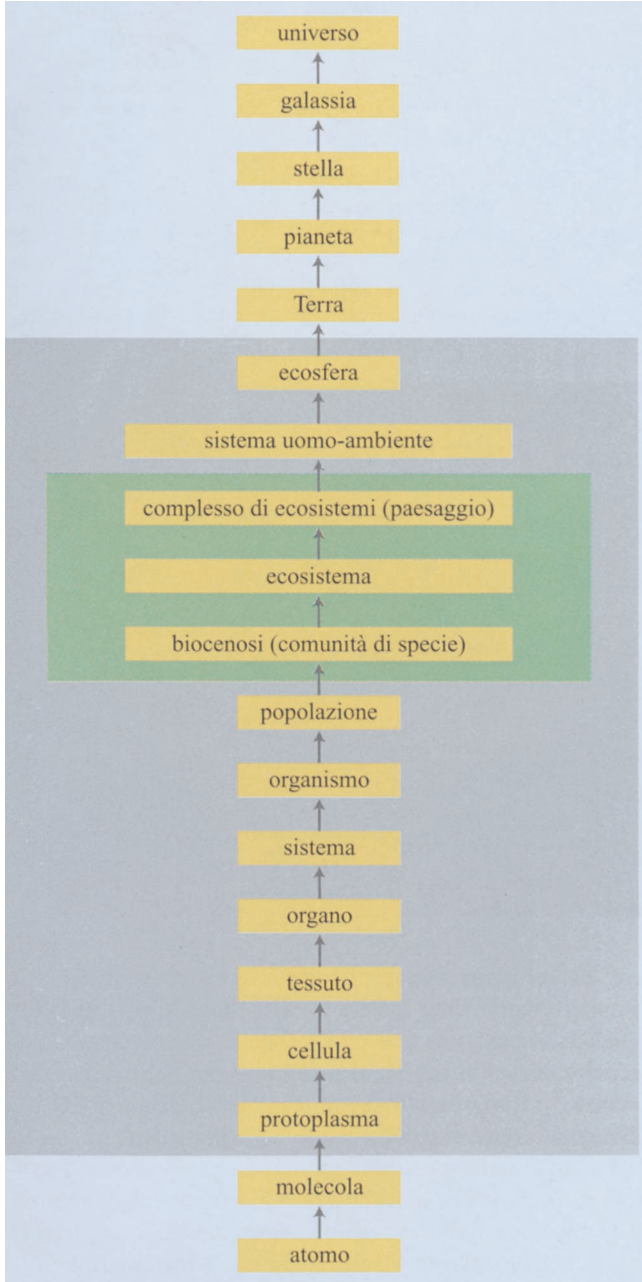

FIGURE 22 The hierarchical order of the different organization forms of organisms (gray square) and of matter and energy, each characterized by a structural and functional diversity. The range of biocoenology is indicated by the green square.

Forms of Diversity

The different forms of biodiversity may be assigned to four types:

Diversity of Elements (Element Pattern of Biodiversity).

1. Taxonomic and syntaxonomic diversity and species and coenosis diversity: Various species and coenosis diver-

sity levels can be distinguished in different spatial units: a, b, g, and d diversity (Goetze and Schwabe, 2000).

α diversity refers to the species diversity of a certain area. It is described, for instance, by several calculation methods and the determination of indices. α diversity is also defined as "diversity within a community."

Gradients between different biotopes (habitats) can be analyzed by β diversity. This procedure is especially suitable for regions with ecological gradients (ecoclines), e.g., forest/open land areas and zonation complexes at water banks; however, it is less suitable for areas with pronounced discontinuities. This diversity type can also be described as "gradient diversity between communities."

γ diversity characterizes the diversity of landscapes. A landscape part (physiotop) consists of several communities, the entirety of which makes up a vegetation complex. In a physiotope certain uniform factor combinations can be found (geological substratum, soil conditions, nutrient balance, water balance, etc.). Units relevant for the investigation of γ diversities are ecosystems and ecosystem complexes. This diversity type can be characterized as "diversity of complex communities."

δ diversity characterizes (analogously to β diversity, where changes in the number of species along an ecological gradient are analyzed) changes in the number of vegetation types along an ecological gradient.

2. Diversity of life-forms: The concept "life-form" comprises the whole complex of species-specific qualities of an organism, which developed in adaptation to the particular conditions of a certain habitat (morphological, physiological, and ethological characteristics). Such life-forms can be typified. A life-form type belongs to a group of species, which often have different systematic ranks but have acquired, adapting to the conditions within a habitat, analogous morphological, physiological, and ethological characteristics and modes of life in the course of evolution and thus have the same life-form. For animals, life-form types can be classified according to feeding habit (e.g., phytophagous, zoophagous, parasitic, and detritophagous; filter feeders, substrate eaters, grazing animals, sap feeders, stinging suckers, gatherers, predators, trappers, and parasites), according to mode of locomotion (e.g., burrowing, crawling, climbing, jumping, flying, and running animals), and according to place of residence (edaphon, atmobios and herbicolous organisms = living on or in plants; phyllobios and lignicolous organisms = living on or in wood; epizoa, endozoa, and others).

For plants, different life-forms can be distinguished according to the way in which they survive the unfavorable season (classification after Raunkiaer), according to adaptations of the water balance (xerophilous, mesophilous, hygrophilous, and hydrophilous), according to light requirement (heliophytes and skiophytes), according to soil factors, and according to diet.

3. Diversity of spatial structures: A habitat can be divided into three different spatial structure types: stratotope, choriotope, and merotope. Such a differentiation is essential for the recording and analysis of synusia within a biocoenosis.

4. Trophic diversity: Classification into producer, consumer, and decomposer levels with further subtypes.

5. Phenological diversity: Characterization of time structures, diurnal and seasonal changes, periodic phenomena within a year, etc.

6. Genetic and population-specific diversity: Characterization of genetic variability and of the genotype spectrum, phenomena of homo- and heterozygosis and of gene drift, mutation rate of individual populations, and others.

7. Biochemical diversity: Characterization of different plant ingredients (e.g., alkaloids), partly important as biochemical defense against phytophages or scents as attractant for flower-visiting animals (Feeny, 1977).

Diversity of Interactions (Dynamic Pattern of Biodiversity). Among themselves, species create bi- and polysystems and thus form so-called biocoenotic links. These interactions between the organisms induce the emergence of characteristics which may contribute to stabilizing the system (quasi-stability in the species composition). Such interaction patterns can be divided into probioses (mutualism, symbiosis, and commensalism) and antibioses (predation, parasitism, etc.).

Mechanisms Causing Diversity (Causing Pattern of Biodiversity). Basically two different processes causing biodiversity can be distinguished: effects in evolutionary times (separation, speciation, and radiation) and effects in ecological times.

1. Effects in evolutionary times: In evolutionary time periods, biodiversity is attained by speciation (allopatric and sympatric). Of great importance in this case are the separation of originally linked populations, the subsequent differentiation of the separated populations, the development of isolation mechanisms, and the formation of different ecological niches. A decisive factor for high diversity rates is a slight extinction. An especially high species diversity is elicited by radiation. Examples include Darwin's finches (Geospizinae) on the Galapagos Islands (Lack, 1947) and the honeycreepers (Drepanididae) and fruit flies (Drosophilidae) of Hawaii (Mayr, 1943).

2. Effects in ecological times: In ecological time periods, a biocoenosis rich in species can only develop when communities immigrate and are newly formed. In this context, the number of ecological niches to be realized plays a decisive part. The ecological niche is not a spatial unit but rather the dynamic relation system of a species with its environment. It is composed of an autophytic/autozooic and an environmental dimension. The autophytic/autozooic dimension comprises the phylogenetically acquired morphological and physiological (and, for animals, also ethological)

characteristics of the species, and the environmental dimension is the sum of all effective ecological factors. Where both dimensions overlap, the ecological niche of a species is realized (Schmitt, 1987). The breadth of the niche depends on the degree of specialization of the ecological niches which realize it. Niche overlaps can only be tolerated by species with a greater niche breadth.

Process of Functioning (Functional Pattern of Biodiversity). The question to what extent biodiversity contributes to the functioning of biocoenoses is controversial. There is no doubt that many organism species are constantly linked by certain interactions and that these relations may be obligatory. Such an interaction structure has only system character when it can be differentiated from other systems and when an independent matter flow is ascertainable. The differentiation of biocoenoses and ecosystems, however, has first a merely hypothetical character. Therefore, only theories can be developed in response to the questions of how much redundancy a biocoenosis or an ecosystem may tolerate without being impaired in the maintenance of their functional balance and whether there are upper and lower limits of biodiversity. The theory of biodiversity is closely linked with the ecosystem theory.

The more diverse the system, the more diverse must be its functional structure to stabilize the system. The element pattern and the diversity of interactions primarily contribute to this stabilization. Matter (nutrient) and energy flow are required to maintain the system and attain quasi-stability. The stabilization processes include matter and nutrient absorption, transformation, and transfer (as input–output reaction).

Intrabiocoenotic Diversity

A biocoenosis is composed of the plant community (phytocoenosis) colonizing a phytotope and the animal community (zoocoenosis) inhabiting a zootope. Owing to the physiognomically dominating higher plants, plant communities can be more easily analyzed and typified than zoocoenoses.

There are different pragmatic approaches to the study of biocoenoses and their diversity:

Investigation of taxonomic groups (zootaxocoenoses): classifying biodiversity

Investigation of functional groups or guilds, respectively (subsystems, smaller units, and functional groups of coexisting species which use the same resources in a similar manner): functional biodiversity

Investigation of certain relations (e.g., plant–insect complexes, food chains, and food webs): interaction biodiversity

Investigation of microhabitats (= synusia): classifying microhabitat biodiversity

More than 90% of all animal species living on land are bound to habitats characterized by their vegetation. The first step in the recording of an animal community may be a phytosociological characterization of the habitat because plant communities or vegetation complexes characterized by plant communities constitute typifiable units under ecological, structural, dynamic, chorological, and syngenetic aspects. Such a characterization of a habitat via its plant communities and plant community complexes is the starting point for a registration and analysis of biocoenological diversity.

The second step is a classification into microhabitats (= synusia); this classification should be based on three different spatial structure types: stratotope, choriotope, and merotope.

The different strata of a forest, for example, are designated as stratotopes; here, it can be distinguished between tree stratum, trunk stratum, herb stratum, etc., each colonized by its own stratocoenosis. Choriotopes, on the other hand, are independent vertical structures of the entire spatial unit or of parts of the stratotope (so-called choriocoenoses) such as the insect community of a tree or a shrub. Finally, in a habitat rich in structures, merotopes can be found (i.e., structure elements within a stratotope or a choriotope, such as organisms living on leaves or on bark or flower visitors) (Fig. 23).

Stratocoenoses. Analyses of taxonomic biodiversity demonstrate that each of these strata has its own animal spe-

STRATOTOPO	STRATOCENOSI	ESEMPI
strutture orizzontali	sottocomunità appartenente allo stratotopo	strato della lettiera strato erbaceo strato dei cespugli strato delle chiome
CORIOTOPO	**CORIOCENOSI**	**ESEMPI**
strutture verticali dell'intera unità spaziale o parti dello stratotopo	sottocomunità appartenente al coriotopo	albero tronco cespuglio carcassa escrementi formicaio nido di uccello
MEROTOPO	**MEROCENOSI**	**ESEMPI**
elementi strutturali all'interno di uno stratotopo o di un coriotopo	sottocomunità appartenente al merotopo	comunità delle foglie comunità del legno comunità della corteccia comunità dei fiori visitatori dei fiori

FIGURE 23 The three different spatial structure types (stratotope, choriotope, and merotope), the coenoses they comprise (stratocoenoses, choriocoenoses, and merocoenoses), and examples for each type.

FIGURE 24 The dominant spider species from different strata in a central European oak–birch forest (data from Rabeler, 1957).

cies inventory, e.g., spider stratocoenoses in central European oak–birch forests. Comparisons of the strata of various plant communities, of the leaf and soil strata of a melic grass–beech forest (Melico–Fagetum), and of an oak–hornbeam forest (Querco–Carpinetum) show distinct differences in the species composition of earthworms in the stratocoenoses, especially in the leaf litter stratum (Rabeler, 1957) (Fig. 24).

Choriocoenoses. Other structural elements include special, clearly differentiable elements, so-called choriotopes; for example, a tree, a shrub, or a single plant, each with its community of phytophagous insects (phytophage complex). The diversity of a choriotope can be demonstrated with the example of a bird's nest (Aßmann and Kratochwil, 1995). Bird species utilize very specific requisites to build their nests. The long-tailed titmouse (*Aegithalos caudatus*) builds highly characteristic nests in juniper (*Juniperus communis*) in northern Germany. An analysis of the nesting material shows that it consists of specific materials: certain moss species, lichen species, algae, etc. The composition depends on the plant community in which the nest is built. It is an orderly, habitat-typical structural diversity. The nest of a great tit (*Parus major*) is built in another way; also, this bird species is mainly found in quite different habitats. The diversity of species entails a diversity of the small structures created by them (Fig. 25).

Merocoenoses. The merotopes are parts of strato- and choriotopes. Strato-, chorio-, and merotopes combine to a special degree structural and functional diversity. Here, we discuss ecological niches, interaction levels, and relation structures between organisms.

	COMUNITÀ DEL GINEPRO (*Dicrano-Juniperetum*)		COMUNITÀ DEL GINEPRO (*Roso-Juniperetum*)		FORESTA DI FAGGIO (*Periclymeno--Fagetum*)
	codibugnolo		codibugnolo		cinciallegra
MATERIALE UTILIZZATO PER IL NIDO	nidi		nidi		nido
	1	2	3	4	5
BRIOFITE EPATICHE					
Hypnum mamillatum	8,9%	23%	12,8%	38%	+
Dicratum scoparium	++	++	-	-	-
Campylopus introflexus	+	+	-	-	-
Lophocolea bidentata	+	-	-	-	-
cf. Dicranoweisia	+	-	-	-	-
Hypnum mamillatum	-	-	+++	-	-
Eurhynchium swartzii	-	-	++	-	-
Dicranoweisia cirrata	-	-	-	+	-
Rhytidiadelphus squarrosus	-	-	-	-	50%
Scleropodium purum	-	-	-	-	40%
Brachythecium rutabulum	-	-	-	-	+++
Eurhynchium praelongum	-	-	-	-	+
Pleurozium schreberi	-	-	-	-	+
LICHENI	11,5%	13,1%	14,6%	9,8%	-
Hypogymnia physodes	+	+	+	+	-
Parmelia sulcata	+	+	+	+	-
Physcia tenella	-	-	+	+	-
Physcia adscendens	-	-	+	+	-
ALGHE					
Ulothrix spec.	+	-	-	++	-
Pleurococcus vulgaris	+	-	-	++	-
MISCELLANEA					
penne	15,8%	19,4%	35,5%	11,6%	-
corteccia di ginepro	64%	12,6%	9,7%	4,7%	-
bacche di ginepro	++	+	+	+++	-
aghi di ginepro	++	+	+	+++	-
tele di ragno	+	+++	+++	++	-
bozzoli di insetti	-	++	-	-	-
erica	-	+	-	-	-
indefinito	-	32%	32%	-	-
resti di foglie	-	-	-	+	-

FIGURE 25 Structural diversities of four nests of long-tailed titmice (*Aegithalos caudatus*) and a comparison with the nest of a great tit (*Parus major*). Plus signs indicate the presence, more or less significant, of traces less than 1% (adapted from Aßmann and Kratochwil, 1995).

The community of flower visitors corresponds to a merocoenosis, with the flowers representing merotopes. First, we find a systematic biodiversity of very different animal groups: Hymenoptera apoidea, Hymenoptera aculeata, Lepidoptera, Coleoptera, etc. Within this flower–flower visitor system, there is a functional diversity introduced by the visitor: for example, food relations (pollen, nectar, and oil) or certain other resource relations, such as the use of the flowers as warming-up places due to their parabolic mirror-like forms, as "rendezvous" places, as food source for predators and parasites, as overnight accommodation (e.g., for bees), or as provider of nesting materials. Flowers even supply scents used to mark swarming paths, as done by the neotropic, scent-gathering euglossine bees (Euglossinae). About 1400 plant species (belonging to 10 families) of oil-producing plants are known worldwide, and approximately 300 wild bee species specialized on them (Vogel, 1988).

Moreover, plants also show different degrees of functionality (functional diversity). For the plant, the margin ranges from symbiotic relations, in which case the pollen-transferring insects are rewarded with food, to parasitism, which can be found in its most distinctive form in specimens of the genus *Ophrys:* The flowers imitate female bees and "sneak" by optical, olfactory, and tactile stimuli into the instinctive behavior of male bees to ensure a transfer of pollinia.

Species diversity and functional diversity always correlate with structural diversity. One example of this is the correlation between the structure of the pollen-gathering device of a bee and certain pollen grain structures.

The structural diversity of a flower–flower visitor merocoenosis is immense:

Optical diversity: the colors of the flowers in the visible and also in the ultraviolet wave range

Olfactory diversity: the multitude of different flower scents

Ethological diversity: the behavioral variety of flower visitors

Phenological diversity: the diurnal and seasonal variation of the occurrence of flowers and their pollinators.

Each plant community has its own animal communities on different levels (e.g., guilds). Often, animals need whole vegetation complexes. On the ecosystem level, the structural and functional diversity levels of different organism groups correlate with their specific abiotic environments. The biocoenoses or biocoenosis complexes are characterized by certain character species. However, each biocoenosis has its own range of diversity types and patterns. The greater the species diversity, the more varied are other diversity types: genetic diversity, space-structural and physiognomic diversity, biochemical diversity, phenological diversity, etc.

Interbiocoenotic Diversity

As a rule, landscapes are not composed of single biocoenoses but, rather, of biocoenosis complexes and a mosaic of different ecosystems. The development of individual vegetation units into associations, for example, is not arbitrary but follows certain rules. It is interesting that regularities on the species–biocoenoses (Thienemann's laws) and biocoenoses–biocoenosis complex levels follow the same natural laws.

In the first case, "The more variable the conditions for life of a site, the larger the species number of the respective community" and "The more the conditions for life of a biotope deviate from the normal and for most organisms optimum conditions, the poorer in species the biocoenosis will become, the more characteristic it gets, the more individuals of the single species will occur."

In the second case, "The more variable the environmental conditions of a habitat complex, the larger the number of its biocoenoses" and "The more the environmental conditions of a habitat complex deviate from the normal and for most biocoenoses optimum conditions, the poorer in biocoenoses the complex will become, the larger and the more characteristic are the occurring biocoenoses" (Schwabe and Kratochwil, 1994).

Does Each Species Have the Same Importance in a Diverse System?

It is undisputed that often the functional importance of species is not known and that there are frequently no indications as to how the species react to stress factors in a certain biocoenosis. There are species of central importance for an ecosystem, so-called keystone species, without which the entire system would break down. Such keystone species include *Phragmites communis,* which builds up large reeds (there are many links between reed and various animal species), and the beaver (*Castor canadensis*), which shapes entire river landscapes (e.g., the boreal regions).

The functions of many species in an ecosystem are not currently scientifically documented. Ehrlich and Ehrlich (1981) formulated the rivet hypothesis: Every species is comparable to a rivet joint in an airplane. Its importance cannot be predicted for any situation. There may be redundant subsystems. No one knows if missing rivet joints can be compensated or if just one missing joint may have severe consequences.

Applied Aspects of Biodiversity

Currently, about 1.5 million of the earth's animal and plant species have been described. Their actual number may vary between 5 and 30 million. For approximately the past 25 years, scientists have predicted the extinction of approximately 1 million species. An exponential tendency can be ascertained: From 1600 to 1900, every 4 years a species was eradicated by man and after 1900 a species was eradicated each year; currently, more than 1 species disappear per day. It is assumed that every hour 1 species is extinguished. By

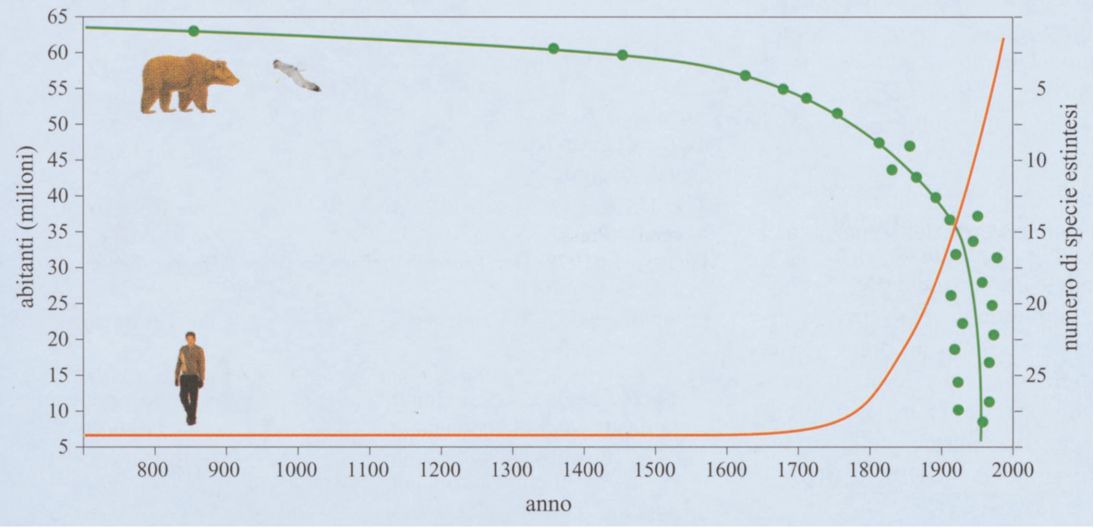

FIGURE 26 Demographic evolution in Germany and extinction rates of mammals and birds (depicted schematically).

the end of the previous century, probably 20–50% of all species had disappeared (Fig. 26).

Under natural conditions, the net growth rate of species is 0.37% in 1 million years (i.e., 0.00000037%), which is an extremely low value. The natural extinction rate has thus been increased 10,000-fold by man; the decrease is at least 100 times higher than the loss of species in the past 65 million years. The rate of loss of genetic diversity on the level of populations is much higher.

The center of especially high biodiversity lies in the tropics, mainly in the tropical mountainous areas. On a few hectares of forest in Southeastern Asia or in the Amazon region, more tree species can be found than in the whole of Europe. In Venezuela's evergreen rain forest, there are at least 90 tree species per hectare. In some regions, the loss of biodiversity is significant: Worldwide, numerous ecosystem types are particularly endangered, including the tropical rain forests, certain marine ecosystems, islands in the sea, high mountain ranges, arctic and subarctic habitats, savannas, steppes, semideserts, large river systems, mangrove forests, many lakes, and also the landscapes in the countries in which we live.

A loss of biodiversity cannot be tolerated for ecological, ethical, religious, aesthetic, and cultural reasons, especially because the destruction of biodiversity is irreversible. To maintain biodiversity, developing theoretical principles and translating them into practical measures is one of the major tasks of the near future. The maintenance of biodiversity is closely linked to the survival of man on Earth and has thus been incorporated into the concept of sustainable development.

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