

## ENCYCLOPEDIA ARTICLE

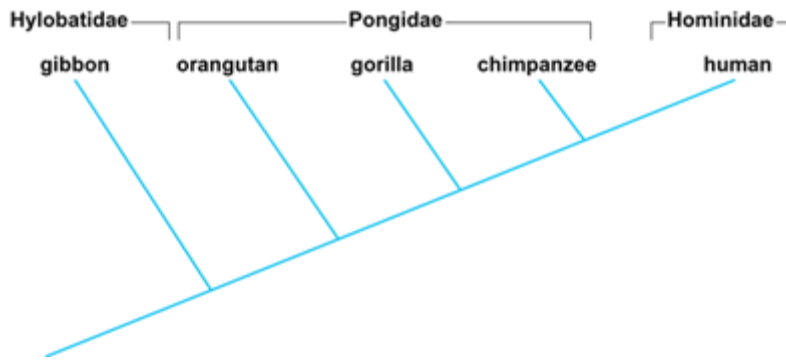
## Macroevolution

Large-scale patterns and processes in the history of life, including the origins of novel organismal designs, evolutionary trends, adaptive radiations, and extinctions. Macroevolutionary research is based on phylogeny, the history of common descent among species. The formation of species and branching of evolutionary lineages mark the interface between macroevolution and microevolution, which addresses the dynamics of genetic variation within populations. The term macroevolution was used by the geneticist Richard Goldschmidt around 1940 to challenge the then prevailing notion that major features of evolutionary history could be understood as simple extrapolations of population genetic principles. The term still often implies this challenge and the expansion of Darwinian evolutionary theory to include evolutionary processes emerging above the species level on time scales encompassing multiple millions of years. Phylogenetic reconstruction, the developmental basis of evolutionary change, and long-term trends in patterns of speciation and extinction among lineages constitute major foci of macroevolutionary studies.

### Systematics and phylogeny

The goals of systematics are to reconstruct the phylogeny of species and to produce a taxonomy of species that reflects their phylogenetic relationships. Phylogenetic relationships are revealed by the sharing of evolutionarily derived characteristics among species, which provides evidence for common ancestry. Shared derived characteristics are termed synapomorphies, and are equated by many systematists with the older concept of homology. Characteristics of different organisms are homologous if they descend, with some modification, from an equivalent characteristic of their most recent common ancestor. Closely related species share more homologous characteristics than do species whose common ancestry is more distant. Species are grouped into clades according to patterns of shared homologies. The clades form a nested hierarchy in which large clades are subdivided into smaller, less inclusive ones, and are depicted by a branching diagram called a cladogram. A phylogenetic tree is a branching diagram, congruent with the cladogram, that represents real lineages of past evolutionary history; that is, it has a time division.

A cladogram or phylogenetic tree is necessary for constructing a taxonomy, but the principles by which higher taxa are recognized remain controversial. The traditional evolutionary taxonomy of G. G. Simpson recognizes higher taxa as units of adaptive evolution called adaptive zones. Species of an adaptive zone share common ancestry, and distinctive morphological or behavioral characteristics associated with use of environmental resources. Higher taxa receive Linnean categorical ranks (genus, family, order, and so forth) reflecting the breadth and distinctness of their adaptive zones. All taxa must have a single evolutionary origin, which means that the taxon must include the most recent common ancestor of all included species. A taxon is monophyletic if it contains all descendants of the group's most recent common ancestor, or paraphyletic if some descendants of the group's most recent common ancestor are excluded because they have evolved a new adaptive zone. For example, evolutionary taxonomy of the anthropoid primates groups the orangutan, gorilla, and chimpanzee in the paraphyletic family Pongidae and the humans in the monophyletic family Hominidae. Although the humans and chimpanzees share more recent common ancestry than either does with the gorilla or orangutan, the chimpanzees are grouped with the latter species at the family level and the humans are placed in a different family because they are considered to have evolved a new adaptive zone. The Hominidae and Pongidae together form a monophyletic group at a higher level (**Fig. 1**). See also: Systematics



**Fig. 1** Phylogenetic relationships of anthropoid primates showing traditional family-level taxa. All apes and humans together form a monophyletic group. The family Pongidae is paraphyletic, and therefore considered invalid by cladistic taxonomists. (After C. P. Hickman, Jr., L. S. Roberts, and A. Larson, *Integrated Principles of Zoology*, 9th ed., 1993)

Cladistic taxonomy or phylogenetic systematics accepts only monophyletic taxa because these alone are considered natural units of common descent. Such taxa form a nested hierarchy of groups within groups corresponding to the structure of the cladogram or phylogenetic tree. Linnean rankings are considered unimportant. Taxa recognized using both the Simpsonian and cladistic taxonomies are standardly used in macroevolutionary analyses of extinction and patterns of diversity through time. The Simpsonian versus cladistic taxonomies often lead to fundamentally different interpretations, however. For example, extinction of a paraphyletic group, such as dinosaurs, would be considered pseudoextinction by cladists because some descendants of the group's most recent common ancestor survive. Birds are living descendants of the most recent common ancestor of all dinosaurs. The dinosaurs as traditionally recognized, therefore, do not form a valid cladistic taxon. See also: Aves; Dinosauria; Phylogeny

### Origins of evolutionary novelty

Comparative studies of organismal ontogeny are used to find where in development the key features of higher taxa appear and how developmental processes differ between taxa. Evolutionary developmental biologists denote the characteristic body plans of taxa by the term Bauplan, and the developmental stage during which key features of the Bauplan are formed by the term phylotypic stage. Developmental stages preceding and following phylotypic stages are subject to profound modification among species, but the phylotypic stages are evolutionarily stable. Specific patterns of gene expression that characterize some phylotypic stages in animal development have been identified through molecular genetics. The major characteristics of animal phyla and their developmental and molecular attributes appear to have arisen and stabilized early in the history of life, during the Cambrian Period. Subsequent evolutionary diversification builds upon the Baupläne established early in animal evolution. See also: Cambrian

### Heterochrony

Particularly important to the evolutionary diversification of life are historical processes that generate change by altering the timing of organismal development, a phenomenon called heterochrony. Heterochronic changes may alter the ontogeny and life history of the organism as a whole or may be limited to certain structures or organs. The different heterochronic processes are described by using an ontogenetic trajectory that describes changes in form occurring throughout the organism's life. Ontogenetic changes are measured relative to the timing of reproductive maturation.

Heterochronic changes can produce either pedomorphic or peramorphic results. Pedomorphosis denotes the retention of preadult characteristics of ancestors in the adult stages of descendants; peramorphosis is the opposite outcome, in which the descendant ontogeny transcends that of the ancestor, adding new features at the final stages. Heterochronic changes can be produced by changing the rates of developmental processes

or the times of their onset or termination. Axolotls of the salamander genus *Ambystoma* illustrate paedomorphosis produced by the heterochronic process neoteny, in which the rate of morphological development is decreased relative to reproductive maturation. The ancestral life history of *Ambystoma* is biphasic, possessing an aquatic larval stage followed by a metamorphosed, terrestrial adult. In the axolotl, reproductive maturity proceeds normally, but metamorphosis does not occur and the adult retains the morphological characteristics of the aquatic larva, including gills and tail fin.

Developmental dissociation occurs when different kinds of heterochronic change alter the development of different parts of the organism independently. Extensive dissociation can fundamentally restructure organismal ontogeny, producing ontogenetic repatterning. However, it is rare that a single heterochronic transformation affects all parts of the organism simultaneously, as seen in the axolotl example above. Dissociation and paedomorphosis together refute the statement that ontogeny recapitulates phylogeny, a claim that preadult stages of organismal development correspond to adult morphologies of ancestors. Ontogeny recapitulates phylogeny only in the unusual event that evolutionary change produces peramorphosis affecting all parts of the organism simultaneously. Ontogeny recapitulates phylogeny for individual structures or organs experiencing peramorphic evolution, whereas reverse recapitulation characterizes paedomorphic transformations. For most taxa, novel morphologies are produced by a mosaic of different heterochronic processes and by changes in the physical location of developmental events within the organism. See also: Heterochrony

### **Key innovation**

A novel morphological or behavioral feature that alters the functional relationship between organisms and their environments is called a key innovation. A key innovation changes the selective factors acting on populational variation and leads to new directions of adaptive evolution. The trophically diverse cichlid fishes illustrate the concept of a key innovation and its evolutionary consequences. The key innovation in this group constitutes changes in the structure of the pharyngeal jaws that permit them to process food. Without the modified pharyngeal jaws, the maxillary and mandibular jaws must both obtain and process food items, preventing the jaws from becoming specialized for obtaining food. The cichlid pharyngeal jaws permit the maxillary and mandibular jaws to specialize for obtaining food in diverse ways, and this has produced an enormous diversity in feeding morphology and ecology among cichlid species. A key innovation or Bauplan of a taxon is evolutionarily stable because many subsequently evolved features are built upon it, causing it to become developmentally and functionally burdened; any major alteration would disrupt the adaptive system and have disastrous consequences. A trophically specialized cichlid fish would be unable to survive, for example, if its pharyngeal jaws lost their ability to process food.

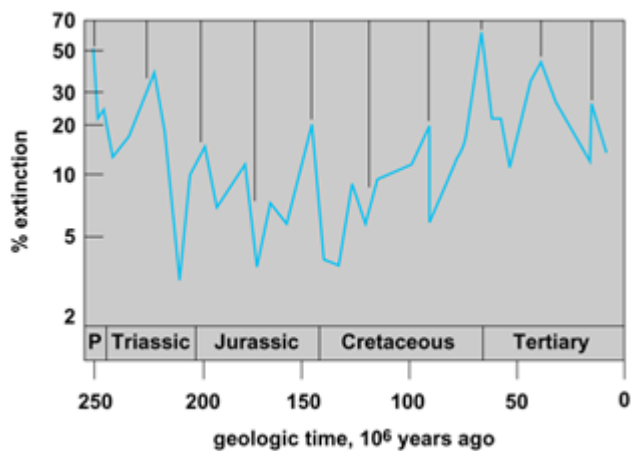
### **Hierarchical expansion**

Traditional Darwinian theory emphasizes natural selection acting on varying organisms within populations as the main causal factor of evolutionary change. Over many generations, the accumulation of favorable variants by natural selection produces new adaptations and new species. Macroevolutionary theory postulates two additional processes analogous to natural selection that act above the species level and on much longer time scales. An evolving lineage ultimately experiences one of two fates, branching speciation or extinction. Lineages that have a high propensity to produce new species and an ability to withstand extinction will dominate evolutionary history to the detriment of lineages that are prone to extinction and that have low rates of speciation. Biological characteristics are transmitted from ancestral to descendant species, and characteristics associated with lineages having high rates of speciation and low rates of extinction will prevail, even if they do not experience variation and selection within populations.

The higher-level process of differential speciation and extinction caused by the varying characteristics of

species or lineages has been called species selection. Because the precise meaning of the term species is controversial, the more neutral terms lineage selection and clade selection are sometimes substituted for species selection. Most species show an evolutionary duration from a few million to approximately 10 million years in the fossil record between geologically instantaneous events of branching speciation. Species selection therefore generally occurs on a time scale of millions of years, rather than the generational time scale of natural selection. Species selection may be the primary factor underlying morphological evolutionary trends at this scale if lineages evolve by punctuated equilibrium, in which most morphological evolutionary change accompanies branching speciation, and species remain morphologically stable between speciational events. See also: Speciation

The fossil record reveals mass extinctions in which enormous numbers of species from many different taxa are lost within a relatively short interval of geological time. For example, approximately 90% of the species and half of the families of shallow-water marine invertebrates were lost within a few million years during the Permian mass extinction (225 million years ago). A major recent discovery is that mass extinctions may occur at a periodicity of approximately 26 million years in the post-Permian fossil record of marine invertebrates (**Fig. 2**). This periodicity may represent periodic bombardment of the Earth by asteroids, causing massive environmental destruction. Some lineages may be better able to survive mass extinction events than others, and the characteristics that make a lineage prone to survive mass extinction may be very different from those that influence species selection between events of mass extinction. Catastrophic species selection denotes differential survival and extinction of lineages during events of mass extinction as determined by character variation among lineages. Prior to the Cretaceous mass extinction, dinosaur taxa dominated mammalian taxa, whereas mammals survived the mass extinction and then diversified extensively. The characteristics of the ancestral mammals may have permitted them to survive environmental challenges to which dinosaurs were susceptible. See also: Extinction (biology); Fossil; Mammalia; Paleontology; Permian



**Fig. 2** Simpsonian patterns of mass extinction in the post-Permian fossil record of marine invertebrates. Mass extinctions (peaks) correspond approximately to 26-million-year intervals (vertical bars). (After D. M. Raup and J. J. Sepkoski, Jr., *Periodicity of extinctions in the geologic past*, *Proceedings of the National Academy of Sciences USA*, 81:801–805, 1984)

Because natural selection, species selection, and catastrophic species selection can differ in the biological characteristics they promote, higher-level processes may undo or reverse evolutionary trends arising from lower-level processes. For this reason, macroevolutionists often resist attempts to explain evolutionary trends strictly from the occurrence of natural selection acting within populations. Species selection and catastrophic species selection are being investigated by paleontological research where processes occurring on geological

time scales of multiple millions of years can be investigated. See also: Organic evolution

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