BOTANY: THE STATE OF THE ART

How Development's Clock Guides Evolution

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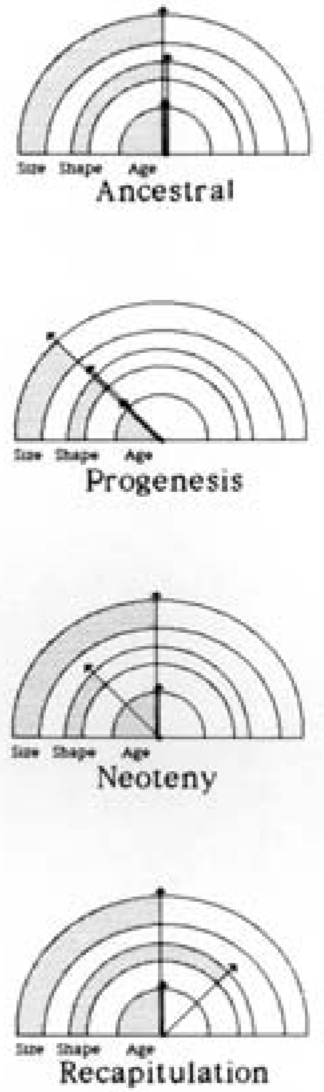
Shifts in the comparative rates at which organisms differentiate, grow, and mature are one source of evolutionary change

Nearly every school child is introduced at some time during his or her education to the hypothesis that ***ontogeny recapitulates phylogeny***. This hypothesis, which over the years has experienced periods of enthusiastic acceptance as well as outright rejection in the scientific community, is usually traced to Professor Ernst Haeckel, a German biologist whose writings on the subject appeared from 1860 to 1880. Briefly stated, the hypothesis ("Ontogeny recapitulates phylogeny.") refers to the apparent sequence of stages that individuals proceed through as they develop and mature, beginning with embryonic stages resembling distant evolutionary ancestors, then stages similar to more recent ancestors, and so on and so on. In the most frequently cited example, early human embryos are said to resemble fish with gill slits, then amphibians with rudimentary tails, etc. According to the hypothesis, each stage in the development of an embryo (ontogeny) reflects an ancestor in the evolutionary sequence (phylogeny) leading up to humans. Thus, in the course of human evolution, fish gave rise to amphibians and they, in turn, to humans.

In spite of the fact that "ontogeny recapitulates phylogeny" is, at best, an oversimplification of a complex process, the expression does focus attention on an important and indisputable fact about evolution—namely, that new species evolve as a consequence of modifications in existing structures. Or, to put it another way, one might say that a careful examination of an organism's ontogeny reveals evidence of ancestral developmental events that have been either elaborated upon or reduced during evolution. Haeckel, unfortunately, felt that his ideas could be extended to practically all aspects of everyday life, including politics, social relations, and even religion. Happily, modern evolutionary biologists who deal with Haeckel's concepts usually restrict their theories to questions about the origin of new plant and animal species.

Probably the most extensive treatment of Haeckel and the biological implications of his theories can be found in *Ontogeny and Phylogeny*, a book by Stephen Jay Gould of Harvard University. Professor Gould, whose own research focusses on the evolution of snail species in Burma, uses a clock analogy to show how developmental alterations can account for evolution. To illustrate this, imagine that an organism's development is laid out in sequence, like the hours of a clock, such that "0" to "1," for example, corresponds to early embryonic development, "1" to "2" to late embryo formation, "2" to "3" to the young individual, and so on. According to Gould's representation, development is a semicircular clock—similar to a sundial—showing different aspects of this sequence and composed of three scales: the first (outer) scale denoting size, the second (inner) scale shape, and the third scale time or age. To use the clock, one follows the progression of size and shape (form) in an individual's lifetime by watching the movement of hands across the different scales. Think of it as the model of existence or, alternatively, as the ancestral type!

What happens to the clock during evolution? If one accepts Haeckel's interpretation (i.e., recapitulation), then evolution produces new species by adding structures onto the end on the ancestral sequence. In other words, "ontogeny recapitulates phylogeny" means that development repeats all the stages (shapes) of an individual's ancestors just as human embryos form rudimentary gill slits, then a tail and then some other seemingly out-of-place structure during the course of their development. According to the clock analogy, recapitulation runs the "shape" hand faster than the "size" and "age" hands.



Developmental "Clocks" Illustrating the Categories of Heterochronic Change Involved in Evolution.

Each clock is set at the stage of reproductive maturity—i.e., flowering. In the Ancestral *clock, "size" and "shape" proceed synchronously over time.* Progenesis *also involves synchrony, but in this case reproductive maturity occurs earlier during ontogeny. By contrast, both* Neoteny *and* Recapitulation *involve developmental changes in the relationships among size, shape, and age. Neoteny, for example, involves a retardation of shape development relative to size and time. On the other hand, recapitulation consists of accelerated shape development.*

Obviously, if one thinks of development in terms of a clock, additional ways of tinkering with the hands, other than recapitulation, ought to be feasible. Theoretically, for example, one could have the shape hand run slowly compared to age and size. Known as ***neoteny***, the result would be an adult with juvenile features; evolutionary biologists use the term ***pædomorphosis*** to refer to the retention of ancestral juvenile characteristics in adults of descendants. Humans, for instance, are often considered to be neotenic in several respects, including the shapes of our skulls, compared to ape-like ancestors. Among zoological scholars, the most famous example of neoteny is the axolotl, a salamander that retains, as an adult, the gills and undeveloped lungs typical of salamander larvae. Not surprisingly, this animal caused considerable difficulty for Professor Haeckel because, after all, axolotl's features hardly fit into a scheme of evolution based on recapitulation. Rather than adding on structures to the end of an ancestral sequence, it abbreviates development by eliminating the later stages of the sequence.

If all three hands of the developmental clock ("size," "shape," and "age") are retarded simultaneously, one obtains a precociously mature individual, small in stature and with juvenile characteristics. This condition, which is known as ***progenesis***, is an alternative evolutionary mechanism that results in pædomorphosis. Several examples of progenetic insect species are known, and, in fact, the hormonal basis of this phenomenon is an area of active scientific investigation. Researchers feel that so-called ***precocenes***, hormones that cause early sexual maturity in juvenile-appearing insects, might be used effectively in controlling insect populations.

Recapitulation, neoteny, and progenesis are all examples of ***heterochrony***, a collective term that refers to any kind of evolutionary change in the timing of developmental events. Although most studies of it concentrate on animal examples, heterochrony is a general biological phenomenon that undoubtedly affects every group of organisms in the world, including plants. Take, for instance, the so-called closed (***cleistogamous***, CL) and open (***chasmogamous***, CH) flowers of violets (*Viola* spp.), *Lamium amplexicaule* and *Collomia grandiflora* studied by Professor Elizabeth M. Lord of the University of California at Riverside. CL flowers normally appear early in the growing season, are reduced in size, and fail to open completely to shed pollen. An adaptation for self-pollination, cleistogamy probably evolved as a mechanism to guarantee fertilization, and subsequent seed set, at a time of year when insect pollinators are scarce. In terms of the developmental implications, the CL flowers reach reproductive maturity (pollen formation) faster than do CH flowers on the same plant, but they fail to complete petal and sepal development. Interestingly, the actual rate of petal and sepal development in CL and CH flowers appears to be identical, at least in *Collomia*. Thus, the change in petal and sepal growth that results in CL flowers involves an alteration in the duration, rather than in the rate, of organ development. In the language of heterochrony, a CL flower is considered to be a progenetic organ.

According to Armen Takhtajan, an expert on systematics at the Komorov Botanical Institute in Leningrad, neoteny also plays an important evolutionary role in generating plant diversity. Alpine meadow races of *Potentilla glandulosa*, for example, appear "juvenile" at sexual maturity compared to races found at middle latitudes or on the coast. Takhtajan cites carpel evolution and the female gametophyte of angiosperms, as well as additional examples of neoteny in plant evolution.

Professor Sherwin Carlquist of Pomona College feels that xylem evolution in species of *Erigeron* (fleabane) in the Family Asteraceae has involved pædomorphic events. Apparently, in the ancestral species, xylem vessels produced by seedlings were shorter than those laid down later in development. Several modern species of *Erigeron*, on the other hand, produce only shortened vessels, even at sexual maturity.

Heterochrony can also be seen in the tissue-culture responses of woody species studied at the Arnold Arboretum. During the last three years we conducted an extensive, comparative investigation to determine the relationship between shoot-tip response in culture and systematics. The results of that study show that responsiveness is sporadically distributed among taxa with species in Subclass Magnoliidae generally failing to grow and species in Subclass Asteridae as well as the orders Ericales, Fabales, and Rosales multiplying rapidly in culture. In attempting to understand the evolution of this physiological diversity, we theorize that differences between taxonomic groups can be explained on the basis of heterochrony by assuming that the ancestral ontogenetic sequence for shoot-tip maturation proceeded from responsive to nonresponsive stages. Among six species of *Cornus*, for example, three fail to respond as seedlings or adults, two re-

Chasmogamous (top) and Both Cleistogamous (CL) and Chasmogamous (CH) Flowers (bottom) of Collomia grandiflora. *CH flowers are about one inch (2.5 cm) long at anthesis. Courtesy Elizabeth M. Lord.*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spond as seedlings only, and a single pædomorphic species (*Cornus canadensis*) responds both as a seedling and as an adult.

As far as practical applications are concerned, the significance of the Developmental clock is that it defines the kinds of new plants that are possible simply by heterochronic alterations in existing ontogenetic patterns. For example, if *Cornus canadensis* is the result of neoteny in dogwoods, conceivably a similar process could generate horizontally growing flowering species in other groups, as well. To think of additional possibilities, just imagine the manifold consequences that could occur every time development's clock starts to run a little differently.

Tick, tock, tick, tock. . . .

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Electron Microscope Views of Collomia *Meristems Developing into CL (left) and CH (right) Flowers. Each pair of photographs shows a different stage in flower maturation. From top to bottom: The first two photographs show the early appearance of petals (c,* corolla*) while in the middle pictures petals, anthers (a) and the developing pistil (g,* gynoecium*) are evident. Later stages in petal, anther, and pistil development are shown in the photographs at the bottom of the figure. Based on the fact that early floral ontogeny in CL and CH is virtually identical, the CL flower in* Collomia *is considered to be a progenetic organ. Courtesy of Elizabeth M. Lord.*