

mitosis, thus delaying differentiation into adult cells (p. 76). The authors point out that this could be considered either hypermorphosis of larval cell mitosis (offset timing of mitosis delayed) or postdisplacement of adult cell differentiation (onset timing of differentiation delayed). A related problem is that a heterochronic change at one level might not be considered heterochronic at another. Cartilage growth ends when it can no longer be fed by diffusion from blood vessels (p. 60). A mutation that increased the number of small blood vessels would thus prolong cartilage growth. Although the blood vessel mutation itself is not a rate or timing change, it would have effected a timing change relative to cartilage growth. Particularly at the level of cellular interactions, the categorization of heterochrony is not straightforward: this raises the uncomfortable possibility that all evolutionary change could be categorized as some type of heterochrony (pan-heterochrony).

Most evolutionary biologists would define heterochrony as the change in timing or rate of a developmental event relative to the homologous timing or rate of that event in the ancestor. It is crucial to identify both the ancestor and the homologous condition to determine the direction of heterochronic change. McKinney and McNamara promote the use of the stratigraphic record to hypothesize ancestor-descendant sequences, and their examples of heterochrony are based on this method. It is generally accepted among evolutionary biologists that neither stratigraphic nor ontogenetic data are useful in polarizing characters (assessing which are primitive and which are derived). Rather, polarity is best determined by looking at homologous conditions in related taxa. Phylogenies based on shared derived characters are necessary to interpret direction of all evolutionary (including heterochronic) change. Moreover, cellular information on heterochrony (the perspective promoted throughout the book) has to come from extant organisms, and polarizing on the basis of stratigraphy, even if it were a valid method, would be impossible. Although the hypothesized direction of heterochronic change may be correct in some of the authors' examples, as a general approach reliance on stratigraphy for evolutionary polarity seriously compromises the validity of the heterochronic conclusions. McKinney and McNamara indirectly address the issue of determining homology (although they do not use the term) in their comparison of the merits of size metrics vs. chronological scales for determining ontogenetic age (they recommend size metrics). Finding practical homology criteria at the level of cellular interactions remains a problem.

Numerous examples of "heterochronoclines," evolutionary sequences that demonstrate paedomorphic or peramorphic trends, are used to illustrate the intrinsic role of ontogeny in directing evolution. The relative roles of extrinsic (natural selection) and intrinsic factors (heterochrony) are discussed, and it is concluded that because of progressive "hardening," development plays less of a role in recent evolution than in the late Precambrian or early Paleozoic. The data presented here (mainly fossil) indicate that most heterochronies are not saltational but gradual or "growth" heterochronies. These are believed to account for much intraspecific variation, including polymorphism. The relationships between heterochrony and life history strategy and other ecological patterns are explored. The familiar dogma that humans are neotenic (slower-growing) apes is debunked in an interesting chapter on human evolution: we grow at the same rate as our ancestors but for a longer time (hypermorphosis = offset delayed).

Is there a single heterochronic process at the cellular level that is responsible for most evolutionary change? The answer awaits the integration of comparative developmental data and well-corroborated phylogenetic hypotheses. The authors have succeeded in stimulating interest in an experimental em-

bryological and phylogenetic approach to heterochronic analysis.

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