

A Guide to the Nomenclature of Heterochrony

Author(s): Kenneth J. McNamara

Source: *Journal of Paleontology*, Vol. 60, No. 1 (Jan., 1986), pp. 4-13

Published by: Paleontological Society

Stable URL: <http://www.jstor.org/stable/1305091>

Accessed: 16-07-2018 10:52 UTC

## REFERENCES

Linked references are available on JSTOR for this article:

[http://www.jstor.org/stable/1305091?seq=1&cid=pdf-reference#references\\_tab\\_contents](http://www.jstor.org/stable/1305091?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



JSTOR

*Paleontological Society* is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Paleontology*

## A GUIDE TO THE NOMENCLATURE OF HETEROCHRONY

KENNETH J. McNAMARA  
Western Australian Museum, Francis Street,  
Perth, Western Australia 6000

---

SINCE Haeckel's Biogenetic Law ('ontogeny recapitulates phylogeny') fell into disrepute early in the twentieth century, there has been intermittent debate, particularly in recent years (de Beer, 1958; Gould, 1977; Alberch et al., 1979; Alberch, 1980; Bonner, 1982; McNamara, 1982a), on the nature of the relationship between an individual's development and phylogenetic history. Important questions under discussion include the following: If a strong causal relationship does exist, what is its nature? How does it work? What is its importance in evolution? How can it be recognized in the fossil record?

The phenomenon of changes through time in the appearance or rate of development of ancestral characters is known as *heterochrony* (sensu de Beer, 1930). It is clear, from the lack of substantial reference to heterochrony in many modern textbooks on evolution, that its impact on the development of evolutionary concepts has diminished markedly during the twentieth century. This stems not only from the fact that Haeckel's Biogenetic Law has generally been discredited, carrying the whole concept of heterochrony as an important factor in evolution with it, but also because of the great proliferation of terms that have been introduced to describe various aspects of heterochrony. For example, a small selection includes: peramorphosis, paedomorphosis, paedogenesis, palingenesis, phyl-embryogenesis, proterogenesis, progenesis and prothetely!

This plethora of terms has contributed to both their frequent misuse and much confusion as to the nature of the relationship between ontogeny and phylogeny. Another reason for the general lack of acceptance of the importance of heterochrony in evolution is probably the paucity of detailed examples, at the species level, described from the fossil record. If due consideration is to be given to the role of heterochrony in evolution, the fos-

sil record must be examined in detail for relevant examples.

During the latter part of the nineteenth century the Biogenetic Law was invoked by a number of workers to explain many aspects of the fossil record. In particular, the evolution of some ammonite lineages was ascribed to the workings of this doctrine. The main proponent of this in ammonites was Hyatt (1889, 1893). Another fervent advocate of the Biogenetic Law was Beecher, who based his classification of the Trilobita on the belief that the phylogeny of the Trilobita was encapsulated within the ontogeny of later trilobites. During the twentieth century, instead of being interpreted in a 'recapitulation' light, the pendulum swung the other way and many trilobites and ammonites were interpreted as having arisen by paedomorphosis (called 'proterogenesis' in ammonites), principally by Schindewolf (1929) for ammonites, and Stubblefield (1936, 1959) and Hupé (1953a, 1953b) for trilobites.

However, recent work, by Gould (1977) in particular, has shown that neither one phenomenon nor the other need necessarily be prevalent. Gould (1977) has done much to unravel the tangled heterochronic web woven by generations of evolutionary biologists and to provide a sound basis on which to examine the role of heterochrony in evolution; and Alberch et al. (1979) have attempted to place the study of heterochronic processes on a more sound, quantitative footing.

The aim of this guide is essentially threefold: to describe concisely each of the heterochronic processes recognized by Alberch et al. (1979); to illustrate how the actions of these phenomena may be recognized in the fossil record; and, in order to facilitate this recognition, to show the morphological and size relationships between inferred ancestral and descendant forms. References are given to detailed examples of each of the processes.

This guide draws heavily on the clarification of the heterochronic processes by Gould (1977) and Alberch et al. (1979). It differs from the work of Alberch et al. (1979) in that it follows a less quantitative approach, with the aim of providing a didactic guide to heterochronic terminology that may be of particular use to paleontologists. A key to the heterochronic processes is presented, and each process is illustrated in simplified diagrammatic form (Figures 2 and 3), in order to aid in the identification of morphotypes produced by heterochrony.

#### WHAT IS HETEROCHRONY?

Heterochrony has been defined as the "changes in relative time of appearance and rate of development of characters already present in ancestors" (Gould, 1977, p. 2, following de Beer, 1930). Such changes in timing of development also occur between parent and offspring within a species as part of general phenotypic variation (e.g., Cock, 1966; Travis, 1981; McNamara, 1982b). If the morphological characteristics of the phenotype derived by heterochrony are of adaptive significance, there may be preferential selection of the derived morphotype and a new species may evolve.

Thus, between parent and offspring, or between successive species, the morphological change during an organism's ontogeny may be relatively increased or decreased. It is important when considering an organism's growth to recognize that it is composed of two basic elements: morphological (i.e., shape) change and overall size change. The decoupling of these two elements and their temporal changes relative to one another may result in heterochrony when either or both are affected by changes in rate of development. Variation in the timing of onset or cessation of morphological development and size change may also result in heterochrony. In some instances there may be no morphological change between ancestor and descendant, but there may be size differences: relative size decrease is *dwarfism* and relative size increase, *giantism*. These terms are self-explanatory and will not be described further, although they are included in the key.

The relationship between size and shape of particular structures is known as allometry

(Gould, 1966, 1977). If the relative size and shape of a morphological feature remain constant with growth of the whole organism, the growth is said to be isometric. More commonly, during juvenile growth, in particular, body size and structural shape changes are dissociated, such that the shape and size of particular structures may alter substantially during ontogeny. With pronounced allometry during ontogeny, size and shape changes can be quite dramatic. Slight alterations to the degree of allometry may have profound effects in the descendant adult.

Allometry may be positive or negative. When allometry is positive for a particular structure the structure increases in size relative to the whole organism and may substantially change its overall shape. It will thus be larger than if its growth had been isometric. When allometry is negative the structure becomes smaller during growth of the organism. An example of positive allometry is the increase in trunk size during growth in humans, while relative reduction in head size occurs by negative allometry (Medawar, 1945).

Extension or contraction of the period during which a particular structure develops by allometry can likewise produce a descendant showing quite different structural features to its ancestor. The classic example of this is the extension of positive allometry of the antlers in the Irish Elk *Megaloceros* (Gould, 1974). Heterochrony is concerned with changing allometries: by the variation of growth rates or by the extension or contraction of the period during which these growth rates operate.

If a descendant passes through fewer stages of ontogenetic development than its ancestor, the descendant adult form will have morphological characteristics which occurred in juveniles of the ancestor. This phenomenon has been termed *paedomorphosis* (Garstang, 1928). Conversely, should a descendant pass through more ontogenetic stages of development than its ancestor, the adult form will have developed "beyond" that of the ancestor. This has been termed *peramorphosis* (Alberch et al., 1979). Both paedomorphosis and peramorphosis express the morphological result of processes affecting the timing of development (Figure 1). They are *not* processes themselves, merely the end result of hetero-

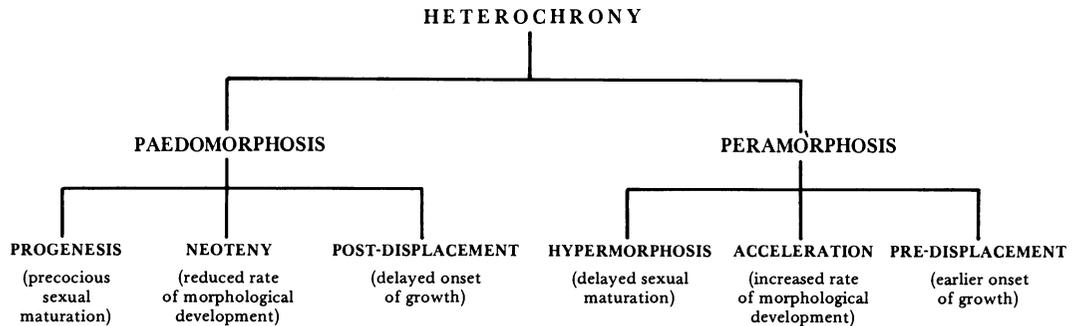


FIGURE 1—The hierarchy of heterochrony.

chronic processes. Paedomorphs and peramorphs may be the same size as their ancestors, or they may be larger or smaller, depending on the heterochronic process which has operated.

In their classification of heterochrony, Alberch et al. (1979) defined heterochronic processes, their morphological expression (i.e., paedomorphosis and peramorphosis), and the resultant phylogenetic phenomena. They regarded the phylogenetic expression of peramorphosis as 'recapitulation,' and of paedomorphosis as 'reverse recapitulation.' I prefer not to use these terms. Firstly, because 'recapitulation' immediately conjures up connotations of Haeckel's all pervasive Biogenetic Law. Secondly, because I consider the term 'recapitulation' to be basically inappropriate: peramorphic processes do more than recapitulate the ancestor's ontogeny. The important point is that the descendant's ontogeny develops further—that is, it is more than just recapitulated. It follows that the term introduced by Alberch et al. (1979) as a counterpart to 'recapitulation,' 'reverse recapitulation,' is similarly inappropriate, and therefore rejected.

Processes that result in either paedomorphosis or peramorphosis are temporal phenomena that occur within species, at the level of successive generations. Effects of these heterochronic processes may appear in the fossil record at the species level, following selection for and genetic fixation of the heterochronic morphotype. Either way, whether the changes are intra- or inter-specific, the processes and resultant morphologies are the same. Thus in this paper paedomorphosis and peramorphosis are also used in a phylogenetic sense.

Certain terms, cenogenesis in particular,

have been used widely in the literature as heterochronic terms when, in fact, they are not involved in changes to the timing or rate of appearance of features at all (Gould, 1977). These terms relate to the introduction of *new* features and, consequently, are not relevant to this guide. *Cenogenesis* (syn. *archallaxis*) sensu de Beer (1930) is the introduction of new features during the juvenile or embryonic stages of development. *Anaboly* was a term used by Severtzov (1927) to describe the introduction of new features at the end of the embryonic stage.

#### IDENTIFICATION OF HETEROCHRONY IN THE FOSSIL RECORD

The observation in the fossil record of heterochronic species can be made both diachronously and synchronously. By observing the time ranges of diachronous species through a stratigraphic succession (assuming that the stratigraphic ranges provide some indication of the true temporal ranges of the species) heterochronic ancestor/descendant relationships can be inferred and either paedomorphosis or peramorphosis can be identified by comparing ontogenetic transformations between successive species (e.g., McNamara, 1982a, 1983a, 1984). Alternatively, it is possible to observe a number of synchronous species, either in the fossil record or at the present day, and identify them as heterochronic species (e.g., McNamara, 1978, 1982b, 1983a). In order to ascertain which is the ancestral form and, consequently, whether the descendant is a paedomorph or peramorph, out-group comparison must be made with material from other time planes, so as to identify the likely ancestral form.

It is possible to identify a series of sequen-

tial ancestor/descendant relationships within a lineage. It has been suggested (McNamara, 1982a) that some evolutionary trends have occurred as a result of the selection of successive heterochronic species through time, resulting in directional speciation. Such trends, termed paedomorphoclines and peramorphoclines (McNamara, 1982a), can occur when new morphotypes, resulting from heterochronic processes, are adaptively significant along an environmental gradient.

Recent critics of the use of the fossil record for evolutionary studies (e.g., Nelson, 1978; Fink, 1982) have advocated the use of ontogenetic character transformations to assess phylogenetic relationships. However, such adherents to the cladistic school are content to analyze the ontogenies of living organisms and attempt to formulate phylogenies from an analysis of organisms only on a single time plane. They do not appear to be prepared to analyze ontogenies of fossil species. Their selectivity of available data, ignoring information from other time planes, makes for weak phylogenetic analysis. Incorporation of information from the fossil record can only improve phylogenetic analysis. To ignore such a welter of information is, to say the least, myopic. By analyzing variation in rates of ontogenetic character changes in successive species through the fossil record, likely ancestor/descendant relationships can be proposed. The aim of this guide is to facilitate such studies.

#### THE HETEROCHRONIC PROCESSES

Most morphological change during an organism's ontogeny occurs during the juvenile phase of growth, particularly during early juvenile development. Cessation or severe reduction in rate of morphological development generally accompanies onset of sexual maturity. Similarly, cessation of increase in size may also accompany maturity and reduced rate of morphological development. However, in many organisms size increase, generally to a specific maximum, which may be related to the period of juvenile growth, continues during part of the adult phase. As noted above, any changes to rate of development, or to onset or cessation of growth can have profound effects on the descendant morphologies, particularly if the growth is allometric. Six heterochronic processes af-

fecting morphological development are recognized.

In order to outline clearly these heterochronic processes, reference will be made to Figures 2 and 3. These figures attempt to illustrate diagrammatic ontogenies of ancestral and descendant forms of an idealized organism. The ancestral form is considered in each case to pass through four arbitrary morphological stages A to D. In each of the paedomorphic situations (Figure 2) the descendant attains only morphological stage C at cessation of growth. However, Figure 2 illustrates how the various paedomorphic processes affect ontogenetic pathways and their relationships to the ancestral ontogeny. Similarly, the ontogenies which have been affected by peramorphic processes (Figure 3), are compared with the ancestral ontogenetic pathway and shown in each case to attain morphological stage E, but by different ontogenetic strategies. It must be stressed that the morphological stages A to E may be either saltatory (as in arthropod development) or gradual; but the same heterochronic processes operate. The idealized organisms in Figures 2 and 3 have appendages that increase in size isometrically, and a central pore that increases in size by positive allometry.

#### PAEDOMORPHOSIS

(Syn. fetalization, proterogenesis, lipopaligenesis, superlarvation, reverse recapitulation.) Retention of ancestral juvenile characters in the descendant adult phase can be achieved in three ways: by reducing the rate of morphological development through the juvenile phase of growth (*neoteny*), by precocious sexual maturation (*progenesis*), or by delay in onset of morphological development (*post-displacement*).

*Neoteny* (Kollman, 1885).—(Syn. brachygenesis, metathetely, retardation.) Reduced rate of morphological development during the juvenile phase results in a morphologically retarded adult. This is termed neoteny. If maturity occurs at the same age as in the ancestor, the neotenic adult will be of equal size to the ancestral adult, though morphologically retarded (Figure 4). If, as is often the case during neoteny, onset of sexual maturity is delayed, a longer period will have been spent in the juvenile phase of rapid size increase. Consequently, the adult will be larger

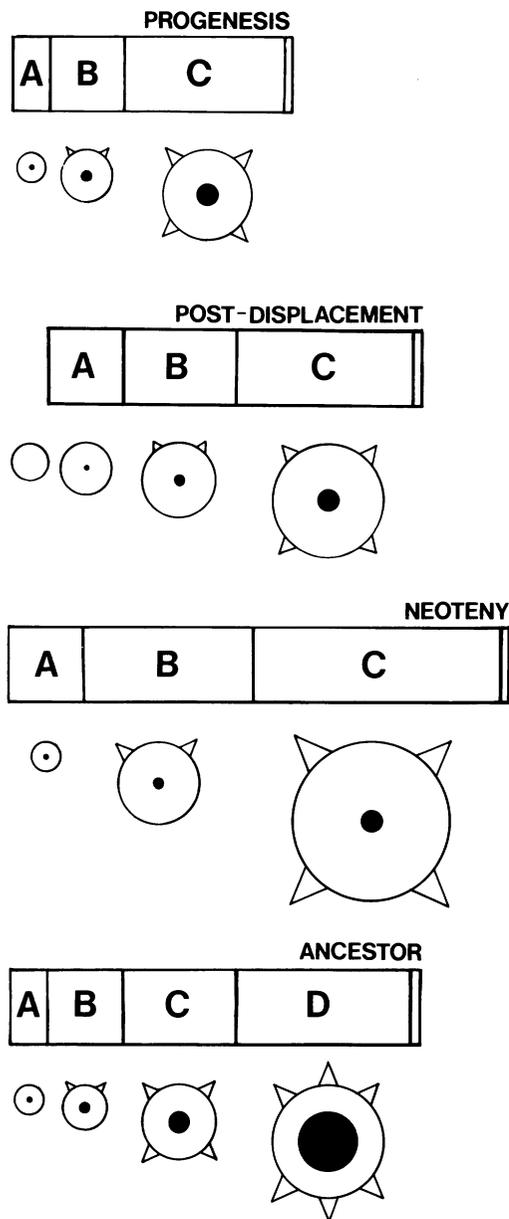


FIGURE 2—Relationship of the three paedomorphic processes to the ancestral form. In *neoteny*, rate of development is reduced. Here, onset of maturity is also retarded, resulting in the descendant adult reaching a larger maximum size. In *post-displacement*, the onset of growth of spots and spines is delayed. Subsequent rate and cessation of growth are the same in the descendant as in the ancestor, but the delayed onset of development means that ancestral juvenile characters occur in the descendant adult. In *progenesis*, precocious sexual maturation results in an adult smaller than in the ancestor. Early

than the ancestral adult, but have morphological characteristics of an ancestral juvenile stage. Thus, by comparison with an ancestral ontogeny A to D (Figure 2) at, for instance, the size at which the ancestor changes from morphological stage C to D, the neotenic form would be only at morphological stage B, on account of the reduced rate of morphological development. Neoteny may only affect some structures, or it may affect the whole organism (termed 'dissociated' and 'global' respectively by McKinney (1984).

Examples of neoteny have been described from the fossil record in molluscs (Gould, 1969, 1970; Nevesskaya, 1967; Hallam, 1982), brachiopods (McNamara, 1983a), trilobites (Ludvigsen, 1979; McNamara, 1981) and echinoids (McNamara, 1982b; McKinney, 1984).

*Progenesis* (Giard, 1887).—(Syn. paedogenesis, prothetely.) If onset of maturity occurs at an earlier stage of development in the descendant, morphological and size changes will be stopped or severely retarded precociously. The resultant progenetic adult will thus retain ancestral juvenile characters, but, unlike the neotenic situation, it will be smaller than the ancestral adult as a shorter period will have been spent in the phase of rapid size increase (Figure 4).

Progenetic forms also differ from neotenic forms in their early ontogenetic strategy. The juvenile rate of development prior to maturity is the same in progenetic forms as in their ancestors (Figure 2). During the same, early ontogenetic period, the rate of development of the neotenic forms is reduced. Progenesis is global, affecting the whole organism. However, certain characters will have a more overtly juvenile aspect than others. In many organisms a certain degree of morphological development occurs after the onset of maturity. Thus a progenetic species differs to some degree from the ancestral juvenile form. In arthropods progenesis can occur in two ways (McNamara, 1983b): by the 'normal' premature maturation (terminal progenesis), or by a shortening of the period spent in each molt stage (sequential progenesis).

←

ontogenetic development is the same in descendant as in ancestor.

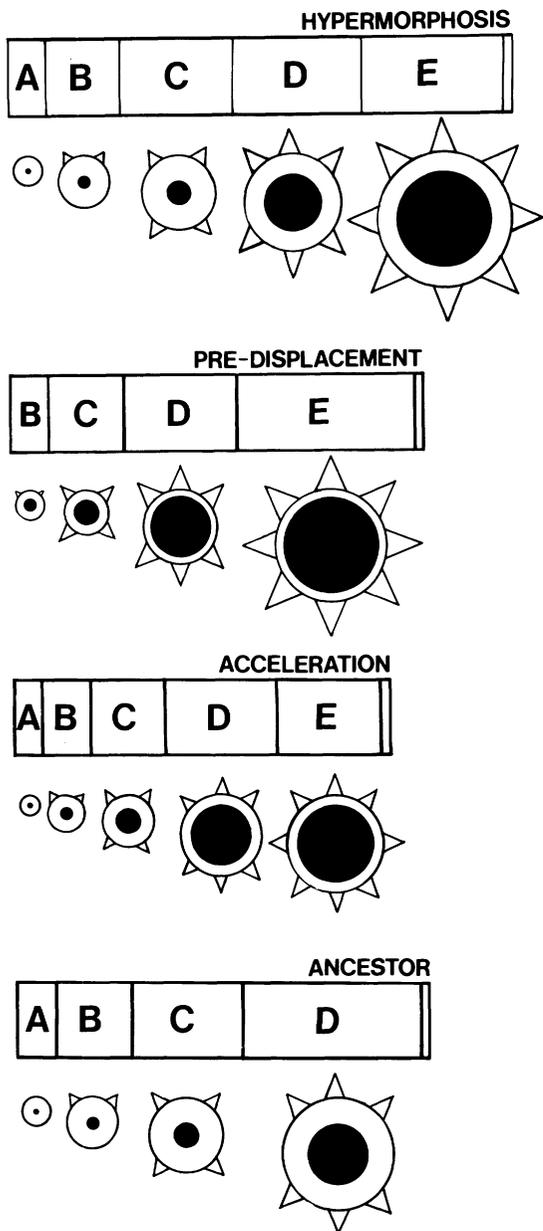


FIGURE 3—Relationship of the three peramorphic processes to the ancestral form. In *acceleration*, increased rate of development results in ancestral adult characters occurring in the descendant juvenile. In this example onset of maturity is also accelerated, resulting in the descendant adult being smaller than the ancestral adult. In *pre-displacement*, onset of growth of spots and spines is initiated at an earlier stage of ontogeny than in the ancestor. Subsequent rate and cessation of growth are the same in descendant and ancestor. However, the earlier onset of development

Examples of progenesis have been described from the fossil record in bivalves (Stanley, 1972), trilobites (McNamara, 1978, 1981, 1983b), ammonites (Wright and Kennedy, 1980), brachiopods (McNamara, 1983a), echinoids (Philip, 1963) and edrioasteroids (Sprinkle and Bell, 1978).

*Post-displacement* (Alberch *et al.* 1979).— Unlike progenesis and neoteny, post-displacement does not arise by changes to rate of development or timing of cessation of development. Indeed, paedomorphosis by post-displacement can occur even if the rate of development and cessation of growth are the same as in the ancestor. Post-displacement occurs by a change in timing of onset of development of certain structures.

By comparison with the ancestor, one or more organs or structures will commence development at a later stage with respect to other parts of the organism. In other words, commencement of development of the organ at stage A occurs when the ancestral organ was at state B, relative to the whole organism (Figure 2). If subsequent rate of development and cessation of growth are the same as in the ancestor, the particular organ or structure that commenced development later will be relatively retarded with respect to the ancestor, having reached only stage C at cessation of growth, whereas the comparable organ or structure in the ancestor would have reached morphological stage D. The adult morphology of the descendant will therefore resemble a juvenile stage of the ancestor. The shorter period of growth will result in the structure being smaller than in the ancestor. Post-displacement only affects certain organs or structures, not the whole organism. Thus, whereas the progenetic adult similarly is smaller and retarded with respect to the ancestor, post-displacement results in only a certain number of organs or structures, not the whole organism, being retarded and smaller. It is feasible for post-displacement and neoteny to operate concurrently, if both

← means that the descendant adult morphology has developed beyond that of the ancestor. In *hypermorphosis*, onset of sexual maturity is delayed, with the consequence that the descendant adult is larger and morphologically more developed than the ancestral adult.

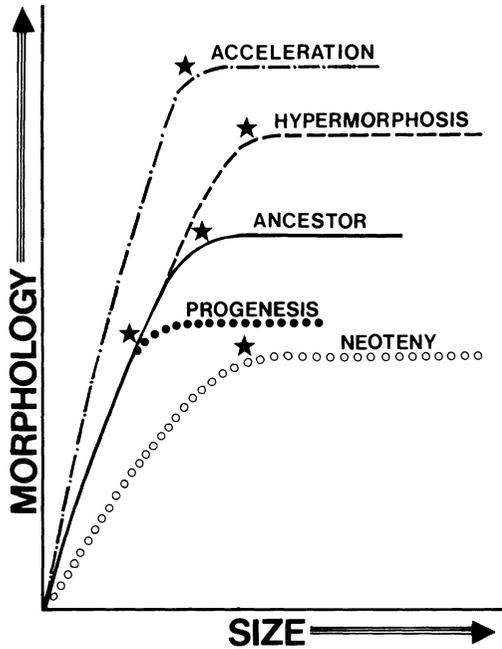


FIGURE 4—Diagrammatic plot of morphological development against size to illustrate the effect of acceleration and hypermorphosis on the ancestral growth curve to produce peramorphic descendants, and of neoteny and progenesis to produce pedomorphic descendants.

onset of growth is delayed and rate of development is retarded.

Examples of post-displacement have been described in zebras (Bard, 1977) and salamanders (Wake, 1966). The reduction in number of lenses in eyes in some lineages of phacopid trilobites (Richter, 1933) may also represent post-displacement.

#### PERAMORPHOSIS

(Syn. adulation, recapitulation, palingenesis.) The occurrence of the ancestral adult morphology in a descendant juvenile stage of development can be achieved in three ways: by an increase in the rate of morphological development (*acceleration*), by delay of onset of sexual maturity (*hypermorphosis*), or by earlier initiation of morphological development (*pre-displacement*).

*Acceleration* (Cope, 1887).—(Syn. tachygenesis.) As its name implies, this peramorphic process consists of an increase in the rate of morphological development during ontogeny. It is the opposite of neoteny. A

small increase in rate of development initiated at an early stage of development can result in quite profound morphological differences between descendant and ancestor, if growth is allometric. In such cases, the descendant will pass through the adult stage of the ancestor during its ontogeny. Maturity may occur when the descendant is the same size as the ancestor; if, however, onset of maturity is also accelerated, the descendant adult may be smaller than the ancestral adult, but be morphologically more advanced (Figure 4). Thus, for example, it can be seen in Figure 3 that, by comparison with the ancestral ontogeny at commencement of stage D, the accelerated organism would, at the same size, be approaching morphological stage E. Acceleration may affect the whole organism, or only certain organs or structures.

Examples have been described in ammonites (Newell, 1949), graptolites (Elles, 1922, 1923; Urbaneck, 1973; Gould, 1977), echinoids (McNamara, 1984) and titanotheres (McKinney and Schoch, 1985).

*Hypomorphosis* (de Beer, 1930).—An extension of the juvenile growth period, caused by a delay in onset of maturation, will result in peramorphosis. This process is the opposite of progenesis. Early juvenile development will commence at the same time and proceed at the same rate as in the ancestor (Figure 3). Extension of late ontogenetic development may result in morphological characteristics quite different from the ancestral adult. The longer period spent in the juvenile phase of growth will result in the attainment of a larger maximum size. The descendant adult will therefore be larger than the ancestral adult (Figure 4). Thus, in Figure 3, instead of becoming mature at the end of morphological stage D, the hypermorphic form will continue developing into morphological stage E; maturity will thus be attained at a larger size than in the ancestor. Hypermorphosis affects the whole organism.

A classic example of hypermorphosis is the evolution of the Irish Elk, *Megaloceros* (Gould, 1974). Hypermorphosis has also been described in echinoids (McNamara and Philip, 1980, 1984; McKinney, 1984).

*Pre-displacement* (Alberch *et al.*, 1979).—As with the operation of pure post-displacement, rate of development and cessation of growth may be the same as in the ancestor.

However, initiation of development of one or a number of organs or structures at a relatively earlier stage of development of the whole organism, with respect to the ancestor, allows a longer period for their growth and development. Thus, by comparison with the same structure in the ancestral form (Figure 3) the peramorphic form will be at stage B when the same structure in the ancestral juvenile was commencing growth. If cessation of growth and rate of morphological development are the same as in the ancestor, the peramorphic structure which initiated growth earlier will be morphologically more advanced and larger than the equivalent structure in the ancestral adult.

Alberch et al. (1979) believed it is possible for all three peramorphic processes, acceleration, hypermorphosis and pre-displacement, to be operating concurrently in a single species. They believed that the peramorphosis in Palaeozoic ammonoids described by Newell (1949), can be explained by the joint effects of the three different processes. Evolution of species within the rugose coral *Amplexizaphrentis*, as described by Caruthers (1910), may have occurred by progressive pre-displacement along a peramorphocline (sensu McNamara, 1982a). McKinney (1984) has described pre-displacement, hypermorphosis and neoteny all occurring concurrently in an Eocene echinoid, illustrating how different morphological features may be simultaneously affected by different heterochronic processes.

KEY TO HETEROCHRONIC PROCESSES

Diagnostic characters of each process relate to change manifest in the inferred descendant with respect to the ancestor's morphology, either of some morphological structure(s) or the whole organism.

1. Descendant adult morphology differs from ancestral adult; size same or different ..... 2  
     Descendant adult morphology same as ancestral adult; size different ..... 7
2. Descendant adult morphology resembles juvenile ancestor (*paedomorphosis*) ..... 3  
     Ancestral adult morphology present in juvenile phase of descendant; descendant morphology then develops 'beyond' that of ancestor (*peramorphosis*) ..... 3
3. Time of onset of morphological development of particular organs/structures de-

- layed; subsequent rate of development same as ancestor ..... *Post-displacement*
- Time of onset of morphological development same as ancestor ..... 4
4. Rate of juvenile development retarded; adult as large as, or larger than, ancestral adult ..... *Neoteny*  
     Juvenile development same as ancestor initially; sexual maturity occurs at earlier stage of development; adult smaller than ancestral adult ..... *Progenesis*
5. Morphological development of particular organs/structures initiated earlier in organism's ontogeny ..... *Pre-displacement*  
     Time of onset of morphological development same as ancestor ..... 6
6. Juvenile rate of development accelerated; adult no larger, often smaller, than ancestral adult ..... *Acceleration*  
     Juvenile development same as ancestor; onset of sexual maturity delayed; adult larger than ancestral adult ..... *Hypermorphosis*
7. Descendant adult smaller than ancestral adult ..... *Dwarfism*  
     Descendant adult larger than ancestral adult ..... *Giantism*

ACKNOWLEDGMENTS

A. Baynes, S. J. Gould, M. L. McKinney and W. J. Kennedy kindly read the manuscript and offered suggestions for its improvement.

REFERENCES

ALBERCH, P. 1980. Ontogenesis and morphological diversification. *American Zoologist*, 20:653-667.  
 —, S. J. GOULD, G. F. OSTER AND D. B. WAKE. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology*, 5:296-317.  
 BARD, J. B. L. 1977. A unity underlying the different zebra striping patterns. *Journal of Zoology*, 183:527-539.  
 BONNER, J. T. (ed.). 1982. *Evolution and Development*. Springer-Verlag, Berlin, 356 p.  
 CARUTHERS, R. G. 1910. On the evolution of *Zaphrentis delanoui* in Lower Carboniferous times. *Quarterly Journal of the Geological Society of London*, 66:523-538.  
 COCK, A. G. 1966. Genetical aspects of metrical growth and form in animals. *Quarterly Review of Biology*, 41:131-190.  
 COPE, E. D. 1887. *The Origin of the Fittest*. Macmillan, New York, 467 p.  
 DE BEER, G. R. 1930. *Embryology and Evolution*. Clarendon, Oxford, 116 p.  
 —. 1958. *Embryos and Ancestors*. Clarendon, Oxford, 197 p.  
 ELLES, G. L. 1922. *The graptolite fauna of the*

- British Isles. Proceedings of the Geologists' Association, 33:168–200.
- . 1923. Evolutional palaeontology in relation to the Lower Palaeozoic rocks. Report of the British Association for the Advancement of Science, 91:83–107.
- FINK, W. L. 1982. The conceptual relationship between ontogeny and phylogeny. *Paleobiology*, 8:254–264.
- GARSTANG, M. 1928. The morphology of the Tunicata, and its bearing on the phylogeny of the Chordata. *Quarterly Journal of Microscopical Science*, 72:51–187.
- GIARD, D. 1887. La castration parasitaire et son influence sur les caractères extérieurs du sexe male ches les crustacés décapodes. *Bulletin scientifique du département du Nord*, 18:1–28.
- GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews*, 41:587–640.
- . 1969. An evolutionary microcosm: Pleistocene and recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 138:407–532.
- . 1970. Land snail communities and Pleistocene climates in Bermuda: a multivariate analysis of microgastropod diversity. Proceedings of the North American Paleontological Convention, part E, 486–521.
- . 1974. The evolutionary significance of 'bizarre' structures: antler size and skull size in the 'Irish Elk', *Megaloceros gigantans*. *Evolution*, 28:191–220.
- . 1977. *Ontogeny and Phylogeny*. Belknap, Cambridge, 501 p.
- HALLAM, A. 1982. Patterns of speciation in Jurassic *Gryphaea*. *Paleobiology*, 8:354–366.
- HUPÉ, P. 1953a. Contribution à l'étude du Cambrien Inférieur et du Précambrien III de l'Anti-Atlas Marocain. Notes et Mémoires du Service des Mines et de la Carte géologique du Maroc, 103:41–402.
- . 1953b. Classification des trilobites. *Annales de Paléontologie*, 39:1–110.
- HYATT, A. 1889. Genesis of the Arietidae. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 16:1–238.
- . 1893. Phylogeny of an acquired characteristic. *Proceedings of the American Philosophical Society*, 32:349–647.
- KOLLMAN, J. 1885. Das Ueberwintern von europäischen Frosch- und Tritonlarven und die Umwandlung des mexikanischen Axolotl. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 7:387–398.
- LUDVIGSEN, R. 1979. The Ordovician trilobite *Pseudogygites* Kobayashi in eastern and Arctic North America. *Life Science Contributions of the Royal Ontario Museum*, 120:1–41.
- MCKINNEY, M. L. 1984. Allometry and heterochrony in an Eocene echinoid lineage: morphological change as a by-product of size selection. *Paleobiology*, 10:407–419.
- AND R. M. SCHOCH. 1985. Titanothere allometry, heterochrony, and biomechanics: revising an evolutionary classic. *Evolution*, 39:1352–1363.
- MCNAMARA, K. J. 1978. Paedomorphosis in Scottish olenellid trilobites (early Cambrian). *Paleontology*, 21:635–655.
- . 1981. The role of paedomorphosis in the evolution of Cambrian trilobites. *Open-File Report of the U.S. Geological Survey*, 81-743:126–129.
- . 1982a. Heterochrony and phylogenetic trends. *Paleobiology*, 8:130–142.
- . 1982b. Taxonomy and evolution of living species of *Breyinia* (Echinoidea: Spatangoida) from Australia. *Records of the Western Australian Museum*, 10:167–197.
- . 1983a. The earliest *Tegulorhynchia* (Brachiopoda: Rhynchonellida) and its evolutionary significance. *Journal of Paleontology*, 57:461–473.
- . 1983b. Progenesis in trilobites, p. 59–68. *In* D. E. G. Briggs and P. D. Lane (eds.), *Trilobites and Other Arthropods: Papers in Honour of H. B. Whittington, F.R.S. Special Papers in Paleontology*, 31:59–68.
- . 1984. Taxonomy and evolution of the Cainozoic spatangoid echinoid *Protenaster*. *Paleontology*, 28:311–330.
- AND G. M. PHILIP. 1980. Australian Tertiary schizasterid echinoids. *Alcheringa*, 4:47–65.
- AND —. 1984. A revision of the spatangoid echinoid *Pericosmus* from the Tertiary of Australia. *Records of the Western Australian Museum*, 11:319–356.
- MEDAWAR, P. B. 1945. Size, shape and age, p. 157–187. *In* W. E. LeGros Clark and P. B. Medawar (eds.), *Essays on Growth and Form*. Clarendon Press, Oxford.
- NEVESSAKAYA, L. A. 1967. Problems of species differentiation in light of paleontological data. *Paleontological Journal*, 4:1–17.
- NELSON, G. J. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Systematic Zoology*, 27:324–345.
- NEWELL, N. D. 1949. Phyletic size increase, an important trend illustrated by fossil invertebrates. *Evolution*, 3:103–124.
- PHILIP, G. M. 1963. Two Australian Tertiary neolampadids and the classification of cassiduloid echinoids. *Paleontology*, 6:718–726.
- RICHTER, R. 1933. *Crustacea*, p. 840–863. *In* *Handwörterbuch der Naturwissenschaften*. Jena.
- SCHINDERWOLF, O. H. 1929. Ontogenie und phylogenie. *Paläontologische Zeitschrift*, 11:54–67.
- SEVERTZOV, A. N. 1926. Über die Beziehungen zwischen der Ontogenese und der Phylogenese der Tiere. *Jenaische Zeitschrift für Naturwissenschaft*, 56:51–180.

- SPRINKLE, J. AND B. M. BELL. 1978. Paedomorphosis in edrioasteroid echinoderms. *Paleobiology*, 4:82-88.
- STANLEY, S. M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology*, 46:165-212.
- STUBBLEFIELD, C. J. 1936. Cephalic sutures and their bearing on current classifications of trilobites. *Biological Reviews*, 11:407-440.
- . 1959. Evolution in trilobites. *Quarterly Journal of the Geological Society of London*, 115:145-162.
- TRAVIS, J. 1981. Control of larval growth variation in a population of *Pseudacris triseriata* (Anura: Hylidae). *Evolution*, 35:423-432.
- URBANER, A. 1973. Organization and evolution of graptolite colonies, p. 441-514. *In* R. S. Boardman, A. H. Cheetham and W. A. Oliver (eds.), *Animal Colonies*, Dowden, Hutchinson & Ross, Stroudsburg.
- WAKE, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. *Memoirs, Southern California Academy of Sciences*, 4:1-111.
- WRIGHT, C. W. AND W. J. KENNEDY. 1980. Origin, evolution and systematics of the dwarf acanthoceratid *Protacanthoceras* Spath, 1923. (Cretaceous Ammonoidea). *Bulletin of the British Museum (Natural History) (Geology)*, 34: 65-107.

MANUSCRIPT RECEIVED 10 MARCH 1983

REVISED MANUSCRIPT RECEIVED 8 FEBRUARY 1984

### PALEONTOLOGICAL SOCIETY CANDIDATES FOR OFFICE, 1986 ANNUAL BALLOT

At its meeting in Orlando, Florida, on October 30, 1985, Council of The Paleontological Society selected the following candidates for Society offices from nominees proposed by the Nominating Committee:

For: President-Elect (1986-87) N. Gary Lane, Bloomington, Indiana  
 Councilor (1986-88) Roger J. Cuffey, University Park, Pennsylvania  
 Program Coordinator (1986-89) Jennifer A. Kitchell, Ann Arbor, Michigan  
 Paleobiology Editors (1986-89) Richard Cowen and Philip W. Signor, Davis, California

This slate will be submitted to the Membership on the Annual Ballot in August 1986. Additional nominations made in accordance with provisions of Section 3, Chapter 2 of the By-Laws will be accepted by the Secretary until July 1, 1986, and will be included as special tickets with the regular ticket announced above.

John Pojeta, Jr.  
Secretary