

Of coiled oysters and big brains: how to rescue the terminology of heterochrony, now gone astray

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SUMMARY During the past decade, the terminology of heterochrony, heretofore consistent and workable, has become internally illogical and incoherent as the unfortunate result of an extension of terms, properly devised to describe shifts in developmental timing of shapes and features, to the rates and timings that cause these shifts. All the resulting, and extensive, confusion in the literature arises as a pure consequence of this error in logic and nomenclature, and not at all from disagreement about the important empirical questions described by this central concept and phenomenon in the integration of evolution and development. In particular, the claim that the same feature in human evolution (the paedomorphic shape of the human cranium) expresses either neoteny or the apparently opposite phenomenon of hypermorphosis only records the terminological error, and not any factual disagreement—for this neotenic feature has probably

arisen by a prolongation of juvenile growth patterns inappropriately designated as “hypermorphosis of rate.” I show that a prominent and unchallenged case of neoteny in fossil oysters arises by exactly the same evolutionary mode. When we restore the terminology of heterochrony by the “paedomorphic” intellectual event of dropping these inadaptable terminal accretions (the illogical extension of shape categories to describe rates), then the concept of heterochrony will again make proper distinctions by designating a clearly meaningful category of evolutionary changes originating by shifts in timing for features already present in ancestors. “It’s not all heterochrony”—and this particular statement of “less is more” represents heterochrony’s strength as an interesting subset with definite meaning, rather than an illogical hodge-podge apparently applicable to all phenomena, and therefore explaining nothing.

I present one long argument, in twelve steps, for recovery of a term and concept.

1. The burgeoning literature of heterochrony has, in the past decade, become fatally confused by a logical error in widely adopted proposals for an expanded terminology. This erroneous scheme becomes incoherent by including incommensurable and contradictory categories under one taxonomic rubric (and not by any major disagreement about empirical issues). In the worst expressions of this confusion, the same phenomenon (by everyone’s explicit agreement) has been placed into diametrically opposed and logically incompatible categories (see steps 8–10).

2. In the current context of excitement about the “coming of age” (to true operationality) of studies in linkages between development and evolution (after more than a century of attention since Haeckel’s original formulations), our need for clear, consistent, and logical terminology becomes all the more pressing. Raff (1996), for example, writes, “Heterochrony has been the single most pervasive idea in evolutionary developmental biology.”

Several authors have recognized, and decried, the current terminological morass. For example, McKinney (1999) cited the “bloated, baroque jargon describing patterns produced

by largely unknown mechanisms.” And Klingenberg (1998) writes in more measured tones, but with equal frustration, “Differences between analytical frameworks have generated confusion in terminology and methods, as they may lead to contradictory interpretations of the same evolutionary events. Miscommunication stemming from the use of incompatible concepts underlies a number of current controversies, most notably that regarding human heterochrony.” The current situation may be likened to Isaiah’s famous lament (53:6): “All we, like sheep, have gone astray; we have turned every one to his own way.”

When confusion becomes so extensive and entrenched, scientists often despair, assuming that the depth of the problem must correlate with a required complexity of resolution (an issue that they then choose not to address, given our profession’s understandable aversion to definitional issues devoid of direct empirical content). But, in this case, the error can be traced to a simple point source, with all subsequent confusion, despite its baroque nature, arising consequentially. Thus, a correction of this logical error—simple to describe and to effect—could resolve this unfortunate and frustrating situation without undue fuss and wrangling. (In an ironic, if analogical, sense, this style of resolution mirrors the

primary utility of heterochrony itself: the tracing of complex and ramifying results to small alterations in basic components at the outset of a process.)

3. Science does not oppose, and will often welcome, an evolution of terminology as techniques grow and understanding deepens, often leading to new formulations that, while still internally consistent and useful, may run orthogonally, or even inversely, to the original definitions. But science cannot tolerate a change or expansion of meaning that produces unrecognized illogicalities or contradictions, thus depriving terms of clarity and utility, and potentially leading the development of a field backward into confusion.

Indeed, heterochrony itself underwent such a natural and fruitful change to an entirely revised significance (see documentation in Gould 1977 and 1992 as well as discussion in Raff 1996 and Klingenberg 1998). Haeckel originally coined “heterochrony” to describe exceptions to global recapitulation based upon changes in developmental timing of one organ with respect to others in the same body. (In his standard example, the vertebrate heart appears, by functional necessity, earlier in ontogeny than the timing of its phylogenetic origin would warrant). But, in reformulating the subject, De Beer (1930) redefined heterochrony as a change in developmental timing of an organ or feature relative to the same structure in an ancestor.

Thus, heterochrony moved from a descriptive term for exceptions to universal recapitulation to a defining term for all directions of change in developmental timing in phyletic sequences (both peramorphic, as recapitulation requires, and paedomorphic, in direct opposition to recapitulation). Since recapitulation had been overthrown, and since appropriate interest now centered on the full panoply of changes in developmental timing, this redefinition gained full approbation without sowing confusion, and has remained in force ever since (Gould 1977; Alberch et al. 1979).

4. Although De Beer extended Haeckel’s usage from organs within the same animal to organs in phyletic sequences, the terminology for categories of heterochrony has always (until the recent confusion) retained logical coherence and clear definition by designating changes in developmental timing for structures, organs, features, traits, or shapes. In other words, the categories of heterochronic alteration have always been defined by changes in the “things” produced, not by changes in the rates of production. For example, in the first explicit extension of this terminology to underlying genetic bases, Ambros (1997) properly defined the heterochronic genes of *C. elegans* in terms of the morphological results produced by changes in rates associated with mutant alleles. (Alterations of rates specify the modes and mechanisms of heterochronic shifting. These rates describe processes that produce the results, and should not be listed among the categories of results themselves.)

Thus, the slowing down of a somatic feature’s rate of

change in shape generally leads to heterochronic results (usually paedomorphosis, or retention of an ancestral juvenile shape in an adult descendant). Different modes of change in rates and timing may lead to different names for the results (progenesis for paedomorphosis by accelerated sexual maturation; neoteny for paedomorphosis by delayed somatic maturation), but the categories of heterochrony must still describe results (two different modes of paedomorphic outcomes in the example above). That is, one cannot designate the slowing of a rate, in itself, as a category of heterochrony applied to speeds rather than features. A slowed rate of somatic development cannot be called “paedomorphosis of speed,” although such slowing generally leads to paedomorphosis in a resulting morphology.

The point may seem obvious, if not pedantic, but I shall show how a mixing of rates and features yields an illogical and internally contradictory terminology that many of us have, unfortunately, adopted without recognizing the ineluctable and unfortunate consequences.

To cite key passages from works that established the concept of heterochrony in the evolutionary terms of modern usage, De Beer (1930) explicitly defines heterochrony as developmental shifting of structures, not of rates (whereas change in rates describes the underlying mechanism of shifting): “The strengths of the internal factors of development can vary and exert their effects at different rates with the result that the time of appearance of a structure can be altered . . . The principle of heterochrony will make it possible for any structure to appear later or earlier as well as at the same corresponding time, when compared with a previous ontogeny.”

De Beer’s explicit discussions and examples of individual modes in heterochrony all reinforce this definition in terms of shifting features, not alterations in rates. For example, in discussing hypermorphosis, or heterochrony produced by extension of ontogenetic curves beyond previously adult limits, De Beer speaks of characters that may then be added or altered, not of the elongated times or intensified rates that engendered these new characters: “If the time when development stops is relatively delayed, it will be possible for the descendant to add characters onto the adult ancestral stage. Referring again to the example of intersexuality in moths, male characters do not normally appear by the time development ceases, but if the time of maturity is postponed, these male characters can and do make their appearance.”

This designation of the categories of heterochrony by the features so engendered (and not by the rates doing the engendering) persisted with full consistency, despite many refinements and alterations, in all the standard sources of this subject. For example, I defined heterochrony (1977) in the glossary of *Ontogeny and Phylogeny* as: “phyletic change in the onset or timing of development, so that the appearance or rate of development of a feature in a descendant ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor’s ontogeny.”

5. The most fruitful terminological schemes in science usually arise in the context of theories and broad issues best clarified or exemplified within the chosen taxonomy. The separation and recognition of heterochrony as a phenomenon in evolutionary studies, and the establishment of a taxonomy for its subcategories, have largely occurred within the context of debate over the role of constraint in phylogeny—particularly, in this case, both the limitations and the enhanced potentials for evolutionary change provided by the developmental shifting of features already present in the ontogeny of ancestral forms.

6. Thus, heterochrony encompasses a clearly restricted set of evolutionary changes with a definite theoretical meaning and thrust: phyletic alterations based upon changes in developmental timing of ancestral features, and not upon novel features introduced for the first time into a phyletic sequence.

A misplaced ecumenicism often leads scientists to assume that broadenings of terminology to encompass a wider range of phenomena must represent “a good thing” in the integration and unification thus supposedly promoted. But, sometimes, such proposed expansions produce a strongly retrogressive effect for two primary reasons: because they join phenomena of disparate theoretical meaning, and therefore blur the insights into causal mechanisms that a proper tabulation of relative frequencies for differences can supply; and because they may conflate phenomena of logically distinct status into a single scheme, thereby importing incoherence into a previously consistent taxonomy based upon legitimate boundaries.

For example, such misplaced ecumenicism once sowed substantial confusion in the study of relationships between ontogeny and phylogeny when, throughout the first half of the 20th century, and following the cooling off (through inability to settle, rather than by resolution) of a formerly acrimonious debate, many scientists began to advocate a “kindly” and inclusive fusion of von Baer’s theory about embryonic retention, with Haeckel’s theory about acceleration of ancestral adult features into earlier stages of a descendant’s ontogeny (see extensive documentation in Gould 1977). These fusionists decided to call both theories “recapitulation,” arguing that both versions permitted the extraction of phylogenetic information from early ontogenetic stages, even though the causal mechanics could scarcely be more different (conservative retention of early stages versus active pressing back of previously adult features). The initial 19th century debate, however, had properly paired these views as directly opposed, with Baerian retention as the potential refutation of Haeckelian recapitulation.

7. The current wave of misplaced ecumenicism in the terminology of heterochrony arose in the late 1980s and early 1990s when some researchers, correctly noting the artificiality of strict separation between size and shape in the standard formalisms (De Beer 1930; Gould 1977; Alberch et al.

1979), then made a logical error in arguing that the categories of heterochrony must therefore be extended to include alterations in rates and sizes themselves, and not retain their previous restriction to alterations in the developmental timing of features produced by these changes in rates. Klingenberg (1998) described this unfortunate situation. (In later sections of the same paper, he recognizes and documents the almost ludicrous conceptual tangles thus entailed, but he never grasps the solution because he fails to identify the fallacy of logical inconsistency in the expanded “ecumenical” taxonomy):

This separation of size and shape [in the standard formalisms] has been abandoned by many recent authors, who have applied the terms originally devised for shape to size data as well. . . . Shape results from the relative sizes of an organism’s parts; the changes in developmental processes that determine the sizes of organs and of the whole organism are also the changes that affect shape. Therefore, it is logical to apply the same formalism for heterochrony . . . As a consequence of this shift in definition, the terms that originally were used for heterochrony of shape now are applied to both size and shape measures.

But formalisms, for utilitarian reasons, often parse messy natural continua into admittedly artificial “end member” categories with different theoretical meanings or workable definitions. What else, after all, does “formalism” mean? I don’t think that we can fairly criticize a division of letters into vowels and consonants because vocal cords operate in the production of both categories. And I don’t need to expand my taxonomy of musical forms to include street noises and factory clanks in an ecumenical classification of sound because I have just recognized that the B train under my home on New York’s West Side produces the same pitches as Bach’s B-minor mass.

Just as a syncretic taxonomy of subways and symphonies might lead to the dubious claim of “it’s all music,” so too (and in actuality this time), the incoherent expansion of heterochronic categories to include changes of rates, as well as changes in the developmental timing of features, has led to the claim that “it’s all heterochrony.”

For example, McNamara (1997) writes: “It [heterochrony] permeates every nook and cranny of evolution. Indeed, without it evolution wouldn’t have happened. For it explains everything, from the shape of a delphinium’s flower, to a horse’s foot, to the song of a bird.” This boast has become so common in the literature that Raff (1996), in justified opposition, entitled a chapter of his book, *The Shape of Life*, “It’s Not All Heterochrony.”

But how many legends of King Midas must we cite before we learn the dangers inherent in too much of an apparently good thing? When we start calling any change of speed a heterochrony of rate, then heterochrony loses all meaning by encompassing all phenomena, and permitting no distinctions. At this point, heterochrony becomes little more than a fancy (and superfluous) description of evolution itself. All

change, after all, must be describable as a modification in some kind of rate! A taxonomy that doesn't make distinctions, by excluding some aspects of a universal process from its midst, holds very little utility – although we may be fooled by the siren-like appeal of claims for an all-inclusive status.

Heterochrony designates one particular kind of evolution operating with a relative frequency that must be determined empirically—change by shifts in developmental timing for features already present in ancestors, thus illustrating evolution within constraints or channels of past inheritance—not some technical mumbo-jumbo applicable to all conceivable modes of phyletic alteration. Rice (1997), who develops an interesting graphical and algebraic exemplification for the traditional and restricted definitions of heterochrony as shifted shapes, defends the positive attributes of such rigorous narrowing in clear designations bearing important theoretical meaning: “Rather than being a drawback, though, this leads to another advantage of the narrow definition: saying that something is a case of heterochrony under this definition naturally leads one to look for particular kinds of biological processes, namely those that alter the ontogeny of the character as a unit.”

8. This general point may be illustrated, and a proper solution defended, by considering the actual example that has suffered the most confusion in becoming a focus for fruitless debate, rooted in a bloated taxonomy of false categories, but not in any empirical disagreement about phenomena of nature and evolution.

The hypothesis of important, or even dominant, neoteny in human evolution has enjoyed a long pedigree, and extensive discussion, ever since the overthrow of universal Haeckelian recapitulation brought the general subject into a sharp focus of theoretical legitimacy (see Gould 1977). The claim for prevalent neoteny has been based upon a panoply of putatively juvenilized features in human adults (relative to shared ontogenetic trajectories of our closest primate relatives), including such important aspects of our evolutionary success as our rounded cranium housing a relatively large brain, and a host of less salient (but no less indicative) features, including the sparse distribution of our body hair and the orientation of our great toe.

A general rationale for such extensive neoteny has been sought in the well-documented general slowdown of maturational rates in humans versus other closely related primates (an assertion accepted by all parties to this debate). Since many features of somatic development correlate closely with rates of maturation, this general delay might engender neoteny in such correlated features by retention of juvenile growth rates, even to the final stage of sexual maturation. But this hypothesis, while eminently plausible, must be tested empirically, if only for the obvious reason that plausibilities need not generate actualities.

In particular, in this case, a slowdown and temporal ex-

ension of maturation may also generate the opposite heterochrony of hypermorphosis for features uncorrelated with changes in the maturational rate; these features may continue to develop in shape at their ancestral pace, therefore terminating, in modern humans, with allometric extensions beyond the previously adult form. Within a modern Darwinian context that stresses the mosaic nature of evolution, supporters of human neoteny have always recognized this range of potential outcomes, and have defended neoteny by empirical claims for an important or dominant realized relative frequency among hypothetically legitimate modes of heterochrony. For example, I argued (1977) that the maturational delays, linked by correlated development with many neotenic features, have also engendered opposite hypermorphic outcomes in other parts of the body, most notably in our elongated and strengthened legs: “Retardation in maturation can lead to hypermorphosis and recapitulation in other circumstances.” And Abbie (1958), the most cogent modern advocate of human neoteny, based his case on the empirics of a dominant relative frequency over the major alternative outcome of slowdowns in maturational rates: hypermorphosis. “It is the balance between these two [neoteny and hypermorphosis] in different parts of the body that produces the distinctively human form among primates.”

Moreover, and most importantly, the documentation of a neotenic shape does not, by itself, imply a heterochronic cause. Juvenilized shapes may arise by other routes than a shifting of developmental timing, with the observed resemblance to ancestral juveniles then merely convergent, superficial, or otherwise engendered. In this particular case, an alternative hypothesis for the juvenilized shape of human crania has long been available, and actively advocated in explicit contrast with the heterochronic interpretation. As Franz Weidenreich (1941) and several subsequent anthropologists have maintained, suppose that the human brain becomes large by a non-heterochronic mechanism, and that putatively neotenic features then arise merely as mechanical consequences of how a large brain must shape the yielding and flexible bones of the enveloping face and cranium? I count myself as a strong supporter of the neoteny hypothesis, but I certainly acknowledge the cogency and potential validity of this opposite explanation for the empirical results. The issue must be settled empirically—and heterochrony holds interest and power by representing one meaningful explanation among several alternatives. But if all evolution must be heterochronic by definition, then what will we learn by studying the interactions of development and phylogeny?

9. Advocates for extending the categories of heterochrony to cover rates as well as shapes have promulgated an empty and divisive argument about heterochrony in human evolution by accepting the phenomenology of juvenilized morphology in adult humans, but then advocating hypermorphosis, rather than neoteny, as the primary heterochronic mode. Klingenberg (1998) correctly notes that “the discussion re-

garding human heterochrony has been dominated by contradictory interpretations of the same facts.”

This essential agreement about development of the human brain recognizes two facts: 1) Our relatively large adult brain, housed in its rounded cranium, bears a striking similarity in shape to the juvenile brain of related primates; (this fact must be distinguished from the separate issue of whether—and, if so, in what mode—heterochrony lies behind this evolution in form; see point 8 above); and 2) Our brain reaches its large size by extension of growth—that is, by growing faster and longer than the brains of related primates.

By the properly restricted standard formalisms that define the categories of heterochrony by features that have undergone shifting in the timing of development, the adult human brain, if heterochronic at all, can only be labeled as paedomorphic, or literally child-shaped. Among the subcategories of paedomorphosis, neoteny, or juvenilization by slowdown in change of shape, seems clearly implicated. This framework for posing the question of heterochrony had been clearly articulated, accepted, and understood (although the issue had not been empirically resolved) until researchers began conflating the terminology of heterochrony by mixing the apples and oranges of shape and size in the late 1980s and early 1990s.

By extending the categories of heterochrony beyond the features produced by changes in rates to include the changes in rates themselves, several authors promulgated our current chaos. In the standard terminology for pure sizes and rates, paedomorphs are juvenilized, whereas peramorphs extend their shapes beyond the ancestral adult configuration. In the unwisely extended size terminology, paedomorphs grow more slowly or for a shorter time, and peramorphs grow more rapidly or for a longer duration. For example, in the most comprehensive book dedicated to heterochrony, McKinney and McNamara (1991) define neoteny as “slower rate of developmental events”—and then add that neoteny “produces paedomorphic traits when expressed in the adult phenotype.” They then define hypermorphosis in terms of altered rates as well: “late cessation . . . of developmental events . . . in the descendant.”

The counterproductive terminological chaos, falsely presented as a major reform in the understanding of human evolution, then arose from the “brave” contention that phenomena once viewed as paedomorphic by neoteny (the juvenilized form of the human cranium) must now be reinterpreted as products of the opposite heterochronic process: hypermorphosis, defined as extension beyond a previously adult state, and always classified as a subcategory for the directly contrary result of peramorphosis! McKinney and McNamara (1991), for example, proclaim with force that “this situation reaches its ultimate absurdity in human heterochrony where a truly alarming number of authors state the oxymoron (we paraphrase) that ‘neoteny results in [they

should have said “from”] faster growth by prolongation of the rapidly growing fetal growth stage.’ We hope to clarify that the true situation is that human are generally (and quite simply!) hypermorphic.”

And so we reach the absurdity of paedomorphosis (the juvenilized shape of the human cranium), produced by a subcategory of the directly opposite phenomenon of peramorphosis (an extended and more rapid growth period, or so-called “hypermorphosis of rate” for the human brain). But the absurdity of this situation emerges only from our incoherent terminology, and not at all from nature (for all participants in this discussion agree on the empirical results). And such confusion and contradiction must arise when researchers apply terms explicitly defined for shapes to the rates that generate those shapes.

Paedomorphosis is juvenilized shape, not slowed rates; and peramorphosis is extended shape, not faster growth. The conflation of features and rates can only lead to absurdities because any heterochronic result (a paedomorph or a peramorph) can be produced either by the slowing down or speeding up of some kind of rate. Therefore, if we apply the shape terms to rates, then some paedomorphs (properly defined by shape) will be produced by peramorphs (improperly applied to pure rates), while some peramorphosis (correctly designated by form) will be attributed to paedomorphosis (improperly defined by pure size). Thus, Godfrey and Sutherland (1996), who tried to resolve this confusion, chose a justifiably sardonic title for their paper: “Paradox of peramorphic paedomorphosis: heterochrony and human evolution.”

Several authors have noted the absurdity, but failed to locate the simple solution: “just say no” to the false extensions of heterochronic categories to changes in rates and times.

In an amusing example, Klingenberg (1998) documents the inconsistency and chaos: “This prolongation of brain growth at the high fetal rate is responsible for a marked increase in relative brain size, and it makes modern human clearly peramorphic by hypermorphosis relative to their ancestors. . . . In contrast, the same change renders humans paedomorphic in relation to the ontogenetic polarity of the later postnatal period.” He also recognizes the correct solution in principle: “Authors need to be consistent, using only one formalism at a time, and using each term in only one meaning!”

But Klingenberg then fails to follow his own sage advice because, even while documenting the terminological contradiction and muddle, he doesn’t seem to understand that the debate only implicates words, and not things. That is, he thinks that one of the two “alternatives” must be “right” (neoteny or hypermorphosis), while failing to grasp that a properly defined neoteny of form will often be generated by an extension of time (or speeding of rate) that should not be called hypermorphosis: “I have discussed the question of whether the rounded shape of the human skull is paedomor-

phic because of its similarity to juvenile ape skulls, or peramorphic due to the prolonged growth of the human brain. In that case, developmental information suggests that the latter is more likely.” But our skull is paedomorphic as a consequence of “prolonged growth” that cannot legitimately be designated with a term (peramorphosis) devised to describe features, not the rates that produce them. We must therefore “just say no” to the illogical and incoherent extension of heterochronic categories to changes in rates and times, rather than to their results.

10. When the categories of heterochrony become properly reconfined to the developmental shifting of features, then we may seek an empirical resolution to the fascinating issue of whether the paedomorphic shape of the adult human cranium arises heterochronically by the forward extension of ancestrally juvenile features into the later stages of modern descendants.

Phrased in this coherent and testable way, the hypothesis of neoteny gains strong support from studies of Vrba (1994, 1998) on the achievement of large size and paedomorphic form by the coordinated prolongation of both phases of allometric growth—an early positive allometry leading to substantial relative increase, and a later negative allometry. (Rice’s elegantly simple analysis of human versus chimp growth trajectories [see Rice, 1997] affirms this conclusion). Vrba argues (1998):

Brain growth in humans [occurred through] . . . evolution by proportional growth prolongation: all descendant growth phases are extended by the same factor while each remains at the ancestral growth rate. The results . . . imply that gross brain weight increase toward humans required change in only one growth parameter: prolongation of the nonlinear ancestral growth phases. The restricted and orderly nature of the developmental change hints at a basis in a few genetic changes.

Now, if an admittedly paedomorphic result occurs by a prolongation of juvenile growth rates into later stages of a descendant’s ontogeny—the situation (by Vrba’s analysis) in human ontogeny, made more complex by the biphasic nature of the growth curve, but then affirmed even more strongly by the demonstration that each of the two phases becomes prolonged in the same manner and degree—then the heterochronic result can only be called paedomorphosis by neoteny. This attribution would never have seemed problematic, and the apparently opposite claim for hypermorphosis would never have been made, if our terminology had not become illogically discombobulated by the extension of terms for processes to terms for rates. The decision to call the evolution of the human brain “hypermorphic” can only arise by false application of heterochronic categories to rates, for one might then be tempted to label the ontogenetic extension of the juvenile growth phases as “hypermorphosis of rate.” But this confusing and illogical terminological extension must be re-

jected if we wish to restore clarity and evolutionary meaning to the concept of heterochrony.

Incidentally, although I fully accept Godfrey and Sutherland’s (1996) criticism of my claim (Gould 1977) that the indisputable and general “matrix of retardation” for human development, compared with the rates and forms of pongid relatives, makes human neoteny almost “ineluctable,” I had this situation of the brain’s evolution in mind when I advanced my central argument that neoteny becomes a favored channel for human evolution as a predictable consequence of general retardation in development itself. Retardation by prolongation of juvenile growth rates and tendencies does lead, preferentially, to paedomorphic results—as in the case of the human brain. But I erred in labeling this result as ineluctable, because simple prolongation can also yield other heterochronic results (as I also argued and illustrated in my text), including genuine hypermorphosis (properly defined by an evolution of features “beyond” their ancestral adult form) when the prolongation of rate becomes entirely dissociated from any slowdown in the development of form, and the ancestral allometry just proceeds farther into the extended realm of size—as in the evolution of our elongated legs.

11. Our usual inability to specify the ontogenetic age of fossils has long stood as the greatest impediment to the application of heterochrony to paleontological data. The categories of heterochrony specify phyletic shifts in developmental timing for features of descendants relative to the chronological age or maturational state of the same features in ancestors. The frequent use of size as the only available standard for comparison in fossils—done entirely *faute de mieux*, and always in full recognition of the problems thus entailed—has greatly hampered the study of heterochrony in paleontology, because size cannot serve as a valid surrogate for the desired temporal measure, given the frequency of phyletic change in size (so that similar sizes need not mark similar ages, as the surrogacy argument requires).

Thus, the ability to assess age independently by sclerochronological analysis of growth lines—a far more difficult problem than initial considerations might indicate, because observed periodicities are rarely so regular, or so unambiguous in their astronomical referent, as one might assume—provides a key, only recently turned, for specifying heterochronies in some paleontological material. Jones and Gould (1999) applied this methodology to resolve a classic, but heretofore undefinable, case of heterochrony in the phyletic sequence to increased size and reduced intensity of coiling in the lower Jurassic oyster *Gryphaea*.

The clear trend to paedomorphosis in shape (Fig. 1) had never been denied, but an inability to specify the ages of fossil shells precluded any resolution of mode. In particular, do adult descendants reach their markedly larger size by growing faster or growing longer—a good example of why size surrogates cannot resolve heterochronic questions about age.

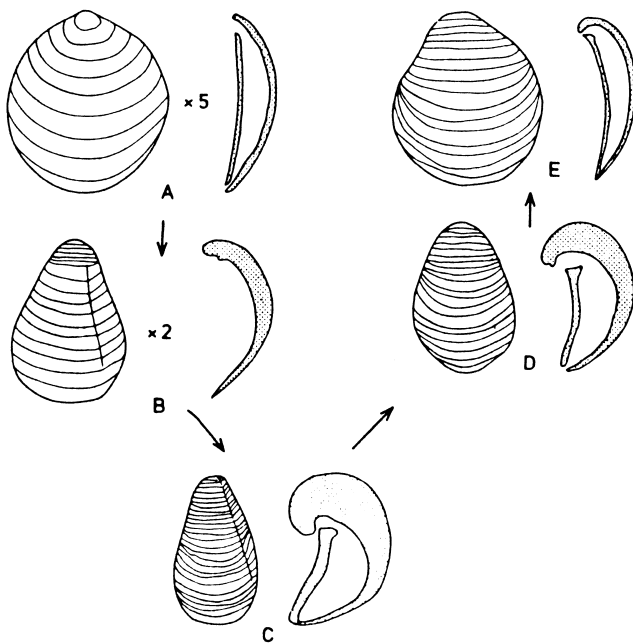


Fig. 1. Pedomorphosis in Lower Jurassic *Gryphaea*. The left sequence (top to bottom) shows ontogenetic stages of the ancestral species drawn at the same size as adults of the phylogenetic series (the right sequence, bottom to top).

If the larger descendant adults reached their pedomorphic shape at the same age as the more coiled and smaller adult ancestors, then we could assert a claim for neoteny, with pedomorphic features engendered by retention of rapid juvenile growth rates (and correlated shapes) into progressively later stages of growth. But if the adult descendants reach their larger size only by growing for a longer time (with ancestors and descendants always reaching the same size at comparable ages), then the pedomorphic shape might not arise by heterochrony at all, for no mechanism for a shift in developmental timing could then be specified, and the juve-

nilized form might have arisen for other reasons, and by other modes.

Our sclerochronological study resolves this issue (see Figs. 2 and 3) by demonstrating that ancestors and descendants have statistically identical life spans, and that all size increase in phylogeny results from faster growth of descendants at comparable ages.

I discuss this case here to emphasize the point that, for this far less salient example than the human brain, where emotions and expectations do not so cloud our concern and judgment, neither the attribution of pedomorphosis, nor the recognition that faster growth at comparable ages implicates neoteny via correlated consequences (for shape) of extending rapid juvenile growth rates into later ontogeny, has ever been questioned. And yet, the case of these oysters corresponds exactly, in mode and style, to the increase of brain size, with pedomorphic shape as a correlated consequence, in human phylogeny. That is, under the falsely expanded taxonomy of heterochronic modes to include pure rates, the case of *Gryphaea* might have been trumpeted as a newly reinterpreted example of “rate hypermorphosis” to extended body size, with accompanying deprecation of previous claims for neoteny!

The two examples illustrate complete correspondence. In both, a phyletic extension of rapid juvenile growth rates leads to marked increase in a structure’s size, with accompanying retention of juvenilized shape—thus yielding outcomes of pedomorphosis by neoteny. One can only invoke the opposite mode of hypermorphosis if one incorrectly applies the heterochronic names to rates rather than features, thus falsely designating a pure increase in rate as a mode of heterochrony, and sowing substantial confusion with no enlightenment.

12. Klingenberg (1998) recognized some of the problems engendered by this incoherent terminological extension, but he despaired of a simple or feasible solution:

Generalizations about evolutionary process on the basis of published results are currently impossible because of

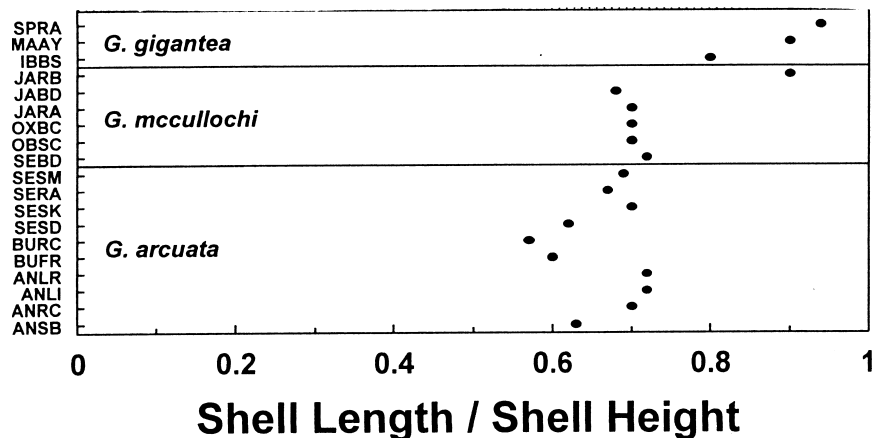


Fig. 2. Mean shell shape of adult *Gryphaea* up the stratigraphic sequence showing pedomorphosis, as increasing length/height ratio characterizes juvenile stages of ontogeny.

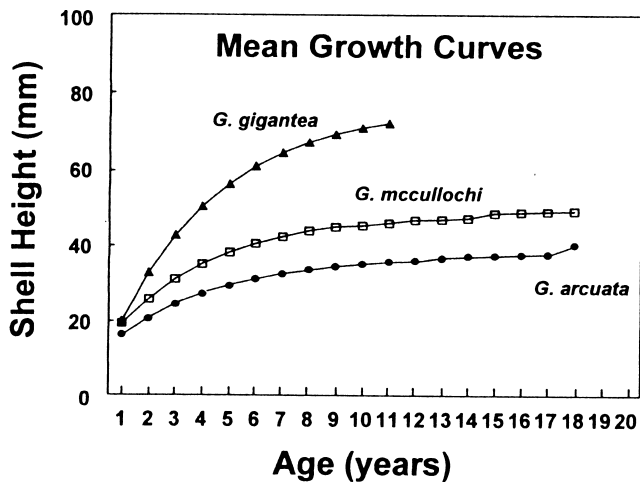


Fig. 3. Increase in size (measured as shell height) at the same age in the phyletic sequence *G. arcuata* → *G. gigantea*.

these discrepancies—one author’s “neoteny” is another author’s “hypermorphosis.” These disagreements about analytical frameworks for heterochrony are deeply entrenched, and there is little or no prospect of a uniform terminology at any time in the near future.

But I would suggest far more optimism in the face of this admittedly tangled situation. For the solution, in fact, is simple, and the primary theme of heterochrony can supply our guide, albeit metaphorically. The confusion has arisen entirely as a consequence of a simple logical error in terminology, and has no basis in empirical disagreements. The categories of heterochrony should never have been applied to changes in rates and times alone. These categories, for reasons of coherence in logic and consistency in application, should remain restricted to the paedomorphic and peramorphic features thus produced—as recognized in all the standard formalisms (De Beer 1930; Gould 1977; Alberch et al. 1979; McNamara 1986, before he became beguiled by the prospect of extension) universally employed before the unfortunate application to rates and times occurred in the late 1980s and early 1990s.

Heterochrony highlights the theme of significant changes in apparently complex situations by relatively simple alterations (with potentially global consequences) in the timing of development. Paedomorphosis, in particular, has long been viewed as a putative “escape from specialization,” an available mechanism for shucking terminal complexities that have shackled an organism’s potential for future development. The evolution of the language of heterochrony now

requires a rescuing event of precisely this type. We need to discard the misguided extensions of heterochronic categories to rates and times. That is, we need to shuck the most recent (and, I would say, senile) accretion, plastered on, about 10 years ago, to the end of the intellectual ontogeny of heterochrony. We should slough off these illogical extensions and return to the simpler and coherent formalisms of a previous intellectual adulthood. Our heterochronic terminology, in short, must undergo evolution by paedomorphosis, thus dropping some inadaptive terminal additions, and returning this vital subject to the coherence and flexibility of its lithe and workable maturity.

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