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Phenotypic Accommodation: Adaptive Innovation Due to Developmental Plasticity

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ABSTRACT Phenotypic accommodation is adaptive adjustment, without genetic change, of variable aspects of the phenotype following a novel input during development. Phenotypic accommodation can facilitate the evolution of novel morphology by alleviating the negative effects of change, and by giving a head start to adaptive evolution in a new direction. Whether induced by a mutation or a novel environmental factor, innovative morphological form comes from ancestral developmental responses, not from the novel inducing factor itself. Phenotypic accommodation is the result of adaptive developmental responses, so the novel morphologies that result are not ‘‘random’’ variants, but to some degree reflect past functionality. Phenotypic accommodation is the first step in a process of Darwinian adaptive evolution, or evolution by natural selection, where fitness differences among genetically variable developmental variants cause phenotype-frequency change due to gene-frequency change. *J. Exp. Zool. (Mol. Dev. Evol.) 304B:610–618, 2005.* © 2005 Wiley-Liss, Inc.

Adaptive responsiveness to conditions in the external and internal environment has long been considered a universal property of living things. Large subdisciplines of the biological sciences, including physiology, endocrinology, neurobiology, ethology, embryology, cell biology, and the molecular biology of gene expression, study the mechanisms of adaptive responsiveness, but its significance for the process of evolution has not been extensively explored.

Elsewhere I have argued that developmental plasticity, or responsiveness to external and internal environments whether adaptive or not, can play an important role in evolution (West-Eberhard, 2003). Here I summarize one aspect of that argument, namely, that adaptive flexibility, or phenotypic accommodation, can facilitate the origin and evolution of morphological novelties. *Phenotypic accommodation* is adaptive mutual adjustment, without genetic change, among variable aspects of the phenotype, following a novel or unusual input during development (West-Eberhard, ’98, 2003).

The role of flexibility in facilitating evolutionary change has been noted by many authors, including most prominently Baldwin (1896, ’02), whose concept of ‘‘organic selection’’ meant fitness enhancement due to phenotypic accommodation; Schmalhausen (’49 [’86]), who saw individual adaptability as a stabilizing force that promotes the origin and evolution of morphological novelties; Goldschmidt (’40 [’82]), who discussed how the ‘‘regulative ability’’ of developmental mechanisms could facilitate and exaggerate change; Frazzetta (’75), who referred to phenotypic ‘‘compensation’’; Müller (’90) on ‘‘ontogenetic buffering’’; and Kirschner (’92); and Gerhart and Kirschner (’97), who consider the mechanisms of phenotypic accommodation within cells and during embryogenesis an aspect of ‘‘evolvability.’’

PHENOTYPIC ACCOMMODATION IN MORPHOLOGY: THE TWO-LEGGED-GOAT EFFECT

Phenotypic accommodation can include adaptive plasticity in all aspects of the phenotype, including not only morphology, but also physiology and behavior. And it can involve developmental plasticity at more than one level of organization. For example, behavioral accommodation may involve flexible responses of many organs (e.g., heart, brain, and limbs) and mechanisms that operate at multiple levels within them (i.e., tissues, cells, and their component

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organelles) (see West-Eberhard, 2003). There are subdisciplines of biology that deal with adaptive accommodation in physiology and behavior, but there is no comparable field devoted primarily to adaptive responses in morphology. Adaptive morphological plasticity is nonetheless well documented, for example in studies of vertebrate muscle and bone (reviews in Slijper, '42a, b; Frazzetta, '75; Wimberger, '94); invertebrate body size and form (e.g., see Bernays, '86; Strathmann et al., '92); and in plants, perhaps the best studied group of organisms with respect to morphological plasticity (reviews in Bradshaw, '65; Schlichting, '86; Sultan, '87, 2000).

A handicapped goat studied by Slijper ('42a, b) can serve to illustrate the phenomenon of morphological phenotypic accommodation. Slijper's goat was born with congenital paralysis of its front legs, so that it could not walk on all fours. It managed to get around by hopping on its hind legs, an example of behavioral accommodation that led to dramatic morphological accommodation as well. When the goat died an accidental death at the age of 1 year, Slijper dissected it and published a description of its altered morphology, which included changes in the bones of the hind legs, the shape of the thoracic skeleton and sternum, changes in the shape and strength of the pelvis, which developed an unusually long ischium. Changes in the pelvic muscles included a greatly elongated and thickened gluteal tongue whose attachment to the bone was reinforced by a novel trait, a set of numerous long, flat tendons.

This example of phenotype accommodation shows how developmental responses can mold the form of a morphological novelty. In Slijper's goat, novel morphology came not from a series of mutational changes, but from reorganized expression of capacities that were already present. In the remainder of this article, I show how such immediate responses can be converted to evolutionary change and facilitate the origin of adaptive novelties.

PHENOTYPIC ACCOMMODATION AND THE ORIGINS OF NOVELTY

A morphological innovation can be defined as an aspect of morphology that was not present in the immediate ancestors of a species, in a given life stage and sex. Mayr ('59, p 89) defined an evolutionary novelty as ''any newly arisen character, structural or otherwise, that differs more than quantitatively from the character that gave rise to it.'' Müller and Wagner ('91, p 243) define morphological novelty as ''a structure that is neither homologous to any structure in the ancestral species nor homonomous to any other structure of the same organism.'' But this definition is impossible to apply given the reorganizational nature of evolutionary change. Unless ''homologous'' means identical, many novelties must have recognizable homologs in ancestral species which have given rise to them through ontogenetic repatterning (Wake and Roth, '89; developmental recombination of West-Eberhard, 2003, 2005). Some innovations, such as those derived via heterotopy (change in the location of expression of an ancestral trait), may exist alongside the ancestral morphology as homonymous structures in the descendent species. [For a more extensive discussion of the homology concept as related to developmental plasticity and evolution, see West-Eberhard (2003) and references therein.]

The two-legged goat is an instructive example for anyone interested in morphological innovation. It does not matter, for the form taken by the morphological change, whether the pivotal change (inability to walk on the front legs) was induced by a mutation or by an environmental accident. The particular characteristics of the novel morphology, that is, the novel features of the bones, muscles and tendons, arose via mechanisms of developmental plasticity, not owing to the particular genetic or environmental change that may have induced them. Any number of mutations or environmental factors could have triggered a defect in the front legs. Whatever the trigger, it acted as a kind of switch mechanism that controlled a whole suite of morphological changes—a complex, coordinated morphological novelty, a new modular ''trait'' whose developmental independence of others is defined by the integrated response of the phenotype to a new input.

A second important point is that the morphological change was mediated by behavior. Behavior is, of course, a common mediator of normal skeletal and muscle development because it is especially flexible in response to environmental contingencies. It follows that behavior must often be an important mechanism in the origins of novel morphological traits. So we have to list behavior and its neuroendocrinological underpinnings, alongside genomic changes, as among the primary developmental causes of morphological novelty.

Two-legged goats are unjustly maligned if treated as mere freaks with no evolutionary importance. Slijper ('42a, b) compared the morphology of the two-legged goat with that of other bipedal mammals such as humans and kangaroos. Some of its novel morphological features closely resemble the evolutionary novelties of bipedal mammals: its compressed thorax and its elongate ischium resemble those of kangaroos; and the wide sternum resembles that of an orangutan, a bipedal primate that, like the two-legged goat, lacks a tail for support. A bipedal baboon filmed by William H. Hamilton III showed similar behavioral accommodation to disabled front legs (see West-Eberhard, 2003). The baboon's deformity is thought to have been caused by polio, for an epidemic had affected its troop.

Could phenotypic accommodation have played a key role in the morphological innovations of bipedal primates and kangaroos? As far as I know this question has never been answered, probably because it is seldom asked, although it was certainly suggested by the comparisons discussed by Slijper. It seems probable that plasticity has at least played a role, judging by the readiness with which mammals accommodate morphologically to behavioral alterations and extremes, as in human body builders and in potential osteoporosis patients, where weight-bearing exercise and a calcium-rich diet can have marked effects on the size and density of bone. Some of the changes described by Bramble and Lieberman (2004) as associated with the origin of a running gait in humans, including enlargement of the gluteus maximus muscle and elongation of certain bones of the legs, modification of the pelvis, and elongation of the Achilles tendon, could have appeared and then spread rapidly. Given natural selection (in whatever context) for increased running behavior in a human population of highly social adults and their imitative young, changes like those produced in the two-legged goat could come to characterize an entire population in a single generation (Slijper, '42a, b). Head stabilization and energetic efficiency, mentioned by Bramble and Lieberman (2004) as special problems during the evolution of hominoid running, increases in monkeys (Japanese macaques) trained over a period of years to walk upright (Hirasaki et al., 2004).

It is easy to see how a phenotypic accommodation could become a regularly occurring developmental pathway. To give just one example that involves an established trait of a natural population, the skulls of adult spotted hyenas (*Crocuta crocuta*) have a striking medial saggital crest and other attachment sites (cheekbones and forehead) for the powerful muscles used in chewing the bones and tough meat of the hyenas' prey (after Holekamp and Smale, '98; Holekamp, personal communication). The extreme modifications of the head are absent in infants of the same species, and they also fail to develop in captive individuals fed on soft diets. The full development of the exaggerated crest evidently requires years of chewing tough food. That is, normal species-specific adult morphology requires a particular kind of environmental factor—a tough diet—and the exercise that this promotes. It is also possible that, in addition, the skull bones have evolved under genetic accommodation of the response, to be especially responsive to such exercise to exaggerate special features of the skull—this is not known. But one thing is certain: a particular environmental factor (hard diet) and behavioral response (intense exercise of the jaw muscles during chewing) contributes to the normal development of the species-typical morphology.

Novel morphology that involves adaptive phenotypic accommodation is not ''random'' variation, for it begins with an adaptive phenotypic change. Phenotypic accommodation gives a head start to adaptive evolution by producing novel phenotypes likely to be favored by natural selection. In this respect, a theory of adaptive evolution that recognizes the role of phenotypic accommodation differs from one that views selection as operating on random variation due to mutation alone.

In sum, phenotypic accommodation facilitates adaptive evolution in two ways: (1) it provides a head start in adaptation. The new trait is produced by an already organized, adaptively flexible phenotype whose responses have been subjected to natural selection in the past. And (2) being a new developmental pathway associated with a developmental switch (the mutational or environmental inducer), the new trait is modular in nature. That is, it is somewhat independently expressed relative to other traits and therefore independently subject to selection (see West-Eberhard, '92, 2003). How adaptive evolution proceeds from this initial step of phenotypic accommodation is discussed in the next section.

A GENERAL MODEL FOR THE ORIGIN OF ADAPTIVE PHENOTYPIC NOVELTIES

The following model is intended to describe the evolutionary origin of all kinds of adaptive traits—morphological, physiological and behavioral, whether induced by a mutation or an environmental factor—at all levels of organization. This is a brief summary of concepts presented in more detail and with more complete supporting evidence elsewhere (West-Eberhard, 2003):

(a) A novel input occurs which affects one (if a mutation) or possibly more (if environmental) individuals. Individuals may experience novel inputs due to evolution in another context (e.g., which moves them into a new environment, or has novel pleiotropic effects on the phenotype via other pathways).

(b) Phenotypic accommodation: Individuals developmentally responsive to the novel input immediately express a novel phenotype, for example, because the new input causes quantitative shifts in one or more continuously variable traits, or due to the switching off or on of one or more input-sensitive traits (causing a reorganization of the phenotype). Adaptive phenotypic adjustments to potentially disruptive effects of the novel input exaggerate and accommodate the phenotypic change without genetic change.

(c) Initial spread: The novel phenotype may increase in frequency rapidly, within a single generation, if it is due to an environmental effect that happens to be common or ubiquitous. Alternatively, if it is due to a positively selected mutation, or is a side effect of a trait under positive selection (Müller, '90), the increase in frequency of the trait may require many generations.

(d) Genetic accommodation (change in gene frequencies under selection): Given genetic variation in the phenotypic response of different individuals, the initial spread produces a population that is variable in its sensitivity to the new input, and in the form of its response. If the phenotypic variation is associated with variation in reproductive success, natural selection results; and to the degree that the variants acted upon by selection are genetically variable, selection will produce genetic accommodation, or adaptive evolutionary adjustment of the regulation and form of the novel trait.

This model requires that at least some individuals in a population are responsive to the new input. As already discussed, the capacity to respond to diverse inputs is likely a property of all living things. The model also depends, for an evolutionary response to selection, on the presence in the population of genetic variation for the developmental change. This also is a realistic assumption for most populations, given the well-documented commonness of genetic variation revealed by electrophoresis, and the evolutionary response of virtually all traits subjected to artificial selection (e.g., see Lewontin, '74; Maynard Smith, '89; West-Eberhard, 2003, 2005).

Standard quantitative genetics models show how threshold selection can lead to the change in frequency of a trait (e.g., see Falconer and MacKay, '96). Previous authors have presented ideas similar to those presented here regarding the origins of novel traits. Wagner and Chiu (2003, p 266), for example, wrote: ‘‘the origin of new characters requires epigenetic opportunity for the new morphological states to occur [i.e., a novel input that provokes a developmental response]. Genetic factors are required for the heritability and subsequent fixation of new morphological states [one possible outcome of genetic accommodation]. This requirement does not imply, however, that the specific nature of a new character is in any sense determined or explained by the mutations that make the character heritable’’ [as just discussed, the nature of the new character comes primarily from the reorganization of ancestral developmental pathways].

There is no conflict between this model and the standard view of adaptive evolution as involving variation, selection, and gene-frequency change. But the analysis includes steps of the process that are usually left out, steps with important implications that are sometimes overlooked, for example, the fact that it does not matter, for the initiation of a novelty, whether the original induction is mutational or environmental; and the fact that environmentally induced traits can initially spread without positive selection (all that is needed is recurrence of the inducing factor).

This departs from the view, which may be encouraged by gene-for-trait modeling of evolution by natural selection, that the recurrence or spread of a novel trait is due to the spread of a particular allele, and the associated idea that only genetically induced, mutational or genetically recombinant, novelties have evolutionary potential. Because environmental factors can affect many individuals at once they may be more effective initiators of selectable evolutionary novelties than mutations, which initially affect only single individuals (West-Eberhard, 2003, 2005). In effect, environmental induction jump-starts adaptive evolution by immediately producing a population of phenotypic variants upon which selection can act. Then, if the phenotypic variance is partly due to genetic variation among individuals, adaptive evolution in response to selection can occur.

In this model, as in Waddington's ('53) concept of genetic assimilation, adaptive evolution depends on evolutionary change in the threshold for a newly induced response, as well as quantitative genetic change in the propensity or ''liability'' to produce the novel trait. But genetic accommodation differs from genetic assimilation in several important respects. For example, it considers genetic change in both the form (e.g., under selection for increased efficiency) and the frequency (e.g., due to change in threshold of expression) of a trait, whereas genetic assimilation treats only the latter. Most importantly, genetic accommodation can lead to a decline in trait frequency and diminished genetic control, or to the establishment of a polyphenism with adaptive conditional expression of alternative forms. Genetic assimilation, by contrast, implies the evolution of increased genetic control and the evolutionary change toward increased frequency or fixation of a trait. For a more detailed comparison of genetic assimilation, genetic accommodation, and the Baldwin effect see West-Eberhard (2003).

Could phenotypic accommodation alone, without gene-frequency change, lead to adaptive evolution? It is sometimes pointed out that developmental plasticity can lead to evolution without gene-frequency change, if the spread of an environmentally induced trait is entirely due to the spread of its environmental inducer, as in the fixation of a conditional alternative phenotype under conditions that induce it, or in the ''behavioral inheritence'' of traits in humans (Avital and Jablonka, 2000). But this would not be Darwinian adaptive evolution, or evolution by natural selection, the subject of this article. Darwin's theory of evolution by natural selection is based on the principle that the spread of a trait in a population is due to the *fitness effect* (advantageousness) of the trait. It is the increased reproductive success, or fitness, of the bearers of the trait that causes the trait to spread. The Darwinian fitness-effect condition is not met if the trait spreads due to the spread of its inducer alone, independent of the fitness effect of the trait. So evolution by increased environmental induction alone may be described as phenotypic evolution—a change in the frequency of a particular phenotype in a population—but not as Darwinian adaptive evolution.

RECIPROCAL CAUSATION IN THE EVOLUTION OF BEHAVIOR AND MORPHOLOGY

There is the potential for circular reinforcement in the evolution of morphology when it is affected by plasticity, especially behavioral plasticity and learning. Diet can affect morphology via phenotypic accommodation during use, and morphology in turn can affect diet, both by phenotypic accommodation due to learning and by making the new diet more profitable. Observations by Greenwood ('65) and others on the African Lake cichlids showed that individuals of a mollusc-feeding species reared on a soft diet in an aquarium develop pharyngeal jaw morphology like that of closely related soft-diet insectivorous species. Then, beginning in the mid 1970s, Liem and Kaufman ('84) demonstrated the reciprocal effect of morphology on diet. When two alternative morphs, one with a mollusc-specialized jaw (the molariform morph) and the other with a soft-diet jaw (the so-called papilliform morph), have an abundant supply of soft food, both prefer the soft diet. But when food is scarce they divergently specialize in accord with their morphological specializations: the fishes with the mollusc-feeder jaw morphology take a greater proportion of molluscs, and those with the soft-food morphology specialize on soft food. So, in conditions of scarcity, morphology affects diet and the resultant divergent behavior would reinforce selection in divergent directions.

A similar phenomenon is well documented in Darwin's finches of the Galapagos islands (Price, '87; Grant and Grant, '89): in times of food scarcity large-beaked finches learn to prefer and efficiently crack large hard seeds, while smaller-beaked individuals learn to concentrate on, and efficiently exploit, small soft seeds. This promotes intermittent diverging selection on the extremes, and generates divergent trends in different populations and species. There is, then, evidence that developmental plasticity in the form of morphology- and diet-associated learning has contributed to the explosive radiations in both the African cichlids and the Galapagos finches (West-Eberhard, 2003).

SIGNIFICANCE FOR RESEARCH ON THE ORIGINS OF MORPHOLOGICAL NOVELTY

A developmental-plasticity approach to the origins of novelty suggests new avenues of research on the evolution of morphology. To explain the origins of morphological novelty, developmental biology needs to broaden its focus beyond genomic innovation to include behavior and even learning as key mechanisms in the evolution of morphology. These mechanisms need to be included in both microevolutionary and macroevolutionary analyses of change.

Microevolutionary analyses

From observations like those discussed here, I offer the following testable hypothesis: species-specific morphological novelties can result from the evolution, or environmental induction, of species-specific behaviors, and need not involve morphology-specific genetic change (though such change is likely to occur eventually, as genetic accommodation leads to the reorganization of gene expression in traits favored by selection).

This hypothesis suggests a broadened experimental approach to research on the origins of morphological novelty. Suppose you are interested in the origin of the exaggerated sagittal crest in hyenas. In a traditional approach, you might propose breeding experiments to ascertain the heritability of crest height in species that already have a sagittal crest. You might map cranial morphology onto a phylogeny to look for similar structures in related species. Both studies would illuminate the evolution of the crest. But an approach considering developmental plasticity might go further, to examine the correlation between dietary toughness and muscle and bone development, or to examine the possibility of crest induction (e.g., by dietary alteration) in related species that do not normally possess a raised crest.

There are, of course, some taxa in which such plasticity experiments have actually been done. One of the best known is the cichlid fishes, already discussed in the section on reciprocal causation (above). Following the discovery that diet affects feeding morphology in cichlids (Greenwood, '65), various investigators, including Liem and associates (Liem and Osse, '75; Liem and Kaufman, '84), Hoogerhoud ('86), Meyer ('87, '90), Wimberger ('91, '92), and Galis (Galis, '93; Galis et al., '94), experimentally examined the effects of diet on morphology in other cichlid species. These studies confirmed effects of diet on the pharyngeal jaw morphology. The Central American cichlid *Cichlasoma citrinellum* has two trophic morphs: one that feeds primarily on snails and another that has a softer diet. Meyer ('90) found that the alternative pharyngeal jaw morphologies of the two morphs can be reversed in at least some individuals by reversing their diets. He also pointed out that these two body forms parallel the differences between two alternative forms that are very common in fishes, the snail feeder having a body shape like a ''benthic'' or bottom-feeding form, and the soft-food morph resembling a ''limnetic'' form that feeds in the water column. These studies support the hypothesis that recurrent trophic morphologies in cichlids can arise due to phenotypic accommodation under different dietary regimes.

Macroevolution, or major morphological change

Macroevolution may be different in scale to microevolutionary change, but it still requires explanation at a microevolutionary level. That is, it requires explanation in terms of adaptive evolution by natural selection and gene-frequency change within populations. No matter how major the trait, no matter how momentous at the family or phylum or body-plan level, analysis still has to go to the microevolutionary level to find out how the trait began. This suggests another kind of new avenue of research for developmental biologists interested in macroevolutionary aspects of evolution.

To cite just one example, consider the likely role of developmental plasticity in the origin of an undeniably major morphological novelty—a new appendage in a fly. In some genera of sepsid flies (Diptera, Sepsidae), a novel appendage is formed by the fourth sternite of the males. It has evolved independently in several different genera (Eberhard, 2001). In relatively unspecialized species (e.g., *Archisepsis diversiformis*), males have sternal bristles that are rubbed against the female during courtship. In somewhat more elaborate versions (e.g., in an unnamed species of *Pseudopalaeosepsis*), male sternites have bristled lateral lobes that are semi-articulated and have attached muscles capable of moving them back toward the posterior end of the fly. And in the most highly elaborated examples (e.g. *in Pseudo-palaeosepsis nigricoxa*), the sternal lobes are long, highly articulated, and capable of limb-like movements both toward the posterior and ventrally, forming a novel appendage complete with segments, muscles, and nerves.

Phenotypic flexibility has likely played an important role in the evolution of this hinged, limb-like structure. First, behavioral movements have evidently taken the lead with abdominal courtship movements preceding the morphological specializations. Then, in somewhat more specialized species, where the lateral lobes are defined, a break in the cuticle allows its pre-existing flexibility or bendability to play a role in the versatility of the males' courtship movements (Eberhard, 2001). The increased modularity of the sternite—now two pieces rather than one—contributes to its flexibility.

The ease with which muscle can be recruited to (or exaggerated at) new attachments, as exemplified in the two-legged goat described earlier, and in these flies, is impressive. But the mechanisms must be different in the flies, where individuals emerge from complete metamorphosis with their adult appendages fully formed and presumably unmodified by exercise. During their development, the walking legs of insects begin as rudiments that grow and then are folded and grooved where they will later become segmented (Chapman, '98, p 343)—a sequence that is not unlike that suggested by the appendage-like lobes of sepsid flies, where the simpler arrangement is a bendable groove or notch, and the more specialized form an articulated structure. It would be of interest to know whether pupal movements play any role in the development of adult insect muscle and cuticular morphology.

Could locomotory appendages like legs or wings have started by a process something like that observed in the diversification of sepsid courtship devices? And if they did, at what point during appendage evolution might the major genes associated with such structures have been co-opted for their development? At what point would you expect to have the newly independent modular parts associated with their own imaginal disks? Such questions cannot be answered, or even asked, in studies of the development of fully formed appendages like those of *Drosophila*. But Julia Bowsher, a graduate student at Duke, is beginning to answer them using sepsid flies. In a study on the developmental genetics of the sternal lobe of *Themira biloba*, a species whose males have an intermediate degree of specialization, possessing a semi-articulated sternal lobe but not a segmented articulated appendage, Bowsher has discovered that at least three genes—engrailed, extradenticle, and notch—which are expressed during the development of the lobes are also expressed during genital appendage development in *Drosophila*. These genes have evidently been co-opted in the development of the novel lobes. In *T. biloba*, the expression of these genes in the lobes occurs at the same time as their expression in the genitalic appendages, and well after sternite patterning, further supporting the interpretation that ancestral appendage genes have been co-opted for expression of a new appendage-like trait. The lobes of this species develop from a cluster of abdominal histoblasts, not from genital imaginal discs, or from any imaginal disc of their own, though the nests of histoblasts are imaginal-disc-like in being set aside during early development, and then proliferating and differentiating to form a specific distinctive structure.

Developmental plasticity and novel morphology under sexual selection

Sexual selection is noted for its ability to produce extreme morphological novelties (Darwin, 1871 [1874]). We often assume that natural selection—survival selection—is responsible for novelty, but we may need to look more closely at how novel structures are used. It is quite possible that limbs, especially appendages like wings in insects and tetrapods, were originally used in displays that evolved under sexual selection, even though they are now associated with survival selection due to their obvious importance in flight.

Developmental plasticity under sexual selection may have affected the diversity of the mouths of African-lake cichlids, contributing to their rapid and extreme radiations in African Lakes Victoria and Malawi (e.g., Greenwood, '64). The cichlid radiations are a story of diversification in teeth, jaws and mouths, so it easy to assume that these aspects of the radiation are entirely explained as trophic innovations. But male cichlids also fight and court using their mouths (Baerends and Baerends-van Roon, '50). They employ behaviors that require extreme development of the muscles that are also used in feeding, and they have been described as trembling like straining acrobats when they opened their mouths wide in nuptial and aggressive threat displays (Baerends and Baerends-van Roon, '50). Such extreme behavior could not help but have affected the form of their flexible and muscles and bones, and would favor the genetic variants best able to respond. Novel social inputs, as well as novel inputs from the non-social environment, could lead to novel or exaggerated behavioral responses and their morphological accommodation.

DISCUSSION AND CONCLUSIONS

One possible objection to the arguments made here is that the traits formed by phenotypic accommodation and novel combinations of ancestral traits are not truly new. Is all of evolution just shifting and accommodating the pieces? If rigidly circumscribed modularity of structures were the rule then the moving-the-pieces objection might hold. But, as shown by the examples described here, when phenotypic accommodation involves the re-use of old pieces in new places, as seen in the co-option of muscles and the remodeling of bone in the two-legged goat, and of ancestral genes in the novel appendages of sepsid flies, the new morphologies are substantially changed in shape and dimensions as well as in the way they are put together. Even mutational genomic change often involves reorganization, duplication and recombination of parts (examples and references in West-Eberhard, 2003), and yet we do not hesitate to call mutations true genetic novelties. As with the concept of homology, the problem is not simple (for discussion of homology relating especially to the nature of innovation, see Müller, 2003; Hall, 2003; West-Eberhard, 2003).

By the broad definition of innovation discussed near the beginning of this article, phenotypic accommodation, including behavioral accommodation and even learning, can be an important source of morphological novelty because it permits immediate reorganization of phenotypes responsive to novel inputs from environment and genome. Although the components of a reorganized phenotype are not themselves new, the combination that makes it distinctive compared to recent ancestors is new, and the components are newly subject to selection in a new context. There is, therefore, some justification for considering novelties due to phenotypic accommodation, once they have been subjected to selection and genetic accommodation, to be true evolutionary innovations.

All novel traits, including macroevolutionary ones, have to be explained in terms of the developmental generation of variation and ultimately in the context of selection within populations, beginning with individuals and species that lack the novel trait. A plausible transition hypothesis, showing how the ancestral phenotype was transformed to produce a novel form, is an important though neglected part of evolutionary biology.

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LITERATURE CITED

Avital E. Jablonka E. 2000. Animal traditions: behavioural inheritance in evolution. Cambridge, UK: Cambridge University Press.

Baerends GP, Baerends-van Roon JM. 1950. An introduction to the study of the ethology of cichlid fishes. Behav Suppl 1:1–243.

Baldwin JM. 1896. A new factor in evolution. Am Nat 30:441–451, 536–553.

Baldwin JM. 1902. Development and evolution. New York: Macmillan.

Bernays EA. 1986. Diet-induced head allometry among foliage—chewing insects and its importance for graminivores. Science 231:495–497.

Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv Gen 13:115–155.

Bramble DM, Lieberman DE. 2004. Endurance running and the evolution of *Homo*. Nature 432:345–352.

Chapman RF. 1998. The insects. Cambridge, MA: Cambridge University Press.

Darwin C. 1871 [1874]. The descent of man and selection in relation to sex, 2nd edn. [unabridged but re-numbered text, and figures]. New York: The Modern Library, Random House.

Eberhard WG. 2001. Multiple origins of a major novelty: moveable abdominal lobes in male sepsid flies (Diptera: Sepsidae), and the question of developmental constraints. Evol Dev 3:206–222.

Falconer DS, Mackay TRC. 1996. Introduction to quantitative genetics, 4th edn. Essex: Longman.

Frazzetta TH. 1975. Complex adaptations in evolving populations. Sunderland, MA: Sinauer.

Galis F. 1993. Interactions between the pharyngeal jaw apparatus, feeding behaviour, and ontogeny in the cichlid fish, *Haplochromis piceatus*: a study of morphological constraints in evolutionary ecology. J Exp Zool 267: 137–154.

Galis F, Terlouw A, Osse JWM. 1994. The relation between morphology and behaviour during ontogenetic and evolutionary changes. J Fish Biol 45(Suppl. A):13–26.

Gerhart J, Kirschner M. 1997. Cells, embryos, and evolution: toward a cellular and developmental understanding of phenotypic variation and evolutionary adaptability. Malden, MA: Blackwell.

Goldschmidt R. 1940 [1982]. The material basis of evolution. New Haven: Yale University Press.

Grant BR, Grant PR. 1989. Evolutionary dynamics of a natural population. Chicago: University of Chicago Press.

Greenwood PH. 1964. Explosive speciation in African lakes. Proc R Inst 40:256–269.

Greenwood PH. 1965. Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi*, and their taxonomic implications. Proc Linn Soc Lond 176:1–10.

Hall BK. 2003. Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. Biol Rev 78:409–433.

Hirasaki E, Ogihara N, Hamada Y, Kumakura H, Nakatsukasa M. 2004. Do highly trained monkeys walk like humans? A kinematic study of bipedal locomotion in bipedally trained Japanese Macaques. J Hum Evol 46:739–750.

Holekamp KE, Smale L. 1998. Behavioral development in the spotted hyena. BioScience 48:997–1005.

Hoogerhoud RJC. 1986. Ecological morphology of some cichlid fishes. Thesis, Leiden: University of Leiden.

Kirschner MW. 1992. Evolution of the cell. In: Grant PR, Horn HS, editors. Molds, molecules and metazoa: growing points in evolutionary biology. Princeton: Princeton University Press.

Lewontin RC. 1974. The genetic basis of evolutionary change. New York: Columbia University Press.

Liem KF, Kaufman LS. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. In: Echelle AA, Kornfield I, editors. Evolution of fish species flocks. Orono: University of Maine at Orono Press. p 203–215.

Liem KF, Osse JWM. 1975. Biological versatility, evolution, and food resource exploitation in African cichlid fishes. Am Zool 15:427–454.

Maynard Smith J. 1989. Evolutionary genetics. New York: Oxford University Press.

Mayr E. 1959. The emergence of evolutionary novelties. In: Tax S, editor. Evolution after Darwin, Volume One. Chicago: University of Chicago Press. p 349–380.

Meyer A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution 41:1357–1369.

Meyer A. 1990. Ecological and evolutionary consequences of the trophic polymorphism in *Cichlasoma citrinellum* (Pisces: Cichlidae). Biol J Linn Soc 39:279–299.

Müller GB. 1990. Developmental mechanisms at the origin of morphological novelty: a side-effect hypothesis. In: Nitecki MH, editor. Evolutionary innovations. Chicago: University of Chicago Press. p 99–132.

Müller GB. 2003. Homology: the evolution of morphological organization. In: Müller GB, Newman SA, editors. Origination of organismal form: beyond the gene in developmental and evolutionary biology. Cambridge, MA: MIT Press. p 51–69.

Müller GB, Wagner GP. 1991. Novelty in evolution: restructuring the concept. Ann Rev Ecol Syst 22:229–256.

Price T. 1987. Diet variation in a population of Darwin's finches. Ecology 68:1015–1028.

Schlichting CD. 1986. The evolution of phenotypic plasticity in plants. Ann Rev Ecol Syst 17:667–693.

Schmalhausen II. 1949 [1986]. Factors of evolution. Chicago: University of Chicago Press.

Slijper EJ. 1942a. Biologic-anatomical investigations on the bipedal gait and upright posture in mammals, with special reference to a little goat, born without forelegs. I. Proc Konink Ned Akad Wet 45:288–295.

Slijper EJ. 1942b. Biologic-anatomical investigations on the bipedal gait and upright posture in mammals, with special reference to a little goat, born without forelegs II. Proc Konink Ned Akad Wet 45:407–415.

Strathmann RR, Fenaux L, Strathmann MF. 1992. Heterochronic developmental plasticity in larval sea urchins and its implications for evolution of non-feeding larvae. Evolution 46:972–986.

Sultan S. 1987. Evolutionary implications of phenotypic plasticity in plants. Evol Biol 20:127–178.

Sultan S. 2000. Phenotypic plasticity for plant development, function and life history. Trends Plant Sci 5:537–542.

Waddington CH. 1953. Genetic assimilation of an acquired character. Evolution 7:118–126.

Wagner GP, Chiu C-h. 2003. Genetic and epigenetic factors in the origin of the tetraped limb. In: Müller GB, Newman SA, editors. Origination of organismal form: beyond the gene in developmental and evolutionary biology. Cambridge, MA: MIT Press. p 265–285.

Wake DB, Roth G. 1989. The linkage between ontogeny and phylogeny in the evolution of complex systems. In: Wake DB, Roth G, editors. Organismal functions: integration and evolution in vertebrates. New York: Wiley. p 361–377.

West-Eberhard MJ. 1992. Behavior and evolution. In: Grant PR, Horn H, editors. Molds, molecules and metazoa: growing points in evolutionary biology. Princeton: Princeton University Press. p 57–75.

West-Eberhard MJ. 1998. Evolution in the light of developmental and cell biology, and vice versa. Proc Nat Acad Sci USA 95:8417–8419.

West-Eberhard MJ. 2003. Developmental plasticity and evolution. New York: Oxford University Press.

West-Eberhard MJ. 2005. Developmental plasticity and the origin of species differences. Proc Natl Acad Sci USA 102(Suppl. 1):6543–6549.

Wimberger PH. 1991. Plasticity of jaw and skull morphology in the neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. Evolution 45:1545–1563.

Wimberger PH. 1992. Plasticity of fish body shape. The effects of diet, development, family and age in two species of *Geophagus* (Pisces: Cichlidae). Biol J Linn Soc 45: 197–218.

Wimberger PH. 1994. Trophic polymorphisms, plasticity, and speciation in vertebrates. In: Stouder DJ, Fresh KL, Feller RJ, editors. Theory and application of fish feeding ecology. Columbia: University of South Carolina Press. p 19–43.