Homoplasy: From Detecting Pattern to Determining Process and Mechanism of Evolution

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Science **331**, 1032 (2011);
DOI: 10.1126/science.1188545

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.

CORRECTED 1 APRIL 2011; SEE LAST PAGE

Homoplasy: From Detecting Pattern to Determining Process and Mechanism of Evolution

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Understanding the diversification of phenotypes through time—"descent with modification"—has been the focus of evolutionary biology for 150 years. If, contrary to expectations, similarity evolves in unrelated taxa, researchers are guided to uncover the genetic and developmental mechanisms responsible. Similar phenotypes may be retained from common ancestry (homology), but a phylogenetic context may instead reveal that they are independently derived, due to convergence or parallel evolution, or less likely, that they experienced reversal. Such examples of homoplasy present opportunities to discover the foundations of morphological traits. A common underlying mechanism may exist, and components may have been redeployed in a way that produces the "same" phenotype. New, robust phylogenetic hypotheses and molecular, genomic, and developmental techniques enable integrated exploration of the mechanisms by which similarity arises.

Phenotypes and taxa are expected to diverge as evolution proceeds. Thus, when divergent lineages are found to be morphologically similar, explanation is needed. Homoplasy is similarity that is the result not of simple ancestry, but of either reversal to an ancestral trait in a lineage or of independent evolution (convergence, similarity resulting from different developmental genetic mechanisms; or parallelism, similarity resulting from the same developmental genetic mechanisms) (Fig. 1). For example, body elongation in salamanders usually occurs in parallel in different taxa by addition of vertebrae, but increased body length may result from elongation of individual vertebrae, an instance of convergence (Fig. 1B). Independent evolution can result from common adaptive responses to selection pressures, such as changes in phenotype associated with a particular life strategy [e.g., a loss of structural anatomy in aquatic plants; the reduction of leaf blade surface in desert plants; evolution of expanded toe tips (scansors), specialized for clinging in lizards]. An alternative is a more organismal mode of evolution, dependent on developmental and genetic mechanisms that are deeply embedded in the evolutionary history of the lineage and are components of integrated organismal systems (*1*, *2*). To explore this evolutionary mode—the focus of this essay—hierarchical perspectives are essential (*3*). Complex morphological features of organisms are self-regulating from developmental genetic and historical perspectives. Because morphological space is limited by constraints, not all possible morphologies for a particular organism are realized or expressed. This inherent limitation on form increases the likelihood of homoplasy (*4*).

Phylogenetic analysis is necessary to show that derived similarity is not the simple result of common ancestry of taxa being compared. Usually homoplastic features are consequences of convergence or parallelism (Fig. 1, B and C). Structures that appear to have been lost may reappear, but such instances are uncommon (Fig. 1A). Study of the underlying developmental genetic mechanisms may reveal whether the recurrent structure has evolved via a novel mechanism or whether the ancestral mechanism has been deployed repeatedly. Thus, the study of homoplasy requires the integration of genetic, developmental, and phylogenetic resources and perspectives. However, one does not seek homoplasy—it "finds" the researcher and compels one to ask appropriate questions.

How Is Homoplasy Recognized?

Homology is what is perceived as the same trait in different taxa and is a true representation of inheritance and phylogeny at the organismal level (e.g., it is the perceived phenotype, not the processes responsible for generating it). Homoplasy is the diametric opposite of homology (*5*)—underlying similarity that does not result from inheritance at the hierarchical level (e.g., gene, tissue, organ; developmental pattern) being considered (*6*, *7*). Homoplasy is recognized by discordance with other characters in a phylogenetic analysis (Fig. 2). Molecular sequence data have greatly increased our ability to identify homoplastic traits. The various classes of homoplasy (convergence, parallelism, reversals) are not necessarily mutually exclusive (*8*, *9*) and can be difficult to discriminate (*10*). Whereas parallelism and convergence run along a continuum (*11*, *12*), convergence typically occurs over relatively greater phylogenetic distances. This distinction is important in interpreting the genetics of adaptation (*13*); convergence generally results from different genetic mechanisms, while parallelism typically arises from similar genetic causes, providing a heuristic context. Once identified, processes that generate the homoplastic traits become the targets of research.

A New Emphasis on Processes, Mechanisms, and Levels

Although homoplasy historically posed problems for phylogeneticists, it has defined fundamentally interesting questions for modern developmental genetics and evolutionary biology. Using developmental genetic approaches in comparative and hierarchical contexts is essential for identifying and defining processes responsible for similar phenotypes in diverse taxa. Mechanisms responsible for generating phenotypic similarity are found at different organizational levels—the phenotypic or whole organismal, developmental, epigenetic, and genetic levels.

The integration of genetics, signaling patterns and regulation, developmental pathways, and phylogenetics is in its infancy, but promises to open the "black box" of phenotype evolution. By comparing genetic regulatory networks (GRNs), and conducting experiments to alter them, the causal basis of development and evolution is illuminated, and evolutionary pathways that lead to fundamental changes in morphology can potentially be reproduced [synthetic experimental evolution (*14*)]. Although experiments may reproduce ancestral phenotypes, alternative developmental pathways may exist. Exploring the potential range of phenotypes [evolvable states (*15*)] to reveal genetic mechanisms involved with macroevolutionary processes is likely to be fruitful.

Adaptively Driven Homoplasy

Adaptively driven homoplasy may result from similar selective pressure, as in the evolution of reduced body armor and pelvic appendage structures (antipredatory adaptations) in stickleback fishes that occurred repeatedly in populations that invaded freshwater lakes, which are characterized by reduced numbers of predators (*16*, *17*). Pelvic loss results when regulatory mutations occur that cause deletion of a tissue-specific enhancer associated with the *Pituitary homeobox transcription factor 1* (*Pitx1*) gene (*18*). Selection for a reduction in lateral body armor plates involves mutations of the *Ectodysplasin* (*Eda*) locus (*19*). These findings show that major phenotypic changes can be associated with regulatory changes in developmental genetic programs (*20*).

Homoplasy of individual genes is exemplified by convergent adaptive pigmentation in diverse vertebrates due to evolution of gene function (*21*, *22*). The same mutation in the *Melanocortin I receptor* gene (*Mc1r*) was found in light-colored beach mice, as well as a 43,000-year-old mammoth from Siberia. In contrast, different mutations

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in the same gene sometimes explain convergent phenotypes. For example, different mutations in *Mc1r* are responsible for blanched phenotypes of two species of lizards (only distantly related to each other) from the White Sands of New Mexico (*22*), and different mutations in *Agouti* are responsible for independently evolved light coloration in Nebraska Sand Hill and Florida Coast populations of *Peromyscus* (*maniculatus* and *polionotus*, respectively). Finally different genes entirely can be responsible for convergent phenotypes, as is likely the case for independently evolved light coloration of Gulf and Atlantic Coast populations of *P. polionotus*. These examples document that phenotypic convergence involves fine- to coarse-grained genetic changes.

Adaptively driven petal forms in flowers exemplify a complex hierarchical evolutionary history. The perianth (i.e., sterile structures surrounding reproductive parts of the flower), a defining derived feature for flowering plants, usually comprises both outer (sepals) and inner (petals) organs. Petals may have evolved independently at least six times (*23*), arising as modified stamens or bracts through changes in expression patterns of specific homeotic genes (*24*). Petals themselves vary greatly in size, color, shape, orientation, and function, and have been lost repeatedly. However, all petals appear to follow a similar genetic program that involves the expression of a set of organ identity genes that control the development of the floral meristem at a specific place (external to the stamens) and time (following stamen initiation) (*25*). Intriguing questions arise when we consider the homoplastic deployment of a similar genetic regulatory pathway in a similar spatial context to generate second whorl petals, and in a different spatial context to create novel structures (e.g., petaloid stamens in Zingiberales, petaloid bracts in dogwoods). Although their multiple origins make petals homoplasious, the similarity of the underlying mechanisms for petal organogenesis is an example of deep homology (see below).

Hierarchically Determined Homoplasy

Hierarchically determined homoplasy is derived from the conserved internal organization of organisms. Homoplasy at the genome level occurs as an indirect effect, through upward causation. Salamanders have the largest genomes among terrestrial vertebrates (*26*), resulting from balanced growth among chromosomes from transposons and retrotransposons. Genome size is positively correlated with cell size. Because of constraints on organismal size (terrestrial salamanders rarely exceed 15 cm; most taxa are much smaller), there are corresponding constraints on cell number per organ, affecting oganismal form. Cell size is negatively associated with cell cycle, so the larger the cell the slower it divides. Small animals have fewer and more slowly dividing cells. Slowing cell division, reducing the numbers of limb blastema cells (cells that differentiate into the various tissues that compose the limb), can decrease digit number in both frogs and salamanders (*27*) in phylogenetically determined patterns (innermost digit lost first in frogs, outermost in salamanders). Thus, increased genome size may retard ontogenetic trajectories and result in a simplification of morphological complexity (*28*). Such homoplasy in brain morphology has been documented in large-genomed salamanders, frogs, and caecilians (*28*).

Deep homology. Homoplastic traits that are found to share a "deeper" developmental genetic

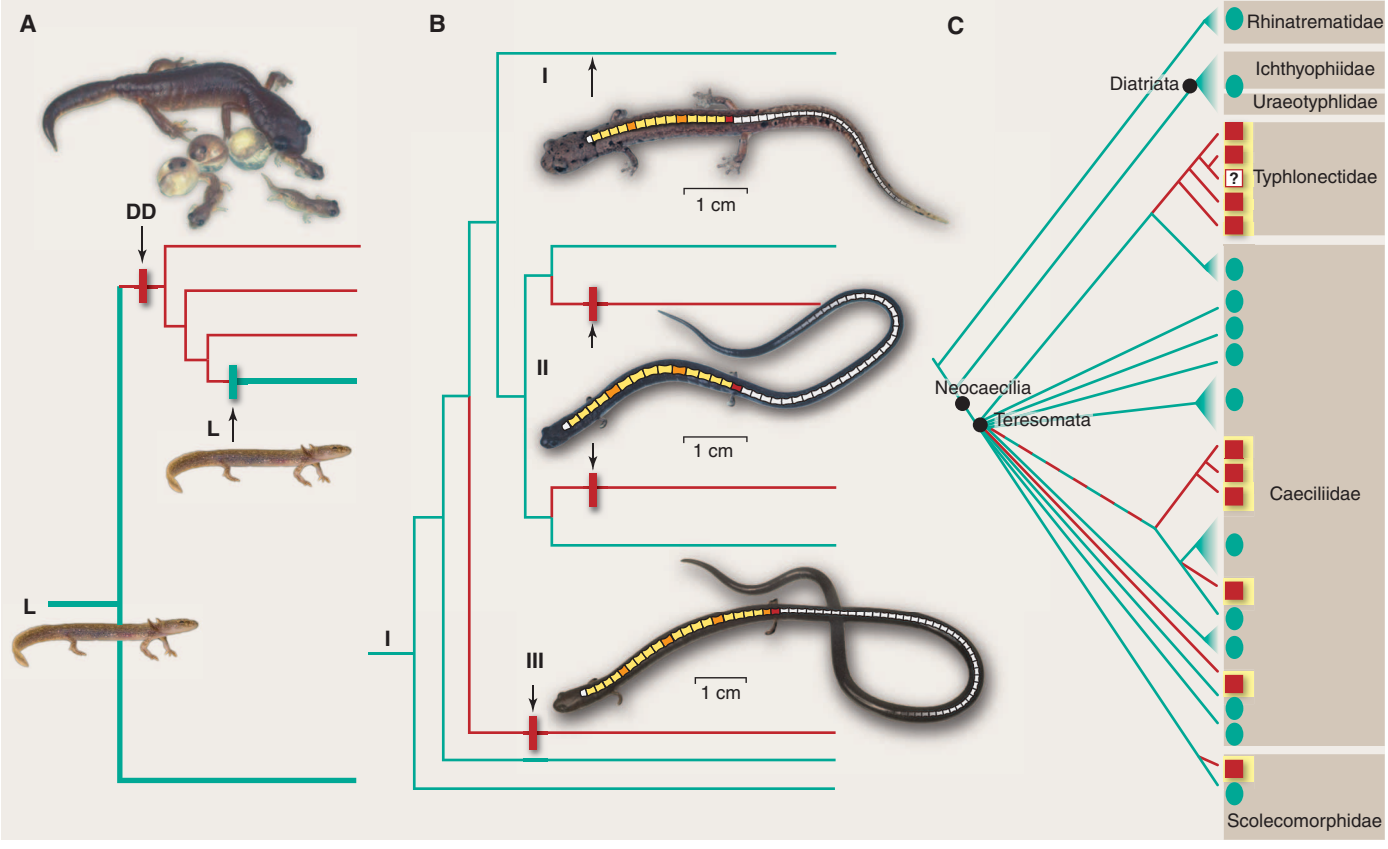

Fig. 1. Homoplasy in a phylogenetic context. (**A**) Example of a reversal in plethodontid salamanders where larvae (L) were lost and replaced by direct development (DD). Larvae re-evolved within the deeply nested genus *Desmognathus* (*47*). (**B**) Convergence and parallelism in two clades of plethodontid salamanders that show similar body elongation due to different pathways. The ancestral mode (I) has 14 trunk vertebrae (highlighted in yellow; every fifth vertebra shown in orange). One mode (which has evolved in two independent lineages) adds vertebrae (II); the alternative mode elongates individual vertebrae (III) (*48*). (**C**) The evolution of viviparity (live-bearing reproduction) in caecilians (Amphibia: Gymnophiona) shows parallelism in five different lineages (*49*, *50*). Red branches indicate lineages with viviparity; red squares indicate genera in which one or more species have evolved the trait; ? indicates unknown reproductive mode, assumed to be viviparous as are other members of the clade; blue branches and circles indicate oviparous (egg-laying) clades. Phylogram after Wilkinson and Nussbaum (*51*).

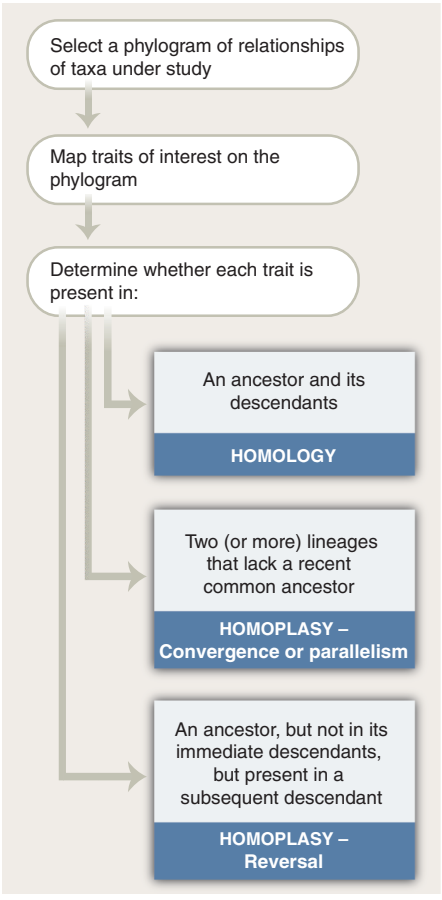

Fig. 2. Flow diagram of the process of detecting homoplasy.

mechanism are said to show deep homology. Common developmental genetic mechanisms have been shown to underlie features that long were considered classic examples of convergent evolution (*29*–*31*). The paired appendages of tetrapods (e.g., salamanders, lizards, mammals) and arthropods (e.g., flies, lobsters, spiders) evolved independently, but integration of phylogenetics, development, and genetics in a hierarchical context shows that homologous gene clusters sharing ancient common ancestry are responsible for the initial outgrowths from the body that become patterned along body axes (front to back, top to bottom, etc.) (*29*, *30*). Patterning in tetrapod appendages, despite considerable variation among taxa, is largely governed by relatively late expression of long-conserved homologous *Hox* genes during development. This also happens in fish fins; the same fundamental process might control even relatively terminal portions of the development of fins and limbs (*30*). Thus, while the morphological structures expressed in adults (e.g., legs of flies and legs of humans, or digits of salamanders and fin rays of zebrafish) are not homologous (because they were not present in a shared ancestor), homology may lie within the organization of *Hox* genes and their regulatory networks, although specific genes might have different expressions. This deep homology (*29*) breaks the ideological constraints associated with homoplasy (*5*) and reveals a continuum rather than a dichotomy (*11*, *12*) of convergence and parallelism at different levels within an organism and among diverse taxa within a clade.

The image-forming eyes of invertebrate and vertebrate taxa are convergent organs that share some core developmental genetic mechanisms that exemplify deep homology (*32*). All eyes, invertebrate and vertebrate, develop through a cascade (*32*) of similar transcription factors despite vast phylogenetic distances. These networks include genes (e.g., *Pax6*) that have been deployed in different ways at different times, and specific pathways that have re-evolved in different lineages by mutation, gene duplication, and intercalary evolution (*30*, *32*). The networks and cascades, which contain homologous genes and members of the same gene families, are not genetically identical. Thus, the end phenotypes might be general homologs at a deep hierarchical level but convergent with respect to end phenotype and phylogeny. Indeed, what has historically been termed "convergence" and attributed to independent evolution in unrelated taxa has a common genetic system associated with trait development (*30*). Comparing underlying mechanisms alone is insufficient if they are not integrated appropriately in developmental and phylogenetic hierarchies.

Metameric growth of plants (production of repeating units) requires the identification of homology in positional, developmental, and functional levels to detect homoplasy (*33*). The outer whorl (sepals) in some monocots (e.g., bananas, Zingiberales: Musaceae) appears identical to the second whorl (petals) (Fig. 3), yet in other monocots (e.g., gingers, Zingiberales: Zingiberaceae and Costaceae), sepals and petals are distinct (*24*), indicating that positioning in the outer whorl alone does not necessarily imply homology of development or function. Furthermore, petaloid staminodes (organs that resemble petals) replace the outer stamens in four of the eight families of the Zingiberales (Fig. 3) (*34*). Similar heterotopic (displacement from normal position) modifications of stamens and petals are found in other flowering plants such as members of the Ranunculales (*35*), which as basal eudicots are phylogenetically distant from the monocots. Deducing the lineage-specific genetic program underlying sepal, petal, stamen, and staminode identity among closely related taxa such as the Zingiberales, and more

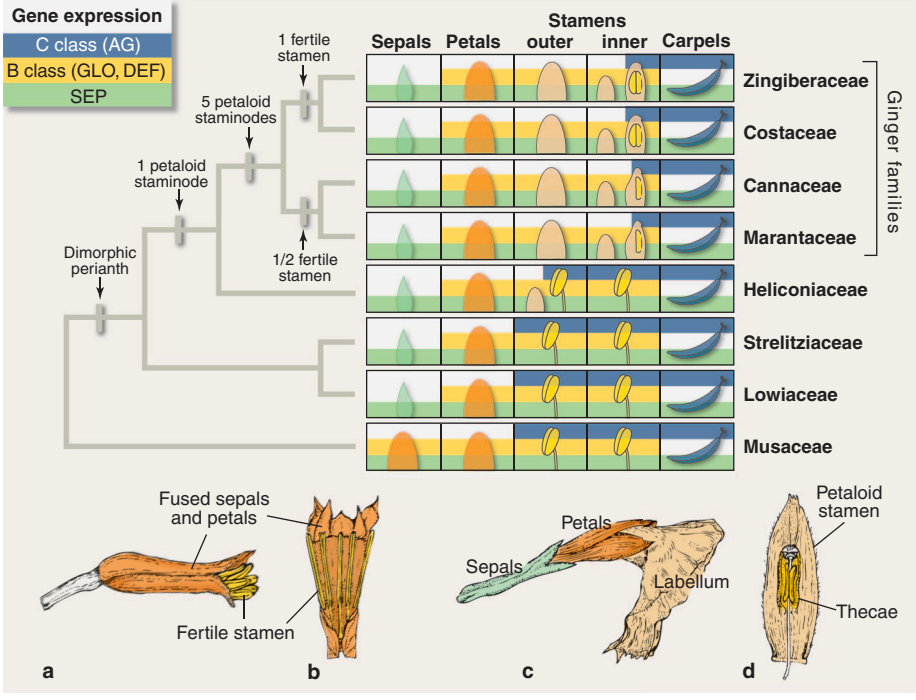

Fig. 3. A model for the developmental evolution of Zingiberales floral organs. The canonical ABC model (*52*) for floral organ identity in taxa outside *Arabidopsis* indicates that the *SEPALLATA* (*SEP*) genes alone are expressed in the sepal whorl (*30*), B-class genes [*GLOBOSA* (*GLO*) and *DEFICIENS* (*DEF*) homologs] code for petals, B- plus C-class genes [*AGAMOUS* (*AG*) homologs] code for stamens, and C-class alone (*AG*) codes for carpels. Expression of members of the *SEP* gene family is likely present in all whorls (*53*). The phylogeny of Zingiberales indicates important character transitions (*34*). For each family, the organs characteristic of each whorl are indicated: green, sepal; orange, petal; yellow, fertile stamen; blue, carpel. The petal-like sepals of *Musa* and petal-like stamens of the four ginger families are indicative of the potential of different genetic programs underlying the positional homoplasy (functional homology). For each family, the hypothesized pattern of B-class (yellow bar) and C-class (blue bar) gene expression for each whorl is indicated. (a and b) *Musa* (Musaceae) flower with petal-like organs in sepal and petal whorls and filamentous fertile stamens. (c and d) *Monocostus* (Costaceae) flower with distinct sepal and petal whorl organs, fused outer and inner petaloids forming the labellum, and (d) a single fertile petaloid stamen from the inner stamen whorl.

distant taxa comprising all angiosperms, requires both a phylogenetic framework to fully explain the mechanisms of organ homology and evolution (Fig. 3) and an understanding of the nature of gene regulation to determine at what level "the same thing" operates in disparate organisms displaying homoplastic parts. Thus, the distinction between convergent and parallel homoplasy (*5*, *10*, *30*, *31*, *36*) fades, to be replaced with new research opportunities.

When Phylogenies Do Not Resolve Phenotypic Trajectories

Although phylogenetic hypotheses are necessary, they are not always sufficient to resolve major questions involving parallelism and reversibility. Mesoevolution (*36*) connotes the problem of parallelism, a transitional condition between true homology (recent common ancestry) and true convergence (independent evolution of similarity), as well as between microevolution and macroevolution. Microevolutionary forces develop associations between regulatory genes of major effect, networks connected with them, and selection, leading to adaptation. Once these relationships are established, bias and constraint are established through homologous GRNs in response to similar environments. Co-option of this genetic system transitions microevolutionary processes governing parallelism (with its reliance on common mechanisms) to macroevolutionary convergence (independent evolution of the same trait). Convergent morphologies may arise from gene and genome duplications, followed by co-option of pathways or parts of pathways and shifts in timing and position of expression. The *CYC*/*TB1* subfamily of *TCP* genes controls floral symmetry across angiosperms; monosymmetric (zygomorphic) flowers have evolved homoplastically from radially symmetric ancestors several times, using the same toolkit of *CYC*-like genes (*37*). Copy number and expression patterns of the homologous genes, however, appear to vary in each lineage characterized to date, an example of mesoevolution.

Reversibility. Dollo's law—organ evolution is irreversible—has been challenged (*38*, *39*); however, examples of homoplastic reversion of organs to an ancestral state are not convincing (*40*, *41*). Although atavism (the sporadic appearance of ancestral traits) long has been invoked as evidence of evolution, such traits do not become fixed. Serially repeated structures (teeth, vertebrae, segments, numbers of phalanges, wings) have re-evolved in different positions within animal bodies, but the developmental genetic and morphogenetic underpinnings are likely to have been retained (*42*). In the case of re-evolved lizard digits, the embryonic condensations of lost digits might have remained and been redeployed, in which case an understanding of the recurrence might come from studying a developmental pathway rather than the expressed trait (*39*, *43*), assuming objections to the phylogenetic hypothesis can be overcome (*41*). Reversals, however, also include regaining the ancestral traits of conditions or states, not specifically organs (Fig. 1A), but the mechanistic bases for such trait reversals usually are not known.

In general, because relaxed selection leads to erosion of unused developmental genetic pathways involved in trait production, lost structures are unlikely to be re-evolved and evolutionary reversals, especially at the level of organs and complex features, are rare at best. The transition from blue to red flowers in *Ipomoea*, which results either from relaxed selection on the blue pathway (which leads to its degradation) or from stabilizing selection on the red pathway, is sufficiently complex that reappearance of the original condition does not occur (*44*). Similar irreversible losses have been observed for self-incompatibility (a postpollination mechanism that prevents self-fertilization) among angiosperms (*45*).

What Does the Future Hold for Understanding Homoplasy, and Thereby Evolution?

Similar environmental pressures are expected to elicit similar adaptive morphologies, suggesting that phenotypic homoplasy is often a consequence of natural selection. However, phenotypic similarity may result from homoplasy at different hierarchical levels [different mutations of the same gene, different genes, or different gene functions (*22*)], suggesting that genetic constraints limit the available variation upon which natural selection can act, thus influencing the course of evolutionary change (*5*, *6*). Convergent evolution may provide insight into both ultimate and proximate mechanisms generating diversity and can inform regarding the extent to which the evolutionary process is both repeatable and predictable (*5*). Sets of developmental genetic mechanisms are deployed repeatedly, under the control of genetic regulatory and epigenetic factors, and the effects can be large (*30*). Morphologically disparate taxa that are only remote relatives share toolkits of body-building and body-patterning genes (*31*). Bounded variation on such general morphogenetic themes can produce homoplastic traits, whose study can illuminate the underlying processes. Although some think that such processes have been overemphasized as evolutionary mechanisms (*46*), we envision great opportunity for understanding phenotypic evolution. It is in this context that study of homoplasy has its greatest promise. Exploration of homoplasy will illuminate the limits on phenotypic evolution, the nature and reasons for biases in its direction, and why "descent with modification" may follow predictable pathways.

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54. Supported by the U.S. National Science Foundation (EF 034939 to D.B.W. and M.H.W., IOS 0845641 and DEB 0816661 to C.D.S.) and the Hellman Faculty Fund (C.D.S.). We thank R. Mueller, P. O'Grady, and E. Rosenblum for comments; Y. Zeng, M. Koo, and T. Renner for assistance with Figs. 1 (A and B), 2, and 3 (A to D), respectively; and many colleagues and students for discussions of principles of evolutionary biology.

10.1126/science.1188545

ERRATUM

Post date 1 April 2011

Review: "Homoplasy: From detecting pattern to determining process and mechanism of evolution" by D. B. Wake *et al*. (25 February, p. 1032). In the legend to Fig. 1B, the third sentence should have read: "One mode (which has evolved in two independent lineages) elongates individual vertebrae (II); the alternative mode adds vertebrae (III) (*48*)." In the legend to Fig. 3, the fourth sentence should have read: "The phylogeny of Zingiberales indicates the relationships of the eight families with important character transitions (*34*)." The fifth sentence should have read: "For each family, the organs characteristic of each whorl are indicated: green, sepal; orange, petal; yellow, fertile stamen; light orange, petaloid stamen/staminode; blue, carpel." The ninth sentence should have read: "(c and d) Monocostus (Costaceae) flower with distinct sepal and petal whorl organs, fused outer and inner petaloid staminodes forming the labellum, and (d) a single fertile petaloid stamen from the inner stamen whorl."