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Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution

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ABSTRACT

Homology is at the foundation of comparative studies in biology at all levels from genes to phenotypes. Homology is similarity because of common descent and ancestry, homoplasy is similarity arrived at via independent evolution. However, given that there is but one tree of life, all organisms, and therefore all features of organisms, share some degree of relationship and similarity one to another. That sharing may be similarity or even identity of structure and the sharing of a most recent common ancestor – as in the homology of the arms of humans and apes – or it may reflect some (often small) degree of similarity, such as that between the wings of insects and the wings of birds, groups whose shared ancestor lies deep within the evolutionary history of the Metazoa. It may reflect sharing of entire developmental pathways, partial sharing, or divergent pathways. This review compares features classified as homologous with the classes of features normally grouped as homoplastic, the latter being convergence, parallelism, reversals, rudiments, vestiges, and atavisms. On the one hand, developmental mechanisms may be conserved, even when a complete structure does not form (rudiments, vestiges), or when a structure appears only in some individuals (atavisms). On the other hand, different developmental mechanisms can produce similar (homologous) features. Joint examination of nearness of relationship and degree of shared development reveals a continuum within an expanded category of homology, extending from homology → reversals → rudiments → vestiges → atavisms → parallelism, with convergence as the only class of homoplasy, an idea that turns out to be surprisingly old. This realignment provides a glimmer of a way to bridge phylogenetic and developmental approaches to homology and homoplasy, a bridge that should provide a key pillar for evolutionary developmental biology (evo-devo). It will not, and in a practical sense cannot, alter how homoplastic features are identified in phylogenetic analyses. But seeing rudiments, reversals, vestiges, atavisms and parallelism as closer to homology than to homoplasy should guide us toward searching for the common elements underlying the formation of the phenotype (what some have called the deep homology of genetic and/or cellular mechanisms), rather than discussing features in terms of shared or independent evolution.

Key words: atavisms, convergence, embryonic development, evolution, homology, homoplasy, parallelism, reversals, rudiments, vestiges, descent with modification.

CONTENTS

I will grant that someone might be able to generate an original thought concerning homology, but I doubt it. (Wake, 1999: p. 24)

I. INTRODUCTION

Homology is the hierarchical foundation of all biology. Consciously or unconsciously, we invoke homology whenever we compare two or more biological units, whether those units are genes, cells, tissues, organs, structures, behaviour or individuals (Hall, 1994*a*; Slikas, 1998; Bock & Cardew, 1999; Papini, 2002).

This review examines the relationships between homology and homoplasy, with respect to common or independent descent and to the mechanisms of embryonic development that underlie both homology and homoplasy. I conclude (see Table 1) that homology as applied to the features of organisms (i.e. to structures, behaviours, and modes of communication) represents the presence of that feature in the last common ancestor, whether the feature is based on shared or upon divergent developmental processes.

Common or independent descent is what Darwin called 'descent with modification', although that phrase is older than its use by Darwin. In an historical sketch added to later editions of *On the Origin*, Darwin noted that:

In 1846 the veteran geologist M. J. d'Omalius d'Halloy published in an excellent though short paper ('Bulletins de l' Acad. Roy Bruxelles,' tom. xiii. p. 581) his opinion that it is more probable that species have been produced by descent with modification than that they have been separately created: [noting that] the author first promulgated this opinion in 1831. (Darwin, 1910: p. xvii)

The origins of my analysis lie in an examination of whether homology and homoplasy represent a dichotomy (homology *versus* homoplasy, or homoplasy as non-homology, which is how they are almost universally regarded) or a continuum of biological processes. In a forthcoming paper I examine the three traditionally recognized classes of homoplasy – convergence, parallelism, and reversals/rudiments/vestiges/atavisms – in relation to whether they form using similar or divergent developmental pathways (Hall, 2002*d*). I conclude that parallel features are constructed using similar developmental pathways, convergent features using divergent or even different pathways, and reversals etc. using ancestral developmental pathways. Reversals, rudiments, vestiges and atavisms are often grouped as such to indicate a close relationship between them. However, this formulation can imply that they are synonyms, or represent a single class of homoplasy. As I argue in Section IV.3 in the present analysis, the four are different but related evolutionary and developmental processes.

It is not surprising that similar features persist over evolutionary time – homology as classically defined – especially when the developmental basis of that feature has been retained, this being a criterion taken by many as an essential element of homology (see Riedl, 1978; Hall, 1994*a*; and Bock & Cardew, 1999 for discussions on this and other aspects of homology). It is also not surprising that different environments or selective pressures can trigger the appearance or reappearance of similar features in organisms that do not share a most recent common ancestor – homoplasy as classically defined (Sanderson & Hufford, 1996). What is surprising is that parallelism on the one hand, and reversals, rudiments, vestiges and atavisms on the other, can produce homoplastic features using similar developmental processes (Reilly & Lauder, 1988; Hall, 2002*d*, and present review). Homoplasy as independent evolution conjures up a vision of different developmental processes, not similar ones. When I speak of developmental processes, I do not include the regulatory genes that initiate developmental processes. This distinction can be made clear using the example of *Pax-6*, the key regulatory gene for eye development in flies and vertebrates (Halder, Callaerts & Gehring, 1995; Pichaud, Treisman & Desplan, 2001). *Pax-6* activates divergent gene cascades and developmental processes in these representatives of two distant phyla to produce features

Table 1. *A summary of the continuum within the expanded category of homology of features*

*Homology**

The feature is present in the last common ancestor and developmental mechanisms are shared; equated by some with synapomorphy of feature and process; =syngeny or generative homology (Butler & Saidel, 2000).

*Homology**

The feature is present in the last common ancestor and developmental mechanisms have diverged; synapomorphy of the feature; =allogeny or generative homoplasy (Butler & Saidel, 2000).

Reversals

The feature is present in all the adults of a taxon, was present in more distant lineages/ancestors of that taxon but not in the most recent common ancestor: =phylogenetic character reversals (Stiassny, 1992).

Rudiments

The feature is an embryonic primordium of a more fully developed feature (a homologue) found in an ancestor and/or in a related taxon, as evidenced by some element of phylogenetic continuity of the feature and shared developmental mechanisms with ancestral or related taxa. Rudiments may be non-functional, have a different function from the embryonic primordium in those taxa in which the feature develops fully, or may serve a developmental role related to the formation of other embryonic primordia. Particular stages in the development of a rudiment would be homologues (at the level of developmental process or stage) of the equivalent process or stage in taxa in which the structure forms fully.

Vestiges

The feature is an adult remnant of a feature (a homologue) that is more fully formed in an ancestor and/or in a related taxon. Evidence of a vestige is some element of phylogenetic continuity of the feature and shared developmental mechanisms with ancestral or related taxa that have the fully formed feature. Vestiges either are non-functional or may have a different function from the fully formed ancestral feature. If fully developed, the adult feature would be classified as a homologue.

Atavisms

A feature that was present in more distant lineages/ancestors and which appears in low frequency in individual members of a population, usually only in one or a few individuals; =taxic atavisms (Stiassny, 1992).

Parallelism

A feature present in related lineages but not in their most recent common ancestor (otherwise homology), as similar genetic and developmental mechanisms in different lineages respond to influences (external or mutational) by producing similar features.

* No attempt is made to devise a new terminology for these two classes of homology; I leave that to braver souls such as Haas & Simpson (1946). As classes of homology of features, both are covered by Lankester's term homogeny, a term that does not take developmental basis into account. The terms 'homologous and non-homologous precursors and processes' (Northcutt, 1990), and 'equivalent and non-equivalent developmental processes' (Hall, 1992; Section III.3), have been proposed for the similarity or divergence of the developmental processes underlying homology.

(eyes) that are not homologous (Hall, 1999). Homology of regulatory genes need imply neither homology of developmental processes, nor homology of the feature that forms, an old idea, that goes back at least to de Beer (1938). We have to envisage at least three levels of both homology and homoplasy when considering establishment of the phenotype: genes, developmental processes, and the feature itself.

Given that homoplastic characters can have an affiliation (shared developmental processes) with characters normally classified as homologous, one is led to ask whether we can find common ground between developmental and phylogenetic approaches to character evolution through a re-examination of the relationship(s) between homology and homoplasy. I think we can. As evidenced by atavisms, reversals, vestiges and rudiments, developmental mechanisms may be conserved even when the structure (complete or incomplete) does not form. Alternatively, different developmental mechanisms can produce similar structures in both closely (Section III.1) and distantly related (Section IV.2) organisms (i.e. in lineages that do, or do not, share a recent common ancestor). The basis may be selection that favours those mutations that reactivate or co-opt developmental processes present in ancestors, and/or developmental processes that are so canalized, modular, or constrained by stabilizing selection that, inevitably, old pathways resurface or persist unexpressed (atavisms and reversals). This notion is similar to Mayr (1960) who argued that the emergence of new structures reflects intensification of existing selection rather than a new selective regime. Such an analysis is consistent with the view elegantly characterized by Jacob (1977) as 'evolution by tinkering' and by Duboule & Wilkins (1998) as 'the evolution of bricolage,' and with the concept of what has been called the deep homology of shared genetic, biochemical, cellular and developmental mechanisms (McShea, 1996; Shubin *et al.*, 1997; Gerhart, 2000; Hall, 2002*d*; Section VI).

So, is the traditional view of homoplasy as the antithesis of homology still appropriate? Would an analysis of the conservation or evolutionary divergence in developmental processes, coupled with an awareness of nearness of relationships, yield a different grouping of the four categories: homology; convergence; parallelism; and reversals, rudiments, vestiges and atavisms? What emerged after many months of grappling, was a continuum: an expanded category of homology, extending from homology → reversals → rudiments → vestiges → atavisms → parallelism, with convergence as the only class of homoplasy. What I thought was an entirely novel synthesis, turns out to be very close to the position initially set forth by E. Ray Lankester 130 years ago (Lankester, 1870*a*, *b*). Nothing is new under the sun. In reaching these conclusions, I review: homology, analogy and homoplasy as classically defined (including the role played by Lankester); the relationship between homology and homoplasy and developmental mechanisms; classes of homoplasy, including convergence, parallelism, reversals, rudiments, atavisms, and vestiges; and finally realign the classes of homology and homoplasy as outlined above. [After this manuscript was submitted, Gould's *The Structure of Evolutionary Theory* was published (Gould, 2002). It includes an analysis of homology and homoplasy back to Lankester and makes, in a remarkable case of convergence, many of the same points made herein, especially the separation of parallelism from convergence on the same basis as argued herein.]

II. HOMOLOGY, ANALOGY, AND HOMOPLASY

Although concepts of affinity and similarity and of essential and adaptive features, have a very long history in biology, this is not the place to retell that history, other than in the very broadest outline (see Bowler, 1984, 1996; Hall, 1994*a*, *b*; Ospovat, 1995; Bock & Cardew, 1999 for details).

The classification system (quinarianism) proposed by William Sharpe MacLeay in *Horæ Entomologicæ* (1819–1821) was based on a distinction between affinity ('A natural series of affinity is such as … shall be found uninterrupted by any thing known …') and analogy ('Relations of analogy consist in a correspondence between certain insulated parts of the organization of two animal which differ in their general structure' (MacLeay, 1819–1821: p. 363, cited from Ospovat, 1995: p. 104).

Cuvier from his studies on adults, and von Baer from his on embryos, regarded animals as fixed within major types, and saw no possibility of shared relationship (homology) between them. The transcendental morphology of Geoffroy allowed transformation between the four types of animals advocated by Cuvier. The 'Great Debate' between Geoffroy and Cuvier in the late 1820s and early '30s was all about homology, analogy and the very nature of how to study morphology (Appel, 1987; Hall, 1999). What MacLeay called a natural series of affinity and Geoffroy analogous structures, we would now call homology and homologous structures. The term *homology* (homologue) was first clearly defined by Richard Owen in 1843 as: 'Homologue … The same organ in different animals under every variation of form and function' (p. 379).

Although much has been written on homology in the past 159 years, views still differ and debates continue to rage. Indeed, no other fundamental concept in biology has generated as much discussion and so many definitions; 19 definitions (types of homology) are listed in the index to Hall, 1994*a* [see also Haas & Simpson (1946) and Fitch (2000)]. Leaving the rest of that history aside, homology may be defined as the continuous occurrence of the same feature (gene, structure or behaviour) in two organisms whose common ancestor also possessed the feature (Fig. 1). By this definition, many would equate homology with synapomorphy, i.e. a shared-derived character (Patterson, 1982). The two features need not be identical but must share sufficient 'similarity' to be recognizable as homologous. Determining similarity is not trivial, however, especially when pair-wise definitions must emerge from any analysis; see Haas & Simpson (1946), Riedl (1978), Gans (1985), Sanderson & Hufford (1996), D. B. Wake (1994, 1996, 1999), Hall (1994*a*, 1999) and Bock & Cardew (1999) for what is meant by similarity in these contexts.

With what do we contrast homology?

Following Richard Owen, who defined an analogue as 'a part or organ in one animal which has the same function as another part or organ in a different animal' (Owen, 1843: p. 374), features that are not homologous are classified as *analogous*, or *analogues* (see Rieppel, 1988, Hall, 1994*b*, and Panchen, 1999 for discussions; see Cohen, 1994, for the same use of homology and analogy in the social sciences).

Another way of comparing and classifying features among organisms is *homoplasy*, a term introduced in 1870 (Lankester, 1870*b*) by E. R. Lankester (1846–1929) to incorporate an evolutionary dimension into Owen's definition. Today, that evolutionary dimension is often equated with a direct correspondence with genes, although, as will be evident in the remainder of this review, both evolution and development reflect much more than the identification of those genes that underlie (but, which on their own, cannot produce) the characters of the phenotype (de Beer, 1938, 1971; Riedl, 1977, 1978; Hall, 1983, 1999, 2001*a*; Weiss, 1994/1995, 2002; Weiss & Fullerton, 2000; Robert, Hall & Olson, 2001).

Ray Lankester was one of the greatest zoologists of his era. We remember him for important studies on virtually every group of animals, as a pioneer of evolutionary morphology, for analyses of germ layers in relation to homology and classification, degeneration as an evolutionary force, and as a proponent of Haeckel's recapitulationist views; Lankester edited and revised the English translation of Haeckel's *History of Creation*

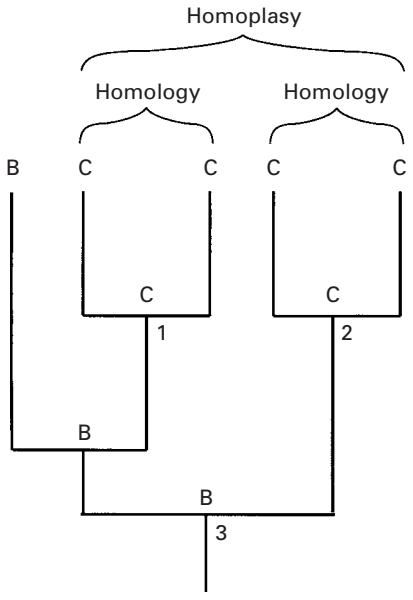

Fig. 1. A representation of homology and homoplasy of feature C, based on traditional definitions (see text). B defines the plesiomorphic state of the feature. Features C and C in lineage 1 are homologues as features because C is found in the closest common ancestor of the taxa with the feature C. C and C in lineage 2 are homologues as features because C is found in the closest common ancestor. However the features in the two lineages are homoplastic because the closest common ancestor (3) lacks feature C.

in 1876. A spellbinding teacher, it was said that Lankester:

> was the only man in London who could hold his lectures at one o'clock, the sacred luncheon-hour, and have them crowded. His lecture-room, and Balfour's at Cambridge, were the two foci from which the new views on morphology and evolution were spread throughout the academic world. (Bidder, 1929: p. 346)

Lankester's life was remembered in eight obituary notices, published in a single issue of *Nature*, all written by leading biologists such as E. S. Goodrich and Henry Fairfield Osborn (Obituary, 1929).

Lankester (1870*b*) dealt specifically with whether Owen's term analogy could be used for homoplasy; see Rieppel (1988), Hall (1994*b*) and Panchen (1999) for discussions. Lankester argued that analogy has a wider significance and could readily embrace features that were homologous or homoplastic:

> Any two organs having the same functions are analogous, whether closely resembling each other in their structure and relation to other parts or not; and it is well to retain the word in that wide sense. (Lankester, 1870*b*: p. 41)

As early as 1866, Ernst Haeckel had concluded that homologous features reflect common descent, a

conclusion that exerted significant influence on 19th century morphologists, many of whom became evolutionary morphologists (evolutionary embryologists) as a result (Nyhart, 1995; Bowler, 1996; Hall, 1999, 2000*a*). It was within this evolutionary tradition that Carl Gegenbaur (1870) defined homology as: '*das Verhältniss zwischen zwei Organen, die gleichen Abstammung besitzen, somit aus der gleichen Anlage hervorgegangen sind*' [the relationship between two organs that share common origin (ancestry) and therefore were derived from the same anlagen]. See Di Gregorio (1995) for Gegenbaur's approach to homology. Ray Lankester (1870*a*, *b*) put forth the same idea.

Neither Gegenbaur nor Lankester were concerned with finding the antithesis of homology. Both placed homology into an evolutionary framework because both were staunch Darwinians: 'in [the various] kinds of animals and plants [we see] simply the parts of one great genealogical tree, which have become detached and separated from one another in a thousand different degrees, through the operation of the great destroyer Time …' (Lankester, 1870*b*: p. 34). To use his own example, Lankester was concerned that although 'the majority of evolutionists' would agree that organs A and B were homologous in animals a and b because a common ancestor possessed the same organ, he saw that the term homology made no reference to evolutionary lineage, indeed it was typological, referring homologues to some ideal type. Consequently, Lankester (1870*b*: p. 36) thought it 'necessary to have two terms in place of the one "homologue"'. His criterion for establishing the two classes was the evolutionary history of the organisms concerned; he coined *homogeny* for similar features shared by two organisms as a consequence of common descent:

> Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called *homogenous*. We may trace an *homogeny* between them, and speak of one as the *homogen* of the other … details not traceable to, and inherited from the ancestor cannot be homogenous. (Lankester, 1870*b*: p. 36, his emphases)

His term *homoplasy* for the second class of similarity was introduced for what Lankester regarded as a single class of evolutionary phenomena. For Lankester, both homology and homoplasy referred to the consequences of the actions of identical or nearly similar forces or environments, in the one case, acting on two or more parts of an organism (what had been called from Owen on, serial homology), in the other acting on parts in two organisms, the parts being exactly or nearly alike:

> Homoplasy includes all cases of close resemblance of form which are not traceable to homogeny, all *details* of agreement not homogenous in structures which are broadly homogenous, as well as in structures having no genetic affinity [i.e. no connection through descent]. (Lankester, 1870*b*: p. 41)

Lankester made it very clear that homogeny and homoplasy were two classes of homology:

> What is put forward here is this, – that under the term 'homology', belonging to another philosophy, evolutionists have described and do describe two kinds of agreement – the one, now proposed to be called 'homogeny', depending simply on the inheritance of a common part, the other, proposed to be called 'homoplasy', depending on a common action of evoking causes or moulding environment on such homogenous parts, or on parts which for other reasons offer a likeness of material to begin with. (Lankester, 1870*b*: p. 42)

He summarized his approach in the article on Zoology in the 11th edition of the *Encyclopædia Britannica*:

> Owen's definition of analogous structures holds good at the present day. His homologous structures are now spoken of as 'homogenetic' structures, the idea of community of representation in an archetype giving place to community of derivation from a single representative structure present in a common ancestor … Darwinian morphology has further rendered necessary the introduction of the terms 'homoplasy' and 'homoplastic' to express that close agreement in *form* which may be attained in the course of evolutionary changes by organs or parts in two animals which have been subjected to similar moulding conditions of the environment, but have not close genetic community of origin [ancestry], to account for their similarity in form and structure, although they have a certain identity in primitive quality which is accountable for the agreement of their response to similar moulding conditions. (Lankester, 1911, vol. 28, p. 1029)

Lankester also introduced the term *homotrophic* for what Darwin (1910) grouped as 'correlations and compensation and economy of growth' (developmental physiology), which, for Lankester (1870*b*: p. 39) reflected the 'delicate balancing of the forces of the organism, which would cause the disturbance of equilibrium in one part to affect simultaneously another part equally and similarly. Organs which stand in this nutritional relation to one another may be termed homotrophic.' The term homotrophic has not survived, although the notion underlying it is recognized as important as reflected in pleiotropy in genetics, inductive interactions in development, and constraints in evolutionary developmental biology, or evo-devo as it has become known (Hall 1983, 1999, 2001*d*; Raff, 1996; Burian *et al.*, 2000; Hall, 2001*b*; Robert *et al.*, 2001; Hall & Olson, 2002).

Nor did the term homogeny take hold. Negative response to the new term was rapid. Lankester published his paper in *The Annals and Magazine of Natural History*.

In a paper in the very next (August) issue, St. George Mivart rebutted the new terminology and the notion that Darwin's theory of evolution necessarily refuted 'that view which represents all organic forms as having been created according to certain fixed types' (Mivart, 1870: p. 114). Mivart thought that abandoning the term homology would be 'prejudicial to science', arguing that 'it is quite possible to have, on the one hand, developmental homogeny between parts which are not ancestrally homogenous, and, on the other, to have ancestral homogeny between parts which are not developmentally homogenous' (p. 116). He proposed 25 different types of homology to support his arguments. Lankester (1870*a*) rebutted Mivart in the same issue, especially in relation to ancestral and developmental homogeny, both of which Lankester thought were tautologies. Mivart was a pragmatist. In *On The Genesis of Species* (1871), which he completed in December, 1870, Mivart cited Lankester's homogeny and homoplasy favourably, reducing his own classes of homology to three; serial, vertical and bilaterally symmetrical. *Genesis* contains many examples of parallelism, which Mivart used to argue that variation was predetermined (and therefore created) rather than random (and selected for).

Like many after him, Mivart held onto Owen's typological and pre-evolutionary conception of homology, although, see Camardi (2001) for an argument that Owen's use of special homology shows an evolutionary orientation. As noted by Boyden (1943) in a paper written to commemorate the 100th anniversary of Owen's formal definition of homology:

> new terms are not indicated here … Owen, defined the terms clearly and used them effectively. There should be no further need of discussion regarding the necessity of clarifying the meaning of the terms homology and analogy. It must be clear to everyone that we have abused them and that we must use them more effectively in the future, if comparative zoology is ever to acquire a sound basis. To remedy the situation Lankester (1870) proposed new terms (homogeny and homoplasy), but new terms are not indicated here … I challenge anyone to misunderstand Owen's essential meanings if only he reads his words. (Boyden, 1943: p. 232)

Olivier Rieppel thought that 'it would indeed appear advantageous to return to Lankaster's [*sic*] (1870) clear-cut terminology, were it not for the universal use, in modern biology, of the term "homology" in an evolutionary context' (Rieppel, 1988: p. 58). Had the term homogeny taken hold, it would have embellished the typological view of homology with the evolutionary gloss of similarity due to common descent. Variants of homogeny were proposed, especially in genetics – 'homogenic' for genes with single alleles (Fisher, 1928); 'homogenetic' for pairing in hybrids of chromosomes from one of the original ancestors (Waddington, 1939); 'homogenetic or normal morphogeny' [morphology], in contrast to 'convergent morphogeny' or 'mere convergence' (Willey, 1911); 'homogenesis' for the similarity of offspring to their parents (Mitchell, 1910) – but none remain in use. 'Homogeny' as biological similarity due to common descent, however, remains as an historical relic in the better dictionaries.

Homoplasy as the term for similarity resulting from evolutionary convergence, parallelism or reversal has endured (Sanderson & Hufford, 1996). While, as discussed above, Lankester saw homoplasy and homogeny as two classes of homology, homoplasy is now contrasted with homology (Fig. 1).

> Homology and homoplasy are terms that travel together; homoplasy being close to, but not quite, the inverse of homology. If homology is 'the same thing' … homoplasy is the *appearance* of 'sameness' that results from independent evolution. (D. B. Wake, 1996: p. xvii)

I want to explore the manner by which homoplasy can be considered, as David Wake put it, as 'not quite the inverse of homology'.

An additional complication is that the category 'homoplasy' or 'homoplastic' is not homogenous, including convergence, parallelisms, reversals, rudiments, vestiges and atavisms (Patterson, 1982, 1988; Wake, 1991; McShea, 1996; Sanderson & Hufford, 1996; Meyer, 1999; Hall, 2002*d*). Such a grouping gives the impression that these are equivalent processes, which they are not, neither with respect to developmental mechanisms, the presence of the feature in all members of a population/species, nor to independent or shared phylogenetic history.

III. HOMOLOGY AND DEVELOPMENTAL MECHANISMS

Homology is a statement about the continuous presence of the 'same' character in two or more taxa sharing a common ancestor. Although a character is any trait or feature of the phenotype, there are many definitions of 'character', and there has been even more discussion of characters and the character concept (M. H. Wake, 1996; Wagner, 2000; and see chapters in Wagner, 2001, and Hall & Olson, 2002).

Without going any further into the history of how developmental mechanisms relate to homology (for summaries, see Spemann, 1915; de Beer, 1938, 1971; Hall, 1994*a*, *b*; and Bock & Cardew, 1999), it is now recognized that homology must be approached hierarchically. Homology at one level, for example a

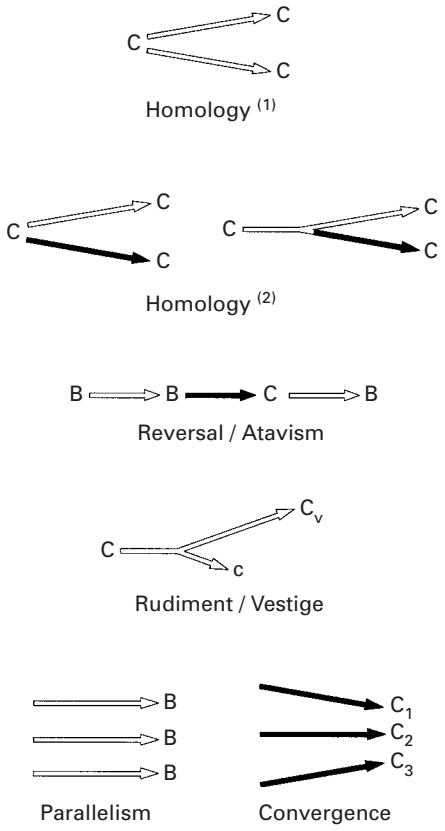

Fig. 2. Diagrammatic representations of the categories of similarity discussed in the text and summarized in Table 1. Unfilled arrows indicate shared developmental pathways. Black arrows indicate a divergent developmental pathway. Homology$^{(1)}$: C is homologous and arises through shared developmental processes. Homology$^{(2)}$: C is homologous and arises from divergent developmental pathways. The divergence may involve the entire developmental pathway (left), only later parts of the pathway (right), or only earlier parts of the pathway (not shown). Reversal/atavism: character B is a reversal (if in all members) or an atavism (if in one or few members) to the ancestral character B. Rudiment/vestige: C_v is a vestige (by definition found in adults) of the more fully formed ancestral character C; c is a rudiment (by definition, embryonic) of the fully formed ancestral character C and of the fully formed character C in the sister taxon. c is shown as utilizing only the early portions of the shared developmental programme. Parallelism: B is found in related lineages (but not in their shared ancestor), and arises through similar developmental processes. Convergence: C_1–C_3 are similar characters produced in distantly related lineages through divergent developmental processes.

feature such as a limb, need not correspond to homology at other levels; the developmental processes that produce the limb, or the genetic cascades underlying those processes. There are many examples of homologues arising via different developmental processes (Fig. 2). Two examples – tetrapod digits and the vertebrate lens – are discussed below. Other examples include: the primary and secondary neurulation that produces the anterior and posterior neural tube in vertebrates; formation of the neural crest by delamination or by cavitation; gastrulation via a blastodisk or a blastopore; formation of primordial germ cells by sequestration of a maternal germ plasm or by induction interaction between regions of the blastula. See de Beer (1938, 1971), Bolker (1992), Hall (1995*b*, 1998, 1999) and Minsuk & Keller (1996) for these and other examples. Gastrulation, neural crest and germ cell formation are especially interesting examples as they demonstrate that development may be modified very early in ontogeny, without affecting the morphology of the adult organ or organisms that forms (Hall, 1995*b*). Nevertheless, many expect homologues to arise using similar developmental processes: 'homology has come to signify an agreement in evolutionary derivation and in embryonic development' (Hubbs, 1944: p. 305; and see Moment, 1945, and Hall, 1995*b*, 1999), although Richard Owen did not:

> There exists doubtless a close general resemblance in the mode of development of homologous parts; but this is subject to modification, like the forms, proportions, functions and very substance of such parts, without their essential homological relationships being thereby obliterated. (Owen, 1848: p. 6)

See Wilson (1894) for a discussion of 'the embryological criterion of homology' in the latter half of the 19th century.

Charles Darwin equated homology of structure with homology of development, homology for Darwin being 'that relation between parts which results from their development from corresponding embryonic parts …' (Darwin, 1910: p. 409). So did many others during the latter half of the 19th century: 'The great argument for the homology of any two parts has been generally held to be the fact of their undergoing the same process of development' (Mivart, 1870: p. 116). Lankester was prompted to revisit homology, as much because of 'an appreciation of the value of developmental changes in indicating the similarities or distinctions of organs' (Lankester, 1870*b*: p. 35) as by his desire to separate homology from Owen's typology, a separation that began even before the publication of *The Origin of Species by means of Natural Selection.*

> … before the appearance of Mr. Darwin's theory many zoologists were turning to embryology as a surer guide than ideal archetypes in tracing the identities of structure in organisms; so that, refusing to commit themselves to the Platonic theory, they were ready to receive the flood of light and explanation which the doctrine of descent shed upon the meaning and nature of homologies. (Lankester, 1870*b*, p. 35)

I discuss digits in tetrapods and development/regeneration of the lens in amphibians as two examples illustrating the divergent developmental bases of homologous features (see Northcutt, 1990; Striedter & Northcutt, 1991; Hall, 1994*b*, 1995*b*, 1999; and Striedter, 1998 for further examples and discussion).

(1) Tetrapod digits

Because homology has traditionally not been viewed hierarchically, as homologous structures, tetrapod digits are expected to arise from and share the same developmental processes. Homology of the feature is expected to extend to (indeed, to be a consequence of) shared developmental processes. However, development evolves.

Homologues (defined at the level of the feature, in this case, tetrapod digits), can form using different developmental programmes (Hall, 1983, 1995*b*). In tetrapods other than urodele amphibians, digits separate from one other during embryonic development as the result of the onset of genetically programmed cell death (apoptosis), a process that removes cells between the digit primordia, leaving interdigital spaces. Such spaces may be complete, as in the human hand and chick foot, or incomplete, as in the webbed feet of ducks. In urodeles, however, differential growth of the digits themselves, rather than apoptosis of the interdigital connective tissue, separates digital primordia (Hinchliffe, 1982, 1994; Shubin *et al.*, 1997). While the mechanisms that separate digits during ontogeny differ, the digits are homologous as features. Although the relationship of urodeles to other amphibians is unresolved, the observation that only urodeles do not use apoptosis, implies that loss of interdigital apoptosis and the use of differential growth is the derived condition. Regarding digits of urodeles as not homologues of other tetrapod digits, leads to such suggestions as that urodeles should be excluded from the 'true' tetrapods, an exclusion which is hard to maintain, based, as it is, on a single (derived) character.

We see (or perhaps assume) that the developmental processes operating early in limb development are conserved across the tetrapods, although detailed information is not available for all these early processes in all groups, let alone in all species. Those early processes include: epithelial-mesenchymal interactions to produce condensations of prechondrogenic mesenchyme; initiation of cell differentiation within each condensation using similar genetic networks and cellular processes; and skeletal growth and morphogenesis by proliferation of chondroblasts and deposition of extracellular matrix (Goodwin & Trainor, 1983; Hinchliffe & Griffiths, 1983; Hall, 1983, 1995*b*, 1999, 2002*d*; Hall & Miyake, 2000). We regard these early processes as homologous; see Section III. 3 for the terminology of homologous developmental processes. It may be, however, that evolutionary changes have occurred in these early processes of digit development but have not been detected; after all, frog digits are not chick digits. The developmental mechanisms specifying a later developmental event – separation of the digits – clearly have evolved; apoptosis *versus* differential growth; see Fig. 2 for a diagrammatic representation under homology.[(2)] Although this late event is not based on homologous developmental processes, digits as features are homologous. Such patterns of conservation of early processes and modification of later ones, which Wagner & Misof (1993) refer to as 'generative processes' and 'maintaining interactions,' respectively, may be common in situations where multiple steps are required to produce a structure (Hall, 1983, 1995*b*, 1999). Even when comparing cascades of developmental processes between different taxa, we may find homology at one level but not at another.

Although von Baer's law of the conservation and generality of early development holds in many situations, processes that occur early in embryogenesis also can evolve. Situations in which one major developmental event, such as an embryonic induction, initiates the development of a feature, can (as in the epithelial–mesenchymal interaction that triggers the chondrogenesis of Meckel's cartilage; Hall, 1983, 2000*b*) or must (as in the induction of mesoderm or neural crest early in embryogenesis, or the formation of homologous skeletal elements by different mechanisms; Bellairs & Gans, 1983; de Sá & Swart, 1999; Hall, 1999) involve changes in early developmental processes. Indeed, there are many examples of modification of developmental processes or stages even earlier in embryogenesis. Alteration in the distribution of maternal cytoplasmic constituents in the egg occurs during oogenesis. Changes in patterns of cleavage or changes in cell lineages occur at the blastula stage. Changes in the mechanism of gastrulation can result in gastrulation from a blastodisk in frogs whose close relatives gastrulate through a blastopore. A direct-developing frog produces a secondary yolk sac from the body wall as otherwise occurs in amniote embryos (Del Pino & Elinson, 1983; Bolker, 1992, 1994; Wray, 1994; Hall, 1995*b*, 1998, 1999; Del Pino, 1996; Minsuk & Keller, 1996; Raff, 1996; Elinson & Fang, 1998).

(2) Lens development/regeneration

Induction of the lens by the optic cup during vertebrate embryonic development is the culmination of a series of interactions between different cell types. These

interactions are presumed to have been highly conserved; indeed, induction of the lens by the optic cup is one of two paradigmatic examples of embryonic induction, the other being primary embryonic induction. It therefore comes as a considerable surprise to find that in two species of frogs within the genus *Rana*, Linnaeus, 1768, *Rana fusca* and *R. esculenta*, two congeneric species of amphibians, *R. fusca* uses the optic cup to induce the lens, *R. esculenta* does not; see Jacobson & Sater (1988) and Hall (1999) for this and other examples of divergent developmental processes producing homologous features. On the assumption that earlier steps in lens induction are conserved in the two species of *Rana*, a truncation of the developmental process when compared with the ancestral condition could explain the difference between the two species. Such a truncation, which could be based in the induction interactions themselves, or in altered timing of eye development relative to general body growth, would be an example of the evolutionary process of heterochrony (Hall, 1983, 1999, 2001*c*, 2002*c*; McNamara, 1995; Zelditch, 2001). Unfortunately, the phylogenetic relationships of ranid frogs are unresolved, and without a robust phylogeny we are unable to pursue the evolutionary history of these developmental changes. This problem is not unique to ranid frogs.

Some vertebrates are able to regenerate the lens if it is removed by a predator, accident or removed surgically. When the lens in a Mexican axolotl *Ambystoma*, is removed, it regenerates from cells of the iris (Wolff, 1895). A lens also regenerates following removal of the lens from two species of frogs within the genus *Xenopus*, Wagler, 1827, *X. laevis* and *X. tropicalis*, but from cells of the cornea not the iris (Freeman, 1963; Tsonis, 2000; Henry & Elkins, 2001). Lens regeneration in both *Ambystoma* and in *X. laevis* (we do not know about *X. tropicalis*), involves dedifferentiation and redifferentiation of cells; this developmental process is conserved. But different cells with different developmental origins (iris cells from neural ectoderm and corneal cells from nonneural ectoderm) dedifferentiate in each genus. This step has evolved, providing an example of the evolutionary process of *heterotopy*, a change in the position where, or the cells or tissues from which the feature forms (Zelditch & Fink, 1996; Hall, 1999, 2001*c*, 2002*c*; Zelditch, 2001). Neither iris nor corneal cells, nor the process of dedifferentiation contribute to the development of the original lens. Thus the developmental mechanisms for lens formation and regeneration differ during the ontogeny of individual species and between species. Indeed, some amphibian species possess more than one mechanism for regenerating the lens (Spemann, 1915).

Clearly, different developmental mechanisms producing homologous features can and have evolved, without affecting homology of the feature (see Hall, 1983, 1995*b*, 1999 for further discussion and examples).

(3) Terminology of developmental processes in relation to homology

A number of recent workers have attempted to provide a terminology to reflect the fact that homologous features may arise from shared or divergent developmental processes and mechanisms, shared or divergent developmental processes representing one such terminology. For this approach to biological homology see Hall (1994*a*, 1995*b*, 1998, 1999) and Gilbert & Bolker (2001).The range of terms proposed includes: *homologous and non-homologous* precursors and processes (Northcutt, 1990; Striedter & Northcutt, 1991); *equivalent and non-equivalent* developmental processes (chapters 10 in Hall, 1992 and 21 in Hall, 1999; Miyake *et al.*, 1992; Hall, 1995*b*; Striedter, 1997); *epigenetic homologues*, to reflect the construction of developmental information during ontogeny (Striedter, 1998); and *syngeny* (generative homology) for characters produced by shared generative (developmental) pathways.

The production of homologous features through shared or divergent processes at genetic, cellular and tissue levels, demonstrates that developmental processes can evolve without affecting the feature produced (Fig. 2). Effectively, the genotype and phenotype can disassociate during the evolution of homologues and homoplastic characters, a process that has been called 'phenogenetic drift' or 'developmental system drift' (Budd, 1999; Weiss & Fullerton, 2000; True & Haag, 2001; Weiss, 2002).

IV. HOMOPLASY AND DEVELOPMENTAL MECHANISMS

As traditionally defined, homoplasy includes a diverse assembly of evolutionary processes which are united by the independent evolution of features (or the presumption of independent evolution), but which, I will argue, are neither united by independent evolutionary history, nor by different developmental mechanisms forming the feature in different taxa (Table 2). Consequently, homoplasy as a category is unsatisfactory, whether one thinks about homoplasy from a developmental or a phylogenetic point of view.

(1) Convergence

The appearance of similar features in independent lineages is *convergence* (see Tables 1 and 2, and Fig. 2).

Table 2. *Homology and homoplasy of features and their relationship to developmental pathways*

Class	Definition	Development
Homology		
	The same character continuously present in two taxa and in their most recent common ancestor (shared ancestry)	Shared or different developmental pathways
Homoplasy		
Convergence	Similarity arising through independent evolution	Different developmental pathways
Parallelism	A feature present in closely related organisms but not present continuously in all members of the lineage	Normally similar developmental pathways
Reversals, atavisms, vestiges and rudiments	A feature, either fully formed or incomplete, and similar to a fully formed feature seen in ancestors within the lineage or in a related taxon	Similar or different developmental pathways

'Independent lineages' is a subjective term. So are other phrases, such as 'lineages that are several outgroups removed from the sister taxon', or 'lineages that are polyphyletic'. The intent of such phrases is to indicate some measure of 'independent' evolution. Given the greater phyletic distances between convergent than other features, we might expect to find greater potential for the evolution of underlying developmental mechanisms and processes in convergence than in other categories. Convergent evolution of wings in insects and birds is a classic example (Shubin *et al.*, 1997). Except in situations where an 'ancestral' developmental mechanism or cascade of regulatory genes has reappeared – one example being convergent larval forms in the four classes of echinoderms (Gordon, 1929; Strathmann, 1988; Wray, 1992, 1996; Hall & Wake, 1999; Hickman, 1999; Kerr & Kim, 1999; Wray & Lowe, 2000) – we expect convergent features to be based on different developmental mechanisms. Convergent features, however, may share all or part of a deeper homology of regulatory genes and/or gene cascades (Duboule & Wilkins, 1998; Abouheif, 1999, McGhee, 2000, and see Conclusions). Although this sounds like a modern idea, it has a long history: 'it is clear that *characters controlled by identical genes are not necessarily homologous* [and that] *homologous characters need not be controlled by identical genes*' (de Beer, 1938: p. 66, his emphasis).

As early as 1838, Charles Darwin had realized the fact of convergence and the difficulties it would raise when separating affinity from analogy (Ospovat, 1995: pp. 111–112). As one example, the search for relationships among the invertebrate animals and for the origin of the vertebrates was bedeviled by the issue of whether segmentation was homologous or convergent across the animal kingdom (Bowler, 1996).

Perhaps the best accumulation and analysis of examples of convergence, and, to my knowledge, the only book devoted entirely to this class of homoplasy, is Arthur Willey's *Convergence in Evolution* (1911). Dedicated to Lankester, it was written to counteract William Gaskell's (1890, 1908) 'earthquake hypothesis' that vertebrates arose from within the crustaceans. [The term 'earthquake hypothesis' was contained in a letter from Thomas Henry Huxley to Gaskell, which Gaskell reproduced at the beginning of his book, *The Origin of Vertebrates*: 'Go on and prosper; there is nothing so useful in science as one of those earthquake hypotheses, which oblige one to face the possibility that the solidest-looking structures may collapse' (Huxley to Gaskell, dates, in Gaskell, 1908: p. i).] Virtually every evolutionary morphologist rejected Gaskell's theory. Among the categories discussed by Willey were mimicry and homoplasy, divergence and parallelism, and convergence at the tissue level (histogenetic convergence), all illustrated with a plethora of examples, as Willey combated what he described as 'more joy amongst morphologists over one attempt at genealogy than over ninety and nine demonstrations of convergence' (1911: p. 53); see Gregory (1951) for well over 100 examples of convergence, and see Bowler (1996) for Willey's views on parallelism and convergence. Willey proposed a 'system of convergence' to show:

> that homoplasy does not cover all the cases which are included under convergence in the wider acceptance of the term 'and that' *all homoplasy is convergence, but all convergence is not homoplasy*. (1911: pp. xii, 11; my emphasis)

(2) Parallelism

Parallelism describes the development of features in lineages that are more closely related (more recently diverged from their last common ancestor) than those that show convergence (Table 1, Fig. 2).

Parallelism reflects the appearance of similar features in related lineages but not present continuously since diverging from their most recent common ancestor. Were the feature present in the most recent common ancestor, the features would be classified as homologues, unless the feature had evolved, subsequently been lost and then re-evolved, in which case it would be classified as a reversal (Section IV. 3*a*).

G. G. Simpson defined parallelism as: 'the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channelled by, characteristics of that ancestry' (Simpson, 1961: p. 78). Simpson was ahead of his time in his consideration of parallelism and convergence, although a close reading reveals a conflation of processes and levels that is, at least in hindsight, unsatisfactory. In *The Meaning of Evolution*, first published in 1949, Simpson argued that there is no fundamental difference between parallelism and convergence. Parallelism was seen in groups of organisms that were already structurally and adaptively similar and which underwent independent changes in the same direction. Simpson thought, although we might now disagree, that this similarity was because 'mutations, like structures, are likely to be more nearly alike in closely than in distantly related animals' (1965: p. 183). Such a similarity would indeed provide an evolutionary mechanism separating parallelism from convergence. However, while the phenotypic effects of mutations may be similar in animals with similar genomes (and developmental pathways), mutation itself has no such basis.

Simpson believed that, 'especially among more nearly related groups, the convergence is likely to involve homologous structures, as is also true of parallelism', and acknowledged that in more distantly related organisms, 'such homologous structures are less likely to be present and convergence may affect organs developed completely independently in each group'. He saw (at least implicitly) that a hierarchical approach was required: 'the convergent wings of pterodactyls, birds, and bats arise from homologous forelimbs, although they do not arise in the same way' (Simpson, 1965: p. 183; see also the discussion in Kellogg & Shaffer, 1993 for the significance of this view for phylogenetics). An elegant recent example is the study by Wagner (2000) of the frequency of occurrence of morphological character states in 56 fossil taxa. Wagner found that, in over 85 % of the taxa, the character states were not added continuously, although the observed character states 'exhausted' the character states available [see also Hall (2002*e*) for a discussion of available morphospace], and discussed these findings in relation to homoplasy, constraint and available morphospace, i.e. hierarchically.

An example that illustrates nicely the relationship between parallelism and convergence, and which was teased out because of the authors' detailed knowledge of the phylogeny of the organisms and of the development of the character under analysis, is elongation of trunk vertebrae in salamanders within the tribe Bolitoglossini. Parra-Olea & Wake (2001) described patterns of trunk elongation based on elongation of existing vertebrae in species in the genus *Lineatriton*, Tanner, 1950, but on increase in the numbers of vertebrae in other genera (*Batrachoseps*, Bonaparte, 1841, and *Oedipina*, Keferstein, 1868). From their phylogenetic analysis they concluded that these patterns represented parallelism within the genus *Lineatriton* but convergence within the family Bolitoglossini, i.e. the distinction between parallelism and convergence need not be arbitrary and can be established given a sufficiently robust phylogenetic analysis. Gould (2002) refers to the distinction between 'parallelism as a positive deep constraint on homology on underlying generators … and convergence as the opposite sign …' (pp. 81–82) and of 'parallelism as a "gray zone" between homology and convergence' (p. 1088).

We expect similar, perhaps identical, developmental pathways to be used in the generation of parallel features; 'If they [character states] are parallelisms, then they should be developmentally and genetically the same' (Kellogg & Shaffer, 1993: p. 412). One example is the 'swords', the colourful, elongated, caudal fins in males of the fish *Xiphophorus*. A sexually selected character, swords evolved early in the history of the genus, and were subsequently lost once and later 're-evolved' at least twice. Retention of the developmental programme is illustrated, both by the similarity of the swords in the more derived species, and by the fact that similar swords can be induced in species within genera whose ancestors did not possess swords (Meyer, 1999).

The term *latent homology* (Osborn, 1902; de Beer, 1971) has been used for situations where the developmental potential for a structure seen in a recent group exists in the developmental programme that produced a different structure in an earlier group within the lineage. This is an old idea:

> But no, I am mistaken; from the beginning of all things the Creator knew, that one day the inquisitive children of men

would grope about after analogies and homologies, and that Christian naturalists would busy themselves with thinking out his Creative ideas; at any rate, in order to facilitate the discernment by the former that the opercular peduncle of the *Serpulae* is homologous with a branchial filament, He allowed it to make a *détour* in its development, and pass through the form of a barbate branchial filament. (Müller, 1869: p. 114)

Visceral arches in agnathan vertebrates and jaws in gnathostomes, lower jaw bones in 'reptiles' and the middle ear ossicles in mammals, and anterior appendages in early arthropods and mouth parts in crustaceans are three oft-cited examples (Hall, 1999, 2002*d*; Abzhanov & Kaufman, 2000). Coding the ancestral and descendant feature as independent (apomorphic) characters, nevertheless identifies them as homoplastic features in cladistic analyses. Coding them using multiple character states (developmental processes and features) reveals the sequence of transformations and the ancestral developmental process (the character) as a latent homologue (Hall, 1995*b*). No clear-cut distinction between homology and homoplasy (parallelism) emerges. Osborn (1902) argued as much in a paper that treated homoplasy as a law of latent homology and separated parallelism (evolution through internal factors) from convergence (similar adaptations to external conditions).

Homoplasy is an alternative perspective on homology, and when we can identify a phenomenon as latent homology we begin to approach an understanding of how homoplasy relates to homology on the one hand and to the production of diversity on the other. (Wake, 1999: p. 45)

The connections are revealed even more fully when we examine reversal, atavisms, rudiments and vestiges.

(3) Reversals, atavisms, rudiments and vestiges

To be identified as a reversal, rudiment, vestige or atavism, a feature must bear a high degree of similarity to a character found in a putative ancestor, a circumstance that raises suspicions concerning the relationship between reversals, rudiments, vestiges and atavisms, on the one hand, and homology or homoplasy on the other.

(*a*) *Reversals*

Reversals represent a reversion to a previous evolutionary state (Table 1, Fig. 2). A reversal is a feature that is phenotypically similar to a feature in earlier members within a lineage, not present continuously in the lineage but present in all members of a later species. One example is loss of the second molar tooth in felids in the Miocene and its reappearance in the extant lynx, *Felis lynx* (Kurtén, 1963). Another is the (re)appearance, as repeated reversals, of ancestral features of the lateral lines, muscles and gill rakers in cichlid fishes, a process that Stiassny (1992) termed phylogenetic character reversals or taxic atavisms, terms that illustrate the closeness between reversals and atavisms.

Reversals are traditionally classified as homoplastic because their occurrence in taxa is such that some recent common ancestor or extant taxon lacks the feature; the presence of the feature in the last common ancestor of any two taxa would lead to the features being classified as homologues.

Similarity of phenotypes and closeness of relationships of taxa with reversals suggest retention of similar developmental mechanisms and common developmental bases; the term reversal thus applies to a phenotype arising in a descendent from a developmental programme retained from an ancestor but not expressed in intervening taxa; see McShea (1996) for an informed discussion of reversal in relation to parallelism.

The existence and consequences of conservation of developmental potential is an old idea, the kernel of which goes back at least as far as Weismann (1886):

A large proportional number of the gemmules in each packet, however, fail to develop, and are then transmitted in a dormant state to future generations, in any of which they may be developed subsequently – thus giving rise to the phenomena of reversion or atavism." (Weismann, 1886 as cited by Romanes, 1893: p. 3)

I should add a caveat concerning the reversibility of evolution. The Belgian palaeontologist Louis Dollo (1893) proposed that organs or complex structures cannot return to a condition shown by an ancestor. [The British entomologist Edward Meyrick stated essentially similar laws in his 1927 revision of the *Handbook of British Lepidoptera*: 'A lost organ cannot be regained and a rudimentary organ is rarely redeveloped' (p. 14)]. Dollo did not deny reversibility entirely, only that complex structures could not be recreated. 'Dollo's Law' can now be viewed against knowledge of the genetic and developmental bases of the formation of structures. The existence of atavisms (see below) means that reversals do not require the re-evolution of the development basis for producing the structure; see Gregory (1936) for an early analysis of the limits of the irreversibility of evolution, and Gould (1970), Hall (1984, 2002*b*), Marshall, Raff & Raff (1994), Lee & Shine (1998) and Teotónio & Rose (2001) for more recent discussions of Dollo's Law and/or the reversibility of evolution.

(*b*) *Atavisms*

When a feature is found only infrequently in individuals within a population or species – hind limb skeletal elements in 1/5000 sperm whales (Berzin, 1972) – but was present in all individuals in an ancestor, that feature is classified as an *atavism*, a reappearance of a previous evolutionary state (Table 1, Fig. 2). Atavistic characters have been described from many organisms and include fully developed lateral toes in horses, atavistic muscles in birds and mammals, dew claws in dogs, bristle patterns in flies, accessory nipples in mammals, and skeletal elements in 'limbless' vertebrates such as snakes and whales. In all cases, all individuals of early members in the lineage possessed the character; three-toed horses of the Eocene and limbed ancestors of snakes being two examples (see Struthers, 1881; Evans, 1955; Howell, 1970; Raikow, 1975; Riedl, 1977; Lande, 1978; Hall, 1984, 1995*a*, 1999, 2002*a*; McKitrick, 1986; Tintant & Devillers, 1995; Verhulst, 1996; Greene & Cundall, 2000; Bejder & Hall, 2002).

The occurrence, as atavisms, of ancestral patterns of tarsal bones in individuals within a single population of the salamander *Taricha granulosa*, Gray, 1850, in California, is an example that is particularly well worked out (Shubin *et al.*, 1995). Members of this population also display, as variants, patterns of tarsal bones found only in more derived taxa. That atavism, reversals and future evolutionary patterns can co-occur in the same population, at the very least leads us to contemplate the likelihood of conserved developmental processes underlying these evolutionary characters (Fig. 2). Indeed, atavisms can be used to establish homology. For example, the presence of an atavistic epibranchial in the urodele *Notophthalmus viridescens*, Rafinesque, 1829, was used by Reilly & Lauder (1988) to argue for homology of the epibranchial skeletal elements in amphibians with the epibranchials in the remainder of the vertebrates. As demonstrated in plethodontid salamanders, teleost fishes and seals, atavisms are a mechanisms for generating morphological variation (Stiassny, 1986, 1992; Wake & Larson, 1987; Wyss, 1988), a taxic atavism being an ancestral character state reestablished by phylogenetic character reversal via the spread of an atavism through the population (Stiassny, 1992).

(*c*) *Rudiments*

Although the terms *rudiments* or *vestiges* (vestigial features/structures) are often used as synonyms, there is a clear distinction between them. Rudiments are partly formed or incomplete transformations of a developmental feature and are found only in embryos (Tables 1 and 2, Fig. 2). Vestiges are evolutionary remnants (historical relics) of an ancestral feature and are found in adults. Examples of rudiments are limb buds in the embryos of limbless vertebrates (the adults lacking limbs; Raynaud, 1985), tooth buds [indeed a foetal dentition] in baleen whales when the adults lack teeth, and rudimentary clavicles in the embryos of toothed whales (reduced to a minute rudiment present at only one stage in the sperm whale, *Physeter macrocephalus*), adult toothed whales lacking clavicles (Berzin, 1972; Yablokov, 1974; Klima, 1990; Hall, 1999, 2001*b*; Bejder & Hall, 2002).

As evidence for evolution, rudiments were of great interest to Charles Darwin. It is not difficult to see why. Darwin regarded embryological origins and then homology as two chief classes of evidence for descent with modification.

> I rather doubt whether you see how far, as it seems to me, the argument for homology and embryology may be carried. I do not look at this as mere analogy. I would as soon believe that fossil shells were mere mockeries of real shells as that the same bones in the foot of a dog and wing of a bat, or the similar embryo of mammal and bird, had not a direct signification, and that the signification can be unity of descent or nothing. (Letter from Darwin to G. H. K. Thwaites, 21 March, 1860, cited from Darwin & Seward, 1903: p. 145)

Rudiments were manifestations of both classes of evidence. It is easy to see how an atavism or character reversal could arise in an organism with an embryonic rudiment of that feature, a chance mutation or even an environmental cue triggering an extension of the development of that embryonic rudiment, especially when we consider that atavisms can be induced experimentally (Hall, 1984).

The presence of an embryonic rudiment is in part the consequence of the sharing of regulatory genes between different tissues and organs and the consequent difficulty of removing a primordium entirely. In the latter case, development would be too disrupted, although the modularity of developmental processes goes some way toward alleviating such disruption (Wagner, 1996; Bolker, 2000; Gass & Bolker, 2002). Organs as diverse as limbs, genitalia and the craniofacial region share regulatory genes (Duboule & Wilkins, 1998; Schneider, Hu & Helms, 1999). An example is the directive role of bone morphogenetic protein-4 (BMP-4) and members of the fibroblast growth factor family in limb, tooth and mandibular development in vertebrates (Lyons, Pelton & Hogan, 1989; Tucker, Matthews & Sharpe, 1998*b*; Tucker *et al.*, 1998*a*, *c*; Chen *et al.*, 2000; MacDonald & Hall, 2001). The sharing of regulatory genes, gene cascades, or gene networks is an important aspect of the deep homology that may underlie both homologous and homoplastic

characters; homologues retain their shared bases, while the processes underlying homoplastic features diverge (Weiss, 1994/1995; Abouheif, 1997, 1999; Hall, 1999; McGhee, 2000; Newman & Müller, 2000).

Because rudiments are embryonic, they are often thought not to serve any function, or, in some cases (foetal dentition in whales, for example), not to have been examined sufficiently closely to determine a function (Gans, 1975, 1985). Embryonic rudiments may have no function in the traditional sense, because the developmental programmes that produce them have not yet been removed through accumulation of mutations, or the rudiments may serve as 'developmental spacers' (Ken Weiss, personal communication) required for developmental processes that produce the functional features required to proceed from one stage to the next (Hall & Miyake, 1995; Hall, 1999). In the latter sense, rudiments play essential roles in development. The notochord is often regarded as a rudiment of the ancestral chordate dorsal 'skeleton' that existed before the cartilaginous vertebral column evolved, and that is retained because of its major role in the induction of the dorsal nervous system (Riedl, 1978; Hall, 1983).

There has been a long interest in how teeth affect the development of other features. Aristotle was aware that all species of deer that lack antlers develop their incisors into tusks. These tusks, found in the tufted deer (*Elaphodus cephalophus*), musk deer (*Moschus moschiferus*) and Chinese water deer (*Hydropotes inermis*), can be as long as 10 cm (Goss, 1983). Tusks are never seen in antlered deer. The effects of tooth development on the development and morphogenesis of the jaws and skull have also long been known to morphologists (Thompson, 1917; Davis, 1964). A developmental and evolutionary basis for how teeth and their associated alveolar bone exert their role in morphogenesis and patterning of the embryonic mammalian dentary bone and lower jaw was proposed by Atchley & Hall (1991), who identified cell condensations as fundamental units (now modules) of both development and evolution. The teeth in baleen whales may play a similar role in the morphogenesis of the jaw bones, if the model proposed by Atchley & Hall [and see in Hall (1999, Chapter 20) and Hall & Miyake (2000)] has any generality, which it appears to have, given its utilization in studies as disparate as the morphology, modularity, origin, evolution and phenotypic plasticity of organs in extant and fossil plants, insects, fish, rodents and primates (Bromage, 1989; Arnold, 1992; Maze *et al.*, 1992; Erwin, 1993; Richtsmeier & Lele, 1993; Lauder, 1994; Leroi, Rose & Lauder, 1994; Carroll, 1997; Cheverud, Routman & Irschick, 1997; Nijhout & Paulsen, 1997; Smith & van Nievelt, 1997; Klingenberg, 1998; Schlichting & Pigliucci, 1998; Lieberman, 1999; Bolker, 2000; Li & Johnston, 2000; Oxnard, 2000; Weiss & Fullerton, 2000).

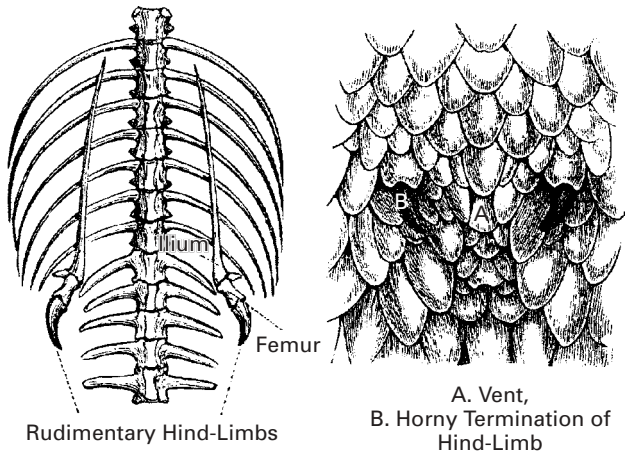

Fig. 3. Vestigial pelvic girdle (ilium) and hind limb (femur) skeletal elements, and a keratinized claw (spur, B) in an adult python. From Romanes (1896), drawn from nature, one-quarter natural size.

(*d*) *Vestiges*

Vestiges are evolutionary remnants (relics) of an ancestral feature, and are found in adults (Tables 1 and 2, Fig. 2). The many examples include reduced wings in flightless birds, reduced eyes in cave dwelling fish, pelvic bones in whales, and pelvic or limb bones in snakes (Fig. 3).

Vestiges exist as what are usually characterized as 'non-functional' and therefore, presumably non-adaptive, adult characters. However, many such characters are retained for functions other than the one traditionally assigned to the character. The adult feature may be retained because its function, or its developmental basis, is linked to other features or developmental pathways. Assessing lack of function, as with assessing adaptation, is always difficult; one needs a thorough, if not total, knowledge of the biology of the organism. Although the reduced wings of flightless birds (ostriches, emus, cassowaries, kiwis and rheas) are non-functional as locomotory appendages, they serve functional roles in balance and communication. Penguins and flightless cormorants use their wings in a locomotor function for underwater propulsion and steering. The pelvic bones of whales may be used in reproductive behaviour; they certainly support the abdominal musculature (Arvy, 1979; Pabst, Rommel & McLellan, 1998). Male boid snakes use their spurs in courtship, and so on.

A possible evolutionary explanation for the retention of rudiments or vestiges is relaxed or indirect selection,

but even here it may be hard to eliminate a role for direct selection (Fong, Kane & Culver, 1995). Accumulation of neutral mutations via genetic drift could also allow features (structures or behaviours) to lose complexity, perhaps in association with positive selection for other features. An example is the reduction of the eyes concomitant with (as a consequence of?) enhancement of the neuromasts and lateral line system in the blind cave fish *Astyanax* (Jeffery *et al.*, 2000). Müller (2002) views vestiges as homologues, arguing (and I agree), that they must be continuously present in the lineage before one can establish homology of the vestiges with its more fully developed ancestral counterpart. This criterion, of course, cannot be applied when a feature has been lost altogether. As Bateman (1996) noted in discussing parallelism, reversals, and parallel reversals in living and fossil land plants, 'morphological losses of features are less amenable to homology reassessment, as it is difficult to find subtle differences among morphological features that do not exist in any of the species in question!' (p. 114).

(*e*) *Distinguishing rudiments from vestiges*

How we identify a rudiment or a vestige raises an interesting issue of comparisons. Do we classify the rudiment or vestige and its fully formed equivalent as one character, two characters, or as one character with two states? Do we identify a character as a rudiment or vestige, and that rudiment or vestige as a homologue (as above), because of its relationship to a more fully developed character in an ancestor or as a consequence of a relationship (similarity, homology) with a more fully developed character in a sister taxon with which it shares a common ancestor? In many cases, we can do both (Fig. 2). Limb buds in snake embryos are rudiments, and elements of the hind limb skeleton in adult pythons vestiges (Fig. 3), both because snakes evolved from a fully limbed ancestor and because homologous structures (limb buds and fully formed limbs) are present in closely related taxa such as lizards, indeed in all tetrapods (Caldwell & Lee, 1997; Cohn & Tickle, 1999; Greene & Cundall, 2000; Wiens & Slingluff, 2001; Bejder & Hall, 2002).

Identifying all elements of the python hind limb skeleton as vestiges, however, is not absolutely straightforward, for reasons that may well apply to the characterization of other elements (especially skeletal and epithelial) as vestiges. Workers agree that the truncated distal element in the vestigial python hind limb is a femur with a terminal claw (Fig. 3). Most would identify the functional unit as a spur (Fig. 3). The femur appears to be a vestige of the fully formed femur found in other tetrapods. Raynaud (1985) identified a cartilaginous element distal to the femoral element in embryos of *Python reticulatus,* indicated that it may remain cartilaginous through life, but was unsure whether it could be homologized to any element of the fully formed limb of other tetrapods. He does note, based on the earlier study by Raynaud & Van Den Elzen (1978), that species with very rudimentary hind limbs, such as the South African skink *Scelotes brevipes*, have a fused tibia-fibula as a cartilaginous element. Two species of fossil 'snakes with limbs', *Pachyrhachis problematicus* and *Haasiophis terrasanctus,* both have tibiae and fibulae (Haas, 1980; Lee & Caldwell, 1998).

A further complication is that the claw in pythons may be neomorphic, i.e. a new structure not found in ancestors. Under experimental conditions, a terminal claw can develop at the distal tip of chick limbs, whether the most distal bony element is a complete limb, a truncated femur or even only isolated digits (Hall, 1978; M. J. Cohn, N. Kley and P. F. A. Maderson, personal communications). Furthermore, claws fail to form in chick embryos carrying the mutation *scaleless*, a mutation that leads to failure of formation of other epithelial structures, such as feathers and scales, while having no direct effect on skeletal tissues (Palmoski & Goetinck, 1970; Abbott, 1975). Claws could be lost and regained, and/or neomorphic claws could develop independently of changes occurring in the skeleton, although in mammals, claws and skeletal tissues share regulatory genes (Hamrick, 2001). As no fossil or extant taxa retains a claw after loss of the distal skeletal elements, it is not currently possible to know whether the claw found in species such as the python is neomorphic or not. Furthermore, a cartilage, sometimes ossified but of unknown homology, may be present as a central support for the claw, further complicating homology assessment. Whether neomorphic or not, spurs are functional; they are used in courtship by male boids (N. Kley and P. F. A. Maderson, personal communications).

As with the tracing of vestigial proximal hind limb elements, we also can trace vestigial digits to their embryonic precursors and to the full complements of digits in ancestors or in sister taxa, and so homologize the vestigial digits. If we examine patterns of digit reduction, we find genera in which various patterns of vestigilization occur in organisms that are very closely related (Greer, 1987). Within squamates, limb reduction has occurred 62 times in 53 lineages. Within the skinkid lizards, size reduction and loss of limb elements has occurred 31 times in 25 lineages. The Western Australian skink, *Hemiergis peronii*, has forms with anywhere between two and five digits. Those with two or

three digits have, as adults, a vestige of digit V. Those with two digits have an additional vestigial digit, and so have two fully formed and two vestigial digits. As embryos, the two-, three- and four-digit forms all develop four unsegmented digital primordia as rudiments (Shapiro & Carl, 2001; Shapiro, 2002; M. D. Shapiro, personal communication), nicely illustrating the difference between rudiments and vestiges.

V. REALIGNMENT OF HOMOLOGY AND THE CLASSES OF HOMOPLASY

Both homology and homoplasy can be defined at different levels without making judgments about homology or homoplasy, or lack of homology/homoplasy at other levels. Indeed, to identify the hierarchical level of homology or homoplasy being specified, we should always speak of 'homologous as limbs, homologous as digits, homologous as a developmental process, homologous as a gene network, etc.,' and ditto for 'homoplastic as …'

The classes summarized in Table 1, in Fig. 2 and discussed below are categories of relationships between features. They would fall into different categories if developmental processes or genetic mechanisms, rather than the feature, were the basis for the categorization. For example, definitions of the homology of features automatically exclude process homology (shared developmental mechanisms leading to the production of similar features), whereas when categorizing homology of features, shared or divergent development provides a basis for delimiting homology. At the level of developmental processes, shared and divergent development are two classes of homology. In part, this reflects the fact that developmental processes can evolve without altering our assignment of the resulting feature as homologous or homoplastic: tetrapod digits, for example. Consequently, we cannot use the criterion 'homologous features share a common development, while homoplastic features do not' to distinguish homology from homoplasy (Table 2). Different categorizations again would result from schemes based on characters and phylogeny (homology, rudiments, reversals, vestiges, atavisms), or process (homology, parallelism, convergence). I have tried to capture these differences in Table 3.

From the examples discussed in Section IV and summarized in Table 1, we begin to glimpse a closer relationship between homology and the classes of homoplasy than suggested by the traditional dichotomy/antithesis of: (*a*) homology *versus* (*b*) homoplasy [convergence, parallelism, reversals, rudiments, vestiges and atavisms]. One of these traditional categories of homoplasy – reversals, rudiments, vestiges and atavisms – groups features that form using similar developmental processes (although underlying genetic control may have diverged). The second, parallelism, also reflects shared processes producing similar features. The third, convergence, is not based on shared development. In contrast to parallelism, convergence reflects different processes producing similar features.

Using development as the criterion to separate homology from homoplasy of the feature (Table 2) results in a different categorization that the traditional one, namely (*a*) homology, reversals, rudiments, vestiges and atavisms; (*b*) parallelism, and (*c*) convergence, where: (*a*) reflects evolutionary changes expected to share developmental processes; (*b*) reflects developmental processes that may have diverged, i.e. the other side of (*a*); while (*c*) reflects divergent developmental processes.

A classification at a different level in the hierarchy – similarity of the developmental processes, rather than of the feature (Table 2) – would group: homology, rudiments, vestiges and parallelism as arising from similar developmental processes; reversals and atavisms as potentially arising from different developmental processes; and convergence as arising from different developmental processes.

Using the developmental component reflects common ancestry or independent evolution, providing a means to refine further the categories: homology reflects evolutionary changes within a lineage and between lineages which share a recent common ancestor; reversals, rudiments, vestiges and atavisms reflect changes within a single lineage and so are aligned with homology; parallelism reflects more distant but related lineages; while convergence reflects divergent/independent evolutionary history in polyphyletic lineages, resulting in: (*a*) homology, reversals, rudiments, vestiges, atavisms, parallelism; and (*b*) homoplasy as convergence, where: (*a*) *reflects phylogenetic conservation or retention of features in organisms with common descent, independent of whether development has diverged, and* (*b*) *reflects similar features resulting from independent evolution*. A dichotomy of categorization of features remains. This combined, incremental use of developmental and phylogenetic criteria, however, expands homology as a category, leaving homoplasy as convergence.

Déjà vu. The first of these final categories, (*a*) is close to, if not identical with, Lankester's homogeny – similarity due to common descent. The second, (*b*) reflects Lankester's homoplasy – similarity reflecting independent evolution – a category that Lankester (1870*b*) used for analogy, parallelism and convergence (see Rieppel,

Table 3. *Categorization of the classes of homology and homoplasy of features (a) on the basis of developmental processes*[a]*, character assessment or synapomorphy of the character, and (b) on the basis of characters and processes*

(*a*)

Process	Character	Shared derived feature (synapomorphy)	Categorization
+	+	+	Homology
−	+	+	Homology
+[b]	+	−(+)	Reversals
+	+/−	+/−	Rudiments
+	+/−	+/−	Vestiges
+[b]	+/−	−(+)	Atavisms
+	+	−(+)	Parallelism
−	−	−(+)	Convergence
+	−	−[c]	Process homology

(*b*)

Character-based	Process-based
Homology	Homology
Reversals	Parallelism
Rudiments	Rudiments
Vestiges	Convergence
Atavisms	

+, Similarity; −, divergence; −(+), normally divergent but possibility of similarity; +/−, possibility of divergence, or insufficient data to decide.

[a] I have not separated developmental processes into genetic and supragenetic mechanisms, not because different categorizations may apply to each level, but because we currently have too little data to do such fine-tuning.

[b] If the reactivation of ancestral (shared) developmental processes involved using different sets of genes or different environmental (epigenetic) cues, then the processes would be categorized as divergent (−) (W. Olson, personal communication.), illustrating the importance of specifying the level in the hierarchy under discussion.

[c] This would be similarity (+) at the level of synapomorphy of processes, again illustrating the importance of specifying the level in the hierarchy under discussion.

1988 and Panchen, 1999 for discussions). Take out parallelism from Lankester's homoplasy and you have homoplasy as I construe it.

I am not alone. Arthur Willey (see Section IV.1) was prescient, both in seeing that phylogenetic relations had to be established before any sense could be made of convergence, and that '*the limitations of convergence coincide with those of homology, and the criteria of the one are inversely those of the other*' (Willey, 1911: p. ix, emphasis mine), an approach that reinforces the dichotomy proposed by Lankester.

VI. CONCLUSIONS

(1) Hall (2002*d*) suggested that examination of nearness of relationships and degree of shared development reveals a continuum within the expanded homology category. The more refined version of that analysis summarized in Table 1 and in Fig. 2, emphasizes a continuum from homoplasy to parallelism, with convergence as the sole class of homoplasy.

(2) This realignment of the categories of homologous and homoplastic features provides a glimmer of a way to bridge phylogenetic and developmental approaches to homology and homoplasy. It will not, and in a practical sense cannot, alter how homoplastic features are identified in phylogenetic analyses, and homoplastic character states are identified *a posteriori*.

(3) Seeing reversals, rudiments, vestiges, atavisms and parallelism as closer to homology than to homoplasy should guide our thinking toward searching for commonalities underlying these features, rather than causing us to regard them as the product of independent evolution (and, by implication, different developmental and genetical bases) and therefore totally apart from

homology. Inevitably, this attempt leads to a search for deeper levels of continuity between homology and homoplasy.

(4) Homoplastic characters turn out to be present to an unexpectedly high degree in phylogenetic analyses of particular lineages (Lieberman, Wood & Pilbeam, 1996; Sanderson & Hufford, 1996; D. B. Wake, 1996; Lockwood, 1999; Lockwood & Fleagle, 1999; Wood, 1999; Hall, 2002*d*).

(5) As emphasized by Lee (2000) in a phylogenetic analysis of lizards and snakes, the distribution of homoplasy is as important as the amount of homoplasy.

(6) Such overwhelmingly convergent evolution may reflect independent evolution when assessed at the level of the phenotypic character. At a deeper level of analysis, it yields insights into the evolution of the ancient genetic pathways and/or developmental processes that underlie character evolution, whether those characters are homologous or homoplastic.

(7) The genetic and developmental bases underlying character formation include shared cellular properties (proliferation, migration, interaction), cellular processes (differentiation, apoptosis, morphogenesis, growth), regulatory genes and gene cascades (Hall, 1983, 1999, 2001*a*, 2002*d*; McShea, 1996; Abouheif, 1997; Wray & Lowe, 2000). These cellular processes evolved early and so have been open to evolutionary conservation or modification for over half a billion years of animal evolution.

(8) Despite the fact that we dichotomize features as homologous or homoplastic, and although many pathways were possible, there has been but one evolutionary and developmental history of life on earth; the biosphere as 'a single, cladistically structured descent group' (Weiss, 1994/1995: p. 222).

(9) There is only one set of historically contingent phylogenetic and mechanistic relationships, some more closely related (shared), others that have diverged to lesser or greater degrees. Consequently, we should be able to construct a relationship among, rather than between, homology and homoplasy that is more representative of reality than coding characters, studying development in isolation, or categorizing evolution as common or independent descent.

(10) The history of life has been descent with modification. Lankester certainly saw this: 'In distinguishing these two factors of a common result [homology and homoplasy] we are only recognizing the principle of a plurality of causes tending to a common end, which is everywhere recognizable …' (1870*b*, p. 42).

(11) Whether we are examining homoplasy (convergence), parallelism, reversals, rudiments, vestiges, atavisms or homology, we are dealing with common descent with varying degrees of modification of features as a result of natural selection tinkering with the genetic and developmental bases responsible for producing those features.

(12) The challenge is to analyse further, and understand more fully, the relationships between degrees of modification and tinkering, conservation and transformation, development and evolution, for the light such analyses will shed on the evolution of the phenotype that results from descent with modification.

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