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Evo-Devo: evolutionary developmental mechanisms

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Introduction

Evolutionary developmental biology (evo-devo, devo-evo or EDB)[1] seeks as a discipline to identify those developmental mechanisms that bring about evolutionary changes in the phenotypes of organisms.

To some, evo-devo arose as a result of the impetus provided by the publication in 1977 of *Ontogeny and Phylogeny* by Stephen J. Gould, who reminded us of the importance of heterochrony (change in timing of development) as a mechanism for evolutionary change. To others, evo-devo arose with the discovery of homeobox (Hox) genes (Lewis, 1978; Gehring, 1985, 1998), a view that equates the discipline with the transformation of developmental biology by molecular genetics, and identifies conserved signaling genes as the most important evolutionary developmental mechanisms. Yet others trace the origins to the work of John Tyler Bonner (e.g. Bonner, 1955, 2000), who, in his search for the origins of multicellularity in the behavior of slime molds was working on evo-devo before most of us were aware that the field was reemerging. The *Dahlem Konferenzen* on "Evolution and Development," held in Berlin (May 10-15, 1981) and published under Bonner's editorship in 1982, brought morphology back to center stage in evolutionary biology. Hence, the origins of evo-devo are multiple, and evolutionary developmental mechanisms many and varied, reflecting the hierarchical organization of organisms and the many levels at which evolutionary change can occur (Hall and Olson, 2003a,b).

Indeed, the origins of evo-devo lie even further back in the comparative evolutionary morphology (evolutionary embryology) that arose in response to the publication of *On the Origin of Species* by Charles Darwin (1859). Darwin's claim that embryology would provide the best evidence for evolution directed most morphologists of the last third of the 19th century to comparative embryology (Bowler, 1996; Hall, 1999a). And so the flowering of evo-devo in the last decades of the 20th century is rooted in the evolutionary embryology of the last decades of the 19th century. The comparative approach we use and analyze in the context of robust phylogenetic analyses today, is no more or less than a

[1] As far as I have been able to trace the use of the term evolutionary developmental biology, Calow (1983, p. 80) used it when discussing what he referred to as a new area of biology concerned with relationships between evolution and development. David Wake talked of a discipline of evolutionary developmental biology in ending a roundtable workshop on "Development and Evolution - The emergence of a new field," held at the Fourth International Congress of Systematic and Evolutionary Biology in Maryland in July 1990, although the published report of the round table did not use the term (Wake *et al.*, 1991). I used it as the title for my 1992 book. For further discussion, see Hall (1992). Also see Robert *et al.* (2001) for how evo-devo relates to other approaches to unite development and evolution.

Abbreviations used in this paper: Devo-evo, developmental evolutionary biology; EBD, evolutionary developmental biology; Evo-devo, evolutionary developmental biology.

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methodologically refined version of the approaches of our late 19th century scientific ancestors.

Looking back

Evo-devo reflects a long search to find and understand relationships between the transformation of an organism within a single generation — development, ontogeny, ontogenetic change — and those transformations that occur between generations — evolution, phylogeny, phylogenetic change (Gould, 1977; Hall, 1992, 1999a; Bowler, 1996). Gould's (1977) emphasis on heterochrony resurrected a theme — alteration in the timing of development as a factor in evolutionary transformation in form — that originated with Ernst Haeckel in the 19th century and was elaborated by Gavin de Beer in the early 20th (de Beer, 1930).

De Beer was seeking processes of embryonic development that could explain morphological evolution. He in turn was heavily influenced by Richard Goldschmidt's discovery that genes could affect the rates of developmental and physiological processes (Goldschmidt, 1918, 1938). If genes controlled rates of such processes, mused de Beer, and if developmental change is related (perhaps causally) to evolutionary change as Darwin and other 19th century morphologists proposed (Hall, 1992, 1999a; Bowler, 1996), then heterochrony could be an important mechanism of evolutionary change: "We may safely conclude that the speeds at which the internal factors work are of great importance in development, and that variation in the relative speed of the various factors may play an important part in the relation of ontogeny to phylogeny" (de Beer, 1954, p. 23).

Heterochrony is what Hall and Olson (2003a) term an *evolutionary developmental mechanism*, i.e., a mechanism operating during embryonic development but that can be modified over the course of evolution and is thus instrumental in effecting evolutionary change in the phenotype.

Another evolutionary developmental mechanism is *heterotopy* — alteration in spatial location of one or more developmental processes — like heterochrony, owes its origin to Ernst Haeckel (see Hall, 1983, 1999a, 2001a and Zelditch, 2001 for reviews). One of Haeckel's primary examples of heterotopy was the origin of germ cells from endoderm or from mesoderm in different animal groups. Other examples may be found in Hall (1999a) and in Zelditch (2001).

TABLE 1

A SAMPLE OF EVOLUTIONARY DEVELOPMENTAL MECHANISMS AT VARIOUS LEVELS OF THE BIOLOGICAL HIERARCHY(a)

Level	Mechanisms
Gene	regulation, networks, interactions, genome size, epigenetic processes (methylation, imprinting, chromosome inactivation)
Cell	division, migration, condensation, differentiation, interaction, patterning, morphogenesis, embryonic induction
Tissue, organ	modularity, segmentation, embryonic inductions, epithelial-mesenchymal interactions, growth
Organism	ontogenetic re-patterning, genetic assimilation, phenotypic plasticity, polymorphism, functional morphology

(a) Evolutionary developmental mechanisms such as heterochrony and heterotopy span all levels.

Now

The desire and ability to produce a special issue of *The International Journal of Developmental Biology (Int. J. Dev. Biol.)* devoted to evo-devo reflects how rapidly the field has grown from embryo to larva to reproductively mature adult. Importantly, we can now identify evolutionary developmental mechanisms other than heterochrony and heterotopy, many of which are reviewed and analyzed in this Special Issue of the *Int. J. Dev. Biol.* and in Hall (2003a), Hall and Olson (2003b) and Hall *et al.* (2003). My aim is to provide no more than a glimpse of the riches ahead.

Heterochrony has had a lively, if controversial, history over the past almost 150 years (Gould, 1977; Zelditch, 2001). Despite claims to the contrary, it is certainly not *the only* evolutionary developmental mechanism (Hall, 2001a; Hall and Olson, 2003b). In part, one can make this claim because evo-devo and evolutionary developmental mechanisms comprise much more than changes in timing of development. In a roundtable discussion held in July 1990, heterochrony, developmental constraints, systematics and homology, were identified as four elements of the then emerging field of evo-devo (Wake *et al.*, 1991). Ten years later, Hall (2000) identified five elements:

- ✓ the origin and evolution of embryonic development;
- ✓ how modifications of development and developmental processes lead to the production of novel features;
- ✓ the adaptive plasticity of development in life-history evolution;
- ✓ how ecology impacts on development to modulate evolutionary change; and
- ✓ the developmental basis of homoplasy and homology (Hall, 2000, p 177); also see Hall and Olson, 2003a, p. xiii.

Even such an abbreviated list demonstrates the breadth of evo-devo, the range of fields in biology impacted upon and integrated by evo-devo — including ecology, molecular biology, palaeontology, life history strategy (Hall, 1992, 1999a, 2002) — and the potential that evo-devo has to form the basis for a new, integrative biology of the 21st C (Hall, 2002).

Looking forward

I noted the importance of molecular biology for evo-devo. Genetics alone, however, does not allow us to understand how phenotypes arise. Evo-devo comprises *all* that is contained in the black box that lies between genotype and phenotype (Hall, 2003b). Evolutionary developmental mechanisms enable us to understand how form is transformed (or maintained static) during evolution, whether that transformation is a minor modification in the shape of a bone or the origin of novel features such as the turtle shell (Burke, 1989a,b; Gilbert *et al.,* 2001), feathers (Prum and Brush, 2002), insect wings (Carroll *et al.*, 1995), or flowers of a plant (Niklas, 1997).

Furthermore, evo-devo enables us to appreciate the commonality and essential continuity that underlies the range of relationships captured by the apparently divergent concepts embraced by the terms homology, homoplasy, parallelism, convergence, rudiments, reversals and atavisms (Hall, 2003c). As argued by Hall (2003c), analysis of nearness of relationship and degree of shared development reveal a continuum within an expanded category of homology, extending from homology → reversals → rudiments → vestiges → atavisms → parallelism. Such an approach leads us to

search for the degree of commonality in developmental mechanisms underlying these features, and thence to their modification as evolutionary developmental mechanisms.

Developmental mechanisms can be conserved between taxa when the structure those mechanisms normally form is either incomplete (as seen in rudiments and vestiges), or appears only in some individuals (as seen in an atavism), both of which dissociate homology of process from homology of structure. Conversely, different developmental mechanisms can produce similar (homologous) features. Hall (2003c) argued that such an approach provides both a bridge between phylogenetic and developmental approaches to homology and homoplasy, and a major rationale for evo-devo. Evolutionary developmental mechanisms really do enable us, perhaps for the first time, to understand the real meaning of modification in "descent with modification," stasis in "morphological stasis", and constraint in "developmental or phylogenetic constraint" (see Hall, 2003d for further elaboration).

Fig. 1. Larval development of the West-African lungfish *Protopterus annectens*. *These, part of the first record of the development of* Protopterus*, drawn by J.S. Budgett from specimens he collected in Africa, typify the search for missing links in embryos and the artistic skill of the 19th century naturalists who went to extraordinary lengths to obtain embryos and larvae. The close similarity of* Protopterus *development to the embryonic development of urodele amphibians was taken as a fundamental demonstration of the close relationship between lungfish and amphibians and as vital information for theories of the origin of terrestrial vertebrates; see Bowler (1996) and Hall (2001b) for further details. Reproduced from Budgett (1901).*

In the late 19th century, evolutionary developmental mechanisms were approached through comparative embryology, analysis of the systematic relationships among and between groups of organisms (Nyhart, 1995; Bowler, 1996; Hall, 1999a), and through a search for missing links, with special emphasis on embryos providing evidence of those missing links (Fig. 1. and see Hall, 1999b, 2001b). In the late 20th century we use all the tools of molecular biology, molecular genetics, developmental biology, phylogenetics and palaeontology in the search for evolutionary developmental mechanisms (Erwin and Wing, 2000; Carroll *et al.*, 2001; Hall, 2002; Wilkins, 2002).

This list implies that evolutionary developmental mechanisms will not all be found in the genes. This is because new mechanisms emerge as development proceeds (Hall, 1999a, 2003b,d; Wilkins, 2002). Evolutionary developmental mechanisms may be genetic, cellular, developmental, physiological, hormonal or any combination of these levels. Development is hierarchical, reflecting emergent developmental processes; the transfer from maternal to zygotic genomic control; cell-to-cell interactions; cell differentiation and migration; embryonic inductions; functional interactions at the tissue and organ levels; growth in all its richness. So too, evolutionary developmental mechanisms reflect each of these levels of control. I have summarized these mechanisms in Table 1, using genes, cells, tissues/organs, and organisms as four levels; see Hall (1999a, 2003b,d), Lewontin (2000) Hall and Olson (2003) and Hall *et al.* (2003) for detailed discussions.

Interactions that are equivalent in all senses to embryonic inductions occur:

✓ between individuals of the same species — as seen in pheromone-based signaling in social insects such as the ant *Pheidole bicarinata* (Nijhout, 1999), and in density-dependent interactions in such amphibians as the New Mexico spadefoot toad *Scaphiopus multiplicatus* (Pfennig, 1992);

✓ between individuals of different species, even of different phyla — as in those predator-prey interactions that elicit a new structure in offspring of the prey species (Stemberger and Gilbert, 1987; Dodson, 1989a,b), interactions often subsumed under the terms cyclomorphosis or seasonal polymorphism and studied using reaction norms; and/or

✓ between species and their biotic and/or abiotic environment — as in seasonal polymorphic caterpillars of the geometrid moth *Nemoria arizonaria*, where the environmental trigger is the concentration of tannin in leaves or twigs of oak trees (Greene, 1999), or modulation of the pelvic girdle in the threespine stickleback *Gasterosteus aculeatus* in response to the combined presence of a predator and low Ca^{++} levels in the lakes (Bell *et al.,* 1993).

There is little to distinguish the causality that underlies such interactions from that which underlies inductive interactions within embryos (Hall, 1992, 1999a, 2003a; Schlichting and Pigliucci, 1998; Hall *et al.*, 2003). Similar mechanisms act within individuals as act between species. Both can be influenced — indeed often controlled — by environmental cues, demonstrating the importance of understanding evolutionary developmental mechanisms (Hall, 2003a).

Within these emergent processes, gene networks and gene cascades (genetic modules) link the genotype with morphogenetic units (cellular modules, namely germ layers, embryonic fields, or cellular condensations), while epigenetic processes such as embryonic inductions, tissue interactions and functional integration, link morphogenetic units to the phenotype. These are summarized in Table 2, where the links between the genotype and phenotype are shown as genetic modules, morphogenetic units, and epigenetic processes. Hall (2003b,d) contains more detailed analyses.

All these mechanisms are either discussed or touched upon in this special issue, indicating the pivotal role that evo-devo is playing and will continue to play unifying our understanding of ontogeny and phylogeny.

Summary

Evolutionary developmental biology (Evo-Devo) as a discipline is concerned, among other things, with discovering and

TABLE 2

EMERGENT UNITS AND PROCESS BETWEEN GENOTYPE AND PHENOTYPE AND THE BASIS OF THE EVOLUTIONARY DEVELOPMENTAL MECHANISMS OPERATING WITHIN EACH[(a)]

Units or processes	basis of evo-devo mechanism
genotype	genes
genetic modules	gene networks; gene cascades
morphogenetic units	cell condensations
epigenetic processes	embryonic inductions, tissue interactions, functional integration
phenotype	inter- and intra-individual/species and ecological/environmental interactions

(a) Note: Units of evolutionary developmental mechanisms such as gene networks/cascades cross over between units in the hierarchy. For further details, see Hall (2003a,b).

understanding the role of changes in developmental mechanisms in the evolutionary origin of aspects of the phenotype. In a very real sense, Evo-Devo opens the black box between genotype and phenotype, or more properly, phenotypes as multiple life history stages arise in many organisms from a single genotype. Changes in the timing or positioning of an aspect of development in a descendant relative to an ancestor (heterochrony and heterotopy) were two evolutionary developmental mechanisms identified by Ernst Haeckel in the 1870s. Many more have since been identified, in large part because of our enhanced understanding of development and because new mechanisms emerge as development proceeds: the transfer from maternal to zygotic genomic control; cell-to-cell interactions; cell differentiation and cell migration; embryonic inductions; functional interactions at the tissue and organ levels; growth. Within these emergent processes, gene networks and gene cascades (genetic modules) link the genotype with morphogenetic units (cellular modules, namely germ layers, embryonic fields or cellular condensations), while epigenetic processes such as embryonic inductions, tissue interactions and functional integration, link morphogenetic units to the phenotype. Evolutionary developmental mechanisms also include interactions between individuals of the same species, individuals of different species, and species and their biotic and/or abiotic environment. Such interactions link ecological communities. Importantly, there is little to distinguish the causality that underlies these interactions from that which underlies inductive interactions within embryos.

KEY WORDS: *developmental mechanism, heterochrony, embryonic induction, emergent properties*

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