

Introduction

The evolution of evo-devo biology

Once seen as distinct, yet complementary disciplines, developmental biology and evolutionary studies have recently merged into an exciting and fruitful relationship. The official union occurred in 1999 when evolutionary developmental biology, or “evo-devo,” was granted its own division in the Society for Integrative and Comparative Biology (SICB). It was natural for evolutionary biologists and developmental biologists to find common ground. Evolutionary biologists seek to understand how organisms evolve and change their shape and form. The roots of these changes are found in the developmental mechanisms that control body shape and form. Developmental biologists try to understand how alterations in gene expression and function lead to changes in body shape and pattern. So although SICB only recently validated evo-devo as an independent research area, evo-devo really started over a decade ago when biologists began using an individual organism’s developmental gene expression patterns to explain how groups of organisms evolved.

To highlight this emerging field, the PNAS Editorial Board has sponsored a special feature on Evolutionary Developmental Biology. This evo-devo special feature contains eight Perspective articles and a review that examine evo-devo’s progress to date, as well as 15 research articles that add new information and focus on the most recent evo-devo biology trends. The majority of the research articles were submitted directly to the PNAS office through our Track II system, and were evaluated by an Editorial Board member. After the initial screening, papers were assigned to an Academy Member-editor who oversaw a process where research manuscripts were rigorously peer-reviewed by experts in the field.

Perspectives

The basis for all evo-devo research covered in this issue is, arguably, the Cambrian “explosion.” This explosion occurred approximately 550 million years ago and lasted only 45 million years. This “brief” period in history resulted in great diversification of metazoan assemblages. These new organisms were unique not only in their abundant diversity, but also in their new body plan complexity as well. In the first Perspective, Conway Morris (1)

reviews why the Precambrian molecular and environmental atmospheres were ripe for a burst of evolutionary expansion. The generation of Cambrian-born organisms with mirror-image body plans is reviewed by Peterson and Davidson (2). These authors cover the origin of “bilaterian” organisms, and review the genetic evolution necessary for their development.

After the Cambrian period, the bilaterian animals split into three major phylogenetic branches, or clades. Each clade provides us a unique insight into evolutionary development. Shankland and Seaver (3) discuss what the annelids (Lophotrochozoa clade) can teach us about body axis and segment formation. Akam (4) and Patel (5) review how molecular embryology tools have been applied to further our knowledge about evolution of arthropod body parts (Ecdysozoa clade). Although the body plans of members from these two clades are very different, both clades belong to the protostome phyla and are linked by a common ancestor. However, precisely what that ancestor is, as well as the evolutionary path that led to the axis inversion between the protostome and deuterostome phylum, is unclear. This “last common ancestor” controversy is the topic of the Perspective by Gerhart (6), whose summation explores a few of the chordate origin hypotheses. Shimeld and Holland (7) discuss the most evolutionarily recent developmental body plan changes in “Vertebrate Innovations.” Finally, Adoutte *et al.* (8) caution us to look carefully at sequence data when rearranging phylogenies or assigning new kinships within any clade or phylum.

Research Articles

The research papers in this Special Feature expound the topics covered in the Perspectives. Chen *et al.* (9) show visually striking bright field and polarized micrograph images of putative Precambrian bilaterian fossils. These support the theory that great evolutionary diversification occurred *before* the onset of the Cambrian period, and again beg the question of how deep in time did the common ancestor of the bilaterian clades arise.

Adami *et al.* (10) argue that, to make a case for or against a trend in the evolution of organism complexity, we must first define biologic complexity. Through separating genomic complexity from struc-

tural or functional complexity, these authors establish an information-based theoretical method for gauging complexity. Their mathematics permits the degree of genomic complexity to be extrapolated into knowledge about the world in which that complexity arose.

A better understanding of evolutionary complexity will also be essential to evaluate newly rearranged phylogenetic trees. Based on the rapidly growing wealth of information gained from DNA sequence analysis and genomic mapping, phylogenetic maps are assigning new kinships while breaking old family ties. Cameron *et al.* (11) discuss the analyses of new 18S rDNA data sets that change our current view of ancestral deuterostome sister groups. Similarly, Miller *et al.* (12) look at the Pax gene sequences in cnidarians to deduce that Pax derived transcription factors do indeed have an ancestral role in neuronal differentiation. Kappen (13) takes a broader approach. She assesses an entire repertoire of homeobox genes in *Caenorhabditis elegans* and compares their sequences and distance matrices to homeobox genes in plants, arthropods, and mammals.

The next series of papers gets at the crux of molecular evo-devo questions: which Hox gene turns on, where does it turn on, and when does it turn on? Peterson *et al.* (14) address this issue by examining the Hox gene cluster transcripts’ role in adult annelid body formation. Like the indirectly developing deuterostome, the sea urchin, the annelid tested does not use Hox cluster expression in larva but rather draws from the complex later in cells “set aside” for generating the adult body. The Hox genes are also the focus of the paper by Gauchat *et al.* (15). They examine expression patterns in hydra and find the Hox paralog genes that define the oral/aboral axis in hydra are not parallel to the anterior-posterior axis formation Hox genes of vertebrates or arthropods. Van Auken *et al.* (16) explore two Hox genes’ expression patterns in *C. elegans* to better define the Hox genes essential for embryonic patterning. Lewis *et al.* (17) examine the homeotic genes Ubx and abd-A and their role in repressing abdominal appendage formation in insects. The cover photograph of this issue comes from an example of their histochemical staining of the Ubx and abd-A proteins in the red

flour beetle. Brown *et al.* (18) look at the *Drosophila* homeotic complex (HOMC) ortholog genes in the red flour beetle and find, through a loss-of-function mutant, that the ancestral gene of HOMC may have served to repress anterior development and confer a trunk-specific identity. *Drosophila* ortholog genes in a different arthropod are also the focus of the report by Damen *et al.* (19). Through comparing expression patterns of segmentation genes in the spider *Cupiennius salei*, they implicate three genes in what might be an ancestrally conserved body plan architecture for all arthropods.

Sarkar *et al.* (20) use the well studied *Drosophila* homeotic genes as a model to trace the evolutionary conservation of a mammalian developmental pathway. This report looks at hedgehog signaling pathways in tooth development. Similarly, Pineda *et al.* (21) look at eye development and conclude that that same genetic regulatory circuit for eye development has been conserved among *Drosophila*, mice,

and *Girardia*. From *Drosophila* eye development we go to *Drosophila* hair follicle development with the work of Sucena and Stern (22), who mapped the difference in hair patterning between two *Drosophila* species to the *ovo/shaven-baby* locus. Based on interspecific complementation tests, they speculate that the different hair and cuticle pattern is governed by the evolution of *cis*-regulatory regions around *ovo/sub*.

The net knowledge gained from all these gene expression studies will bring us to a more complete understanding of bilaterian body plan control and evolution. However, not to be forgotten in the evo-devo revolution, the plant kingdom presents equally intriguing questions about body plan diversification. The review by Graham *et al.* (23) evaluates the elemental body plan changes, like tissue differentiation and asymmetric cell divisions, that spurred the origin of complex plants.

From higher order mammals to primitive plants, perhaps no other research field

uses as many disparate model systems as evo-devo. However, regardless of whether the model system is a complex human vertebra, a simple hydra segment, a fruitfly appendage, or a budding plant leaf, all organisms are used for a common objective. By applying simple molecular phenomena to explain organism body plan architecture, evo-devo is gaining insight into how phylogenies are related. Certainly the old maxim “ontogeny recapitulates phylogeny” could be the evo-devo battle cry; however, in light of the research presented in this PNAS special feature issue, perhaps a more apt saw would be “altering ontogeny formulates new phylogeny.” The Editorial Board hopes this PNAS special feature issue provides a useful resource for evo-devo scientists, and we encourage further submissions of evolutionary developmental biology research.

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