BOOKS: DEVELOPMENT

Evo-Devo Branches Out

Vivian F. Irish

The "modern synthesis," championed by Dobzhansky, Mayr, and Stebbins, among others, proposed that the evolution of novel morphologies occurs by the acquisition and fixation of new genetic mutations. How such genetic changes result in the redeployment of developmental pathways and consequent changes in morphologies has become the center of the emerging field of evolutionary developmental biology, or "evo-devo." This field is still in its infancy though. Much contemporary work is concerned with identifying those developmental genetic differences that may be important to the establishment of new forms. Although many of the advances have come from comparative studies of animal development, the work reported in *Developmental Genetics and Plant Evolution* ably demonstrates that plant evo-devo is fast catching up. Collectively, the chapters in this symposium volume from the Systematics Association present a vibrant view of this growing field.

Developmental Genetics and Plant Evolution
Quentin C. B. Cronk, Richard M. Bateman, and Julie A. Hawkins, Eds.
Taylor and Francis, London, 2002. 559 pp. $168, £105. ISBN 0-415-25790-5. Paper, $72, £45. ISBN 0-415-25791-3.

Any hypothesis of how developmental differences lead to alterations in form relies on correlations among phenotype, phylogeny, and developmental genetic changes. Making such comparisons is not trivial, especially among plant species. Plants grow in an iterative manner, continuously forming organs from the apical meristems. This mode of growth can make it difficult to discern truly homologous structures from structures that appear similar but have arisen independently. Chapters by Hawkins, Baum and Donoghue, Kellogg, and Rudall and Buzgo explore this issue. They point out the great extent to which changes in plant form have been engendered by heterochrony (temporal shifts in developmental pathways) or heterotopy (spatial shifts in developmental pathways). Assessments of heterochrony or heterotopy generally rest on morphological criteria; these authors discuss various hypotheses as to the mechanistic basis for these changes in form. In many cases, it seems likely that such shifts result from the expression of developmental genetic pathways in a new context. As noted throughout the volume, inferring the direction of these evolutionary changes requires a reliable phylogenetic framework.

Despite the inherent difficulties in defining homologous characters, comparisons of developmentally important genes are beginning to yield some tantalizing observations. As is increasingly evident from evo-devo studies of mammals and arthropods, the evolution of very different morphologies paradoxically relies on the reutilization of a relatively small set of master regulatory genes. This theme is becoming apparent for plants as well. A number of chapters deal with the evolving roles of three such gene families: the MADS-box genes, the homeobox-containing *KNOX* genes, and the *TCP* genes. Theissen *et al.* discuss the evidence for duplication and subsequent divergence of MADS-box genes as key events in the specification of reproductive organ identities in the flowering plants. Changes in the expression of the MADS-box transcription factors may also have played an important role in the evolution of new floral characters (discussed by Johansen and Frederiksen; and Teeri *et al.*). Similarly, changes in the expression of the *KNOX* genes may have been a critical factor in the evolution of leaf forms (discussed by Langdale *et al.*; Gleissberg; and Tsiantis *et al.*). The *KNOX* genes appear to have a conserved role in maintaining stem cell identity in the shoot, but their differential expression in lateral organ primordia may have led to the generation of distinct leaf shapes in different species. Although less is known about the *TCP* genes, changes in their spatial regulation are correlated with asymmetric growth patterns in very different developmental pathways (discussed by Gillies *et al.*; Cubas; and Knapp). Together, these observations lend credence to the possibility that the evolution of new plant morphologies relies to a large extent on cis-regulatory changes that result in altered spatial and temporal expression patterns of key master regulatory genes (*1*). That similar insights are emerging from evo-devo studies of animals points to the primacy of regulatory change as an engine for driving the evolution of new morphologies (*2*, *3*).

Green forms. Albrecht Dürer was one of the first European artists to accurately portray the diversity of plant morphologies, as in his watercolor *Large Piece of Turf* (1503).

Defining correlations between changes in the regulation of developmentally important genes and the evolution of new forms is only a first step. In order to test whether such changes are causal, functional analyses need to be carried out. Fortunately, there is considerable potential for genetically manipulating plant species using traditional genetic or transgenic approaches. As illustrated in a number of chapters, such functional analyses are beginning to be carried out in taxa as divergent as mosses and daisies. These analyses presage rapid advances in testing evo-devo hypotheses and in more clearly inferring ancestral versus derived functions.

In the future, it will be interesting to determine the extent to which plants and animals display similarities in the mechanisms by which their developmental pathways evolved. As pointed out in the chapter by Walbot, because plants have no germ line and undergo an alternation of genera-

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tions, selection can act both at the level of defining those cells that will form gametes and at the level of the haploid generation. This may imply that the evolutionary strategies used by plants and animals differ considerably.

Although much of this vast area of research remains to be explored, *Developmental Genetics and Plant Evolution* brings together a variety of approaches and systems where we are beginning to glean some of the answers. As with any multi-author volume, the text is somewhat uneven; some chapters are thought-provoking, and others fairly superficial. Nonetheless, the book does a good job in highlighting the evo-devo potential of many plant systems. Such research will help us determine how changes in developmental pathways have resulted in the diversity of plant forms we see around us today.

References

1. J. Doebley, L. Lukens, *Plant Cell* **10**, 1075 (1998).
2. S. B. Carroll, J. K. Grenier, S. D. Weatherbee, *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design* (Blackwell Science, Malden, MA, 2001).
3. E. H. Davidson, *Genomic Regulatory Systems: Development and Evolution* (Academic Press, San Diego, CA, 2001).

BOOKS: PALEONTOLOGY

Everything You Want to Know and Moa

David W. Steadman

Welcome to New Zealand, where much of the biodiversity crisis is over. People won; native plants and animals lost. In this regard, New Zealand is not alone among oceanic islands. What sets this isolated, partly Gondwanan archipelago apart is its great variety of flightless birds, which includes two endemic orders. Before Polynesians arrived, New Zealand had at least 38 species of birds that could not fly (11 moas, 5 kiwis, 6 ducks and geese, 2 adzebills, 11 rails, a parrot, and 2 passerines). Of these, 29 are now extinct, and most of the 9 survivors are endangered. They and the other indigenous birds are the focus of Trevor Worthy and Richard Holdaway's *The Lost World of the Moa*. The volume is the first book-length paleontological treatment of New Zealand's terrestrial vertebrate fauna, whose native non-bird component consists only of frogs, skinks, geckos, tuatara, and bats. Although the phrase "lost world" sounds a little hokey and might suggest a movie in which people interact with dinosaurs, New Zealand sustained until recently a fauna that would seem fictional if not for the abundant bones it left behind.

The Lost World of the Moa
Prehistoric Life of New Zealand
by Trevor H. Worthy and Richard N. Holdaway
Indiana University Press, Bloomington, IN, 2002. 755 pp. $89.95. ISBN 0-253-34034-9.

Predator and prey. Haast's eagles (right skull) apparently fed on terrestrial birds as large as the giant moa, *Dinornis giganteus* (with a body mass of 200 kg or more).

Any faunal perspective other than paleontological is bound to be limited in New Zealand and its satellite islands. There the "human bolide" (to borrow from Paul Martin) has wiped out about half (70 of 145) of the native species of landbirds over the past millennium or two, with most of the losses occurring before the additionally damaging last two centuries of European influence. Many of New Zealand's surviving landbirds, whether volant or flightless, persist in small populations that occupy only a fraction of their former range. Data reported by Worthy and Holdaway are important to biologists who would like to know the natural distributions and habitat preferences of species in order to set conservation goals.

I love this book, in spite of the criticism I will offer. The authors, independent but prolific New Zealand paleontologists, devote nearly 200 pages to the 11 species of large flightless birds known as moas (Dinornithiformes). They exhaustively cover such topics as morphology, systematics, geographic distribution, extinction, and the history of moa studies. The systematics section is a little compromised by inconsistent use of "ratite" (a sternum without a keel) and "paleognathous" (a configuration of the palate). Although I am not a moaphile, I was glued to my chair while reading Worthy and Holdaway's impressive account of these most famous of New Zealand's birds. On the other hand, their coverage of the immense, extinct Haast's eagle (*Harpagornis moorei*) consumes 90 rather tedious pages, with 30 pages alone devoted to overly precise estimates of its body mass.

This exhaustive coverage of *Harpagornis* is part of the author's highly uneven, "bigger is better" treatment of taxa. The 78 species of snipes, plovers, pigeons, parrots, cuckoos, and passerines—mostly endemic species in endemic genera—are covered in only 28 pages. The 100 currently or formerly resident species of seabirds also get limited press. Whereas no less than 90 photographs or illustrations depict moas, most other avian species (and even genera) are not depicted at all. I would love to see, for example, skeletons of flightless passerines (the acanthisittid wrens *Dendroscansor decurvirostris* and *Pachyplichas yaldwyni*).

The authors provide few comparisons with faunas outside of New Zealand. Although this kiwi-centric approach is to some extent forgivable, biogeographers will be further disappointed that Worthy and Holdaway do not interpret their data in the context of models comparing species richness with land area, elevation, or isolation. They do, however, discuss faunal turnover. Here they teach what may be the most important biogeographic lesson in their and many other fossil-based studies: the species compositions of insular vertebrate faunas have been stable rather than dynamic for more than 100,000 years, cruising unscathed through glacial-interglacial cycles. Large-scale change occurs only when people arrive. Worthy and Holdaway emphatically state, "Indeed, all the species of vertebrate known from New Zealand in the past 100,000 years survived to within the past 2000 years."

On every Pacific island group with a relatively long fossil record (whether Tonga, the Hawaiian Islands, the Galápagos, or New Zealand), the evidence points to pre-human faunal turnover rates at least several orders of magnitude slower than those proposed by ecologists. This finding is not just an artifact of census interval; pre-human colonization and extinction truly were exceedingly rare. Except perhaps for rails, there was no Brownian movement of potential avian propagules to inoculate island avifaunas, nor were the changes in climate and sea-level sufficient to drive extinction. Although concepts of

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