proteins, which mediate short- and long-range interactions between cells. The best-known examples of developmentally important transcription factors are the family of Hox proteins, which are involved in, among many other things, specifying segmental identity along the antero-posterior axis. The interactions between the Hox genes themselves are extremely complex, involving at least six classes of regulatory elements, in addition to autoregulatory feedback mechanisms.

This tight regulatory coupling is probably one of the main reasons for the extreme evolutionary conservation of the architecture of the tightly linked *Hox* gene cluster. *Hox* genes lay down a ground plan in animals that translates amazingly well into major features — segments or modules — of their morphology. The universality of the *Hox* gene clusters has led to the — now often questioned — suggestion that the presence of a linked set of *Hox* genes is a defining characteristic of all animals, the so-called 'zootype'.

Evolution can select only for what is developmentally possible. The evo–devo field has matured, and now that we know conservation abounds, attention must focus on the big question — how does evolution make new and different things? Given the overwhelming similarity and stasis at many levels, ranging from genes and genomes to the interactions of genes in gene networks, how do differences between species arise? How can phenotypic differences be explained, and what, if any, are the rules of change? Carroll *et al.* argue that the answer probably lies largely in changes in the regulation of gene expression. I think that other kinds of molecular mechanism, such as alternative splicing, ribosomal RNA editing and gene duplication, will also be found to have major roles in explaining phenotypic diversification.

With regard to the influence of gene regulatory mechanisms in evolution, the *Hox* genes are prime examples of how selective and differential regulation of gene expression can confer distinct identities on body segments that were originally serially homologous. Such 'individuation' of segments, as Carroll *et al.* call it, results from the partial uncoupling of the underlying developmental program of each segment from the gene networks controlling the development of segments with other identities.

Carroll *et al.* describe how an increasing amount of work on the modular nature of the often extensive and complex regulatory regions of *Hox* and other developmental genes shows that it is neither accurate nor sufficient to try to explain the functions of a given evolutionary toolkit only in terms of the proteins it includes. The function of a protein always depends on the spatio-temporal context of its expression, which can be altered by changes in one or more of its gene's regulatory modules. A protein function can thus be dissociated from its original spatial and temporal pattern of expression, enabling the evolution of new gene and protein interactions, and thereby the evolution of phenotypic novelty or the individuation of particular segments and developmental modules.

Individuation of a module, such as the conversion of the gill arches of fish into functionally new structures such as jaws, or the conversion of arthropod segments used in locomotion into segments used for feeding structures, antennae or genital structures, is the stuff of evolutionary novelty. Modularity

The shrinking world of corals

Australia's Great Barrier Reef hosts the elegance coral, *Catalaphyllia jardinei*, shown above. The picture comes from *Corals of the World* by J. E. N. Veron (3 vols; Australian Institute of Marine Science, A$265). In the Indo-Pacific, the Bennett's butterflyfish, *Chaetodon bennetti* (right), feeds primarily on coral polyps, and is among the species affected by the mass coral mortality — from *World Atlas of Coral Reefs* by Mark D. Spalding, Corinna Ravilious and Edmund P. Green (University of California Press, $45, £29.95), which details the state of the world's coral reefs.