Zootaxa 1668: 55–60 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Invertebrate taxonomy and evolutionary developmental biology*

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**In*: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1–766.

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Abstract

Evolutionary developmental biology (evo-devo) is a new research area where the traditions of evolutionary biology and developmental biology merge together. As in the past there has been a fruitful two-way exchange between evolutionary biology and taxonomy, and also between developmental biology and taxonomy, now the way is open for two-way exchanges between taxonomy and evolutionary developmental biology.

Key words: Evo-devo, evolvability, heterochrony, model species, taxonomy

Introduction

Evolutionary developmental biology (henceforth, evo-devo, as it is usually called today) is a young, lively biological discipline. Evo-devo has its twin roots in two disciplines—evolutionary biology and developmental biology—which until recently have been progressing along independent routes. Comprehensive overviews of its origins, aims and methods are provided by Hall (1998) and Hall and Olson (2003); other useful book-size accounts, more selective in their approach, are Wilkins (2001), Minelli (2003), Carroll et al. (2005), Minelli & Fusco (2008).

As one should expect for a new, or newly re-established field of study, evo-devo is still struggling to define its own identity; the internal debate emerges clearly, for example, from the excellent overviews of Arthur (2002) and Müller (2008).

To some researchers (e.g., Carroll et al., 2005), this discipline is in essence comparative developmental genetics, that is, the comparative study of the spatial and temporal expression patterns of genes with major effects in controlling the processes leading to the establishment of body architecture (antero-posterior and dorso-ventral polarity, segmentation, appendages, and so on) in an adequate sample of model species. But

Accepted by W.A. Shear: 7 Nov. 2007; published: 21 Dec. 2007

others (e.g., Hendrikse et al., 2007) point to problems specific to evo-devo, such as the evolvability of structural traits and the origin of evolutionary novelties. Some theoreticians (e.g., Müller, 2003; Brigandt, 2006) see evo-devo as a research program basically in contrast to the Neodarwinian tradition in evolutionary biology, whereas others (e.g., Minelli in press) regard it as largely in continuity with this tradition, but also complementing it by a more adequate approach to the nature and origin of the intraspecific variation on which natural selection will operate.

Owing to its twin roots, in evolutionary biology and developmental biology respectively, evo-devo has much to say for taxonomy, and vice versa. Both parent disciplines have indeed a long tradition of two-way exchange with taxonomy.

Evo-devo's roots and animal taxonomy

For the relationships between taxonomy and evolutionary biology, it is enough to mention evolution's two giants: Lamarck and Darwin.

In the case of Lamarck, the influence of evolutionary thought is immediately discernible in his monumental *Histoire Naturelle des Animaux sans Vertèbres* (*The Natural History of Invertebrate Animals*) (Lamarck, 1815–22), as in this work the arrangement of taxa goes from the simplest to the most complex of invertebrate animals, exactly the opposite with respect to the traditional (e.g., Linnaean) progression from what was perceived as the highest pinnacle of complexity, i.e. man, down to the lowliest of creatures. In the case of Darwin (1859), the patterns of similarity and difference embodied in the classification offered one of the arguments through which the evolutionary message of the *Origin* was articulated. One might also add the strong positive influence left on Darwin's mind by his own taxonomic practice culminating in his extremely accurate barnacle monographs (Darwin, 1851a, b, 1854a, b).

Two nineteenth-century examples can be also offered of reciprocal positive influence between taxonomy and developmental biology. Spurred by Darwin's evolutionary theory and, to some extent, also by Ernst Haeckel's biogenetic principle (Haeckel, 1866), according to which ontogeny recapitulates phylogeny, numbers of embryologists swarmed to the just-founded biological stations of Europe and the United States, eager to find, in the embryos and larvae of all kind of invertebrates, the most reliable cues as to the phylogenetic affinities of the main animal groups. Their effort, sometimes perhaps off the mark—as twentieth-century critical assessments of the biogenetic principle eventually demonstrated—produced indeed, in some cases, unexpected results of lasting importance. A good example was the appreciation of the close affinities between vertebrates and ascidians (Kowalewski, 1866).

On the other hand, in the early days of comparative biology, when the science of living beings was still dominated by non-evolutionary views, classification provided the only possible framework onto which one could read the evidence obtained through the study of the ontogeny of different kinds of animals. Thus, when formulating his 'law of embryonic development', Karl Ernst von Baer (1828) could only equate the ontogenetic progression in the expression of increasingly more detailed anatomical traits to the classificatory progression in the increasingly specific nature of traits diagnostic of higher to lower taxa, in the order.

Due to its very recent origins, one cannot expect evo-devo to have already much to say in respect to taxonomy, or to have profited much from the latter, in return, but prospects, at least, are far-reaching (Minelli et al., 2007).

Taxonomy's contributions to evo-devo

Let us consider first the possible contributions of taxonomy to advances in evo-devo.

A first, perhaps an obvious contribution is in the suggestions a well-corroborated phylogenetic hypothesis may provide to establishing priorities in selecting model species for experimental studies. Moving away from traditional favourites like *Drosophila melanogaster* and *Caenorhabditis elegans*, evo-devo has been adding more and more species to its model list, from the anthozoan *Nematostella vectensis* to the amphipod *Parahyale hawaiiensis*, from the spider *Cupiennius salei* to a couple of sea urchin species in the genus *Heliocidaris*.

In most cases, the choice has been informed by quite coarse taxonomic criteria (in addition to obvious technical reasons of availability and easy breeding and handling in the lab). In some cases, however, the search for additional species to be investigated in terms of developmental mechanisms has being more sensibly informed by phylogeny, as in the rapidly growing number of nematodes whose embryos are becoming fashionable as an additional (and very informative) source of information to be compared to the better known, but in some ways idiosyncratic *Caenorhabditis elegans*; see, for example, Schierenberg & Lahl (2004), Houthoofd et al. (2006), Schierenberg and Schulze (2008), Zauner and Sommer (2008). Specifically, the modern nematode phylogeny of Blaxter et al. (1998) and De Ley & Blaxter (2002) has been carefully explored to obtain a background for the choice of experimental model species and for the subsequent comparative evaluation of results. I expect that for other major groups of invertebrates, e.g. molluscs, annelids and arthropods, critical lists of evo-devo model candidates will soon be proposed and discussed, as has been recently done for amniote vertebrates (Milinkovitch & Tzika, 2007; Tzika & Milinkovitch, 2008).

However, if a sensibility towards phylogeny is eventually gaining respectability among many experimental biologists, we must also lament that the most elementary caution in correctly identifying newly collected animal stocks to be used in the lab is quite often overlooked. Overlooking this bottom-level use of taxonomy may cause serious trouble, as in the case of an important experimental work performed over the years on leech development: the worms bred in the labs and uniformely regarded as belonging to the species *Helobdella triserialis* eventually were found to belong to three different species (Bely & Weisblat 2006).

On a more technical level, evolutionary developmental biology has burrowed from taxonomy a little bit of cladistic methodology, to employ it in the study of heterochrony. We apply the term heterochrony to all those instances where, in a comparison between more or less closely related species, there are differences in the rate or in the time of initiation or completion of a given developmental process in respect to other developmental processes in the same animals; see the classic treatments of de Beer (1958) and Gould (1977) and the more recent work by McNamara (1986, 1995) and McKinney and McNamara (1991).

Modern approaches to heterochrony are based on comparisons of developmental sequences, defined as lists of different events in the chronological order in which they happen along the ontogeny (Schulmeister and Wheeler, 2004) and including a series of morphological states through which a given embryonic structure passes (Bininda-Emonds et al., 2002). Any developmental sequence is characterized by the particular order of events along the sequence itself. Of any two events, A and B, in a sequence, A may occur before B, or simultaneously with it, or after B. Each of these relationships is an event-pair that can be given a numerical score (Smith, 1997; Velhagen, 1997) and developmental sequences are finally assembled in a data matrix to be analysed under the criterion of maximum parsimony to reconstruct a kind of phylogenetic tree (Jeffery et al., 2002). Up to now, this new approach to heterochrony has been only applied to vertebrate data, but it would be worth applying it also to invertebrates with complex life cycles, like many crustacean and insect taxa. This may even help clarifying our still contentious views about the evolution of arthropod life histories, including the origin of holometaboly (Heming, 2003; Minelli et al., 2006).

The most obvious help taxonomy can offer to the progress of evo-devo is, however, by providing phylogenetic scenarios onto which to map comparative data concerning developmental processes or their outcome. An example is the morphology-based phylogeny of the mecistocephalid centipedes, onto which Bonato et al. (2003) mapped the number of body segments, thus inferring direction, size and reversibility of the evolutionary changes in this trait during mecistocephalid evolution.

Evo-devo's contributions to taxonomy

Let's finally mention briefly some questions where the relationship between taxonomy and evo-devo runs the other way, the former obtaining from the latter either data or interpretative insight.

Most of the major changes in our appreciation of phylogenetic relationships among the major lineages of metazoans have been suggested by comparative molecular evidence, nevertheless a careful assessment of comparative developmental data has been sometimes important in generating, or supporting, new phylogenetic hypotheses. The most obvious example is probably the Ecdysozoa, the supraphyletic assemblage of 'moulting invertebrates' (Aguinaldo et al., 1997) within which morphologically disparate invertebrates like arthropods and nematodes are now currently grouped together.

Knowledge of developmental mechanisms and the appreciation of the evolvability of traits, as expressions of genotypic information ontogenetically translated into phenotypes, may substantially help avoiding one of the most insidious pitfalls in all phylogenetic analyses, that is, a wrong appreciation of the degree to which two characters we want to treat as separate entries in our matrices are in effect mutually independent (Minelli et al., 2007). I would bet in the near future we will witness important progress in invertebrate taxonomy spurred by a careful evaluation of the evolvability of traits, that is, with due attention paid to what an evo-devo perspective can offer.

This will bring to a firmer rejection of residual recapitulatory views. Of course, there is no reason to expect that earlier embryonic or larval stages should *never* be more conservative than later developmental stages, but there are good reasons to suggest that in many instances exactly the opposite is more likely true. In insects, for example, the holometabolous larvae are to a large extent more derived than the corresponding adults. And there are good reasons for that, as the adult, being deprived of a chance of extending the reproductive age over temporally distinct alternative phenotypes—as no more moults are available following the onset of sexual maturity—is much less prone to selection, and thus to heritable change, than the insect's pre-reproductive stages.

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