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BOOK REVIEW

WILLIAMSON D.I.: LARVAE AND EVOLUTION. TOWARD A NEW ZOOLOGY. Chapman and Hall, New York and London, 1992, XVI+223 pp. Hardbound. ISBN 0-412-03081-0. Price GBP 29.95.

I was somewhat surprised when, two years ago, I received a review copy of this book, admittedly upon my request. This feeling became discomfort when I read it. I have long hesitated whether to review it in this journal, and if I finally decided to do so, the main reason was to inform those who, like me, might think that such a book simply *must* contain plenty of material about insects. Two other reasons were that the book is concerned with problems of general interest, and that it will probably become a curiosity in the biological literature. For the inappropriate title is not the only thing to be criticized.

The book concentrates on planktonic larvae of Echinodermata, Hemichordata, some Crustacea, and a few other marine groups exclusively. On the dust jacket, the publisher characterizes it as follows: "This book proposes a radical solution to the otherwise unexplainable incongruities between larval and adult form in a number of invertebrate phyla. The author proposes that after the adult lineage had been established, hybridizations took place by which one animal acquired the larval form of another. Thus is proposed a new, non-Darwinian evolution taking place alongside conventional evolution. The implications of this hypothesis for evolutionary theory and for animal systematics are profound."

To begin with, few would now disagree that some reticulate evolution, and hybridization in particular, took place in the history of living organisms. Certainly, many cases of hybridization could be cited by specialists, with the results being usually more or less intermediate between the two parent organisms. However, Williamson's theory is unusual in two aspects. It proposes (particularly in the case of the Hemichordata and Echinodermata commented upon in more detail below) a hybridization of complex and yet, according to Williamson, entirely unrelated forms, and the result is an ontogenetic succession of life forms of which the first is determined by one parent organism and serves as a carrier from which (or even within which) develops the second form determined by the other parent organism; in other words, an abrupt switch is postulated in the ontogeny from the genetic material inherited from parent 1 to that inherited from parent 2. Williamson calls such an organism a "sequential chimera". An extraordinary theory indeed, and it is therefore not unfair to expect powerful arguments to support it.

I shall ignore some minor issues of the book, such as the apparent conflict of larval and adult characters in some crustacean groups and the presence of trochophore-type larvae in several phyla with "very different" adults. A thorough phylogenetic analysis (and reading the book convinces me that Williamson is not very familiar with such analysis) might solve such cases without postulating horizontal genetic transfers resulting in inserts into the life cycle of larvae borrowed from others. I will concentrate on the main topic of the book (treated mainly in chapters 5 through 9 and 13), which is the Echinodermata.

Reading the book without knowledge from other sources, you might get an impression that the ontogenetic development of the Echinodermata is very unusual: there is a bilateral planktonic larva within which, from internal somatic tissues, later originates a small radially symmetrical juvenile echinoderm which, at a certain stage, breaks the larval body wall and leaves for a benthic or sessile life, while the larval organism sooner or later dies; rarely the deserted larva may continue to live for a prolonged period of days or even weeks. (Williamson on p. 88: "Early juveniles develop as quasiparasites within their respective larvae.") It has been long known that the larval type of Echinodermata is essentially similar to that of the Enteropneusta (Hemichordata), and most authors regarded this as an evidence of relationship while the morphology of adult echinoderms was considered secondarily derived, possibly in connection with an originally sessile life as found in the sea lilies (Crinoidea) (note that, for example, many sea stars undergo a sessile phase during metamorphosis). Williamson takes a very different point of view. He considers that (i) the phylogenies derivable from larval and adult forms of Echinodermata are irreconcilable, and, therefore, (ii) the larvae and adults of echinoderms represent two forms of different origin: primitively, echinoderms lack a larval stage, are basically radial schizocoelous protostomes, and the bilateral deuterostome larva was acquired from enteropneusts by hybridization and inserted at the beginning of echinoderm ontogeny. In places, Williamson even suggests that, particularly, the ectodermal organs in adult echinoderms are not homologous with (i.e., not developed from parts of) those of the larva (pp. 63–64). If this is not enough, horizontal transfer of larvae is proposed even between some groups within Echinodermata, e.g., between brittle stars and sea urchins, which have similar larvae but dissimilar adults (I emphasize the word "dissimilar" since sound phylogenetic argumentation is lacking throughout). Papers (based on biochemical analyses) suggesting close relationships between brittle stars and sea urchins are easily dismissed as possible results of environmental similarities (p. 88).

If Williamson was correct, echinoderms would be truly unique (I cannot resist mentioning the long-abandoned "animal in animali" Swammerdam's encasement theory of holometabolous insect development – see, e.g., Packard, 1909: 641–643). Fortunately, his picture is considerably distorted. First, the echinoderm larva and adult are *not* two different animals. Even if we accepted the idea that separate gene sets could be maintained and switched on or off as a whole within an animal (a similar idea of separate larval and adult genes in insects has been mostly abandoned, at least in its rigid form of non-overlapping gene sets), larval organs (including those ectodermal) are used and rebuilt during the course of metamorphosis. For example, originally, the hydropore (through which the water vascular system communicates with sea water) opens on the larval ectoderm and is taken over into the adult (usually forming the plate of the madreporite) without any disconnection and shifts. Some limited parts of the larva give rise to disproportionately large parts of the adult while other parts "lag" in development and some specialized larval organs are resorbed or even discarded (in many aspects this is analogous to the highly allometric and sometimes destructive metamorphosis of holometabolous insects, particularly those derived groups possessing structures known as imaginal discs). And yet we cannot interpret the echinoderm metamorphosis as a replacement of one organism with another. From the mere fact that the "larval" polyploid cells are destroyed during fruit fly metamorphosis, or that termite or ant reproductives can shed the wings when they are no longer needed, it does not follow that we are witnessing a succession of two different animals.

Second, adult echinoderms are *not* radially symmetrical – many structures disturb the (usually pentaradial) symmetry, particularly as far as the internal organs are concerned. More important, even the structures which *are* radial in the adult do not originate as such. For example, the water-vascular system originates unilaterally (usually from the second left coelomic sac known as the left hydrocoel), and its prospective radial canals originate serially. Only later twisting of the whole structure gives rise to the circular canal and radial canals of the pseudoradial adult. During larval development (Ivanova-Kazas, 1978: 26) or regeneration (Brusca & Brusca, 1990: 828), some sea stars produce temporally paired hydropores or madreporites, of which one later disappears.

Third, nature abounds in examples of extreme sequential ontogenetic polymorphism governed by the same genome, and we should not (and need not) postulate horizontal transfer of genes, and much less so of whole life forms, merely because of such polymorphism, without bringing strong evidence (and, in my opinion, Williamson has failed to bring such evidence). Disappearance of intermediate forms is nothing surprising, but if there are no transitional situations between the gradual relatively non-destructive metamorphosis of enteropneusts and the abrupt more or less destructive metamorphosis of echinoderms, Williamson could have found such transitions in other animal groups, including insects. Indeed, he touches the drastic metamorphosis in some insects (p. 66), and even admits that "perhaps, however, the caterpillar may be regarded as a phase in development transferred from an onychophoran or a myriopod." While the idea of hybridization between distant groups is conceivable in marine animals, which often release at least the sperm into water, I would ask the reader to imagine a pterygote insect copulating with, for example, a centipede (if this was the author's intention).

The corollary of the book: Williamson mixed eggs of *Ascidia* (Urochordata) with sperm of *Echinus* (sea urchin) and, in a few experiments, some eggs purportedly hatched as ciliated blastulae (ascidian eggs normally produce a tadpole larva) and developed further into typical echinoplutei; a few of them metamorphosed into apparently normal sea urchins. This experiment is taken as a proof that the development of a hybrid can be "paternal" from the very early stages. At the time of publication, no karyotypic or other genetic investigation of these specimens had been made. The experiments are not described in sufficient detail to permit judgment about possible contamination with eggs of *Echinus*. Whilst reviewing this book for *Nature*, Cohen (1993) noted that other described cross-fertilizations showed maternal development, at least in the earliest stages (before the zygote-prescribed messenger RNA begins to be transcribed). Also, as Cohen puts it, DNA is prescriptive, not descriptive. In plain language, genes do not bear a rigid information about the final morphology, regardless of the milieu in which they are placed. Modern developmental biology emphasizes the enormous "maternal" effect on the early development, independent of the genes the zygote receives (see, e.g., Lawrence, 1992 for *Drosophila*). Even if we admit that this effect may be much weaker, particularly in marine animals with free spawning and following external fertilization, it would be probably unacceptable for most developmental biologists that the early development of a hybrid between radically different animals could be so completely determined by the genes brought in by the microgamete.

Many other weak points can be found, including the sometimes naive mechanistic ideas about genetic mechanisms, the lack of sufficient discussion of the embryogenesis of those forms of Echinodermata possessing a direct development and the often outdated or dogmatic use or interpretation of some terms and processes (in particular, deuterostomy and coelom formation).

There are some unfortunate books in which an erudite author, based on careful study of facts, makes an entirely false conclusion. With all the open-mindness I am able to show, I am afraid that Williamson's book will become a very prominent example of this category.

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