BOOK REVIEW

SCHWALM, F. E. 1988. Insect Morphogenesis. S. Karger AG, Basel. xix + 356 pp., 94 figs., 14 tables, subject index. $ 261.00 CAN!

Among the most active research areas in Biology today is that dedicated to understanding how genes control embryonic development in animals. Although progress towards achieving this goal has been phenomenal this past decade, principally because of the imaginative use of genetic engineering techniques, it has resulted from intensive study of less than a dozen, easy-to-maintain, "lab animals": the nematode, *Caenorhabditis elegans,* a few sea urchin and annelid species, the amphibian *Xenopus laevis, Drosophila melanogaster,* and the house mouse, *Mus musculus.* Not the least among the dangers of such narrow focus is production of a generation of biologists expert in the burgeoning techniques of molecular biology but unable to teach development from a comparative viewpoint and only at the lowest levels of biological organization. These levels are remote from the personal experience of most students and inaccessible to the senses but for 'laboratories' of high tech equipment. Also, it can be argued (e.g. Bartholomew, 1986. Bioscience 36: 324-329) that to ask *incisive* questions about any aspect of its life, we must know the phylogenetic position of the animal being studied and have knowledge of higher levels in its organization particularly those concerning the whole animal and how it lives. Thus, is there still a place for a 'comparative embryology' such as this volume by Fritz Schwalm.

The book contains a preface by Friedrich Seidel (the "father" of experimental insect embryology), an introduction (3 pp.) and eight chapters concerning, respectively: systematics (4 pp.), imaginal morphology (17 pp.), gametogenesis and sex determination (63 pp.), insect culture and egg collecting techniques (13 pp.), oviposition and parental care (7 pp.), mating, egg structure and fertilization (19 pp.), tables of embryonic development (12 pp.) and a concluding chapter (at 147 pp., the "meat" of the book) on the structural aspects of insect embryogenesis.

In his preface, Seidel summarizes some high points in the early experimental study of insect embryos, emphasizing particularly results from his laboratory in the 1920's that demonstrated the existence of three physiological centres whose activity was required for normal blastoderm (the cleavage centre) and germ anlage formation (the activation centre) and for subsequent differentiation (the differentiation centre) of damselfly (*Platycnemis pennipes*) embryos. In addition, he comments at some length on the negative impact that evolutionary thinking has had on progress in experimental embryology and lauds Schwalm for writing "a monograph on 'pure' morphology" devoid of evolutionary speculation. Chief among the 'destructive' contributions he mentions is Ernst Haeckel's [1866] 'Biogenetic Law' (i. e. "Ontogeny recapitulates phylogeny"), pervasive in the late 19th and early 20th centuries, which suggested that since phylogeny was the "cause" of ontogeny, its experimental analysis was unnecessary. Because of his stature at that time in the

European scientific community, Haeckel was successful for some years in preventing such analysis from beginning. (Haeckel also postulated the existence of an hypothetical ancestral taxon, the "Gastraea" whose adult stage was never found despite numerous attempts to do so and which was thought to be recapitulated in the ontogeny of many modern animals as the *gastrula*). Seidel considers the primary contribution of developmental morphology to be provision of a structural basis for experimental study and implies that use of developmental information to establish homology of structure and to reconstruct phylogeny is of minor importance. The many biologists to-day (*e.g.*, Alberch, Bonner, Gould, Nelson, Smith, etc.) who are attempting to re-introduce consideration of ontogeny into evolutionary thinking, would disagree.

Seidel also discusses the concept of the "Korpergrundgestalt" or *basic body pattern*: an embryonic stage in the development of an animal that clearly identifies the higher level taxon to which that animal belongs. Members of a monophyletic lineage not only express their common phylogenetic origin in an easy to see way for the first time at this stage but diversify from it with subsequent development. For most hexapods, this stage is the "polypod" embryo: a fully segmented form usually bearing paired appendages on most of its body segments. Species as distantly related as bristle tails, mayflies, cockroaches and beetles pass through it on their way to hatching. (One should not confuse this concept with the "Ground Plan" of phylogenetic systematists which constitutes the collective, ancestral character states of a taxon).

In his introduction, Schwalm refers briefly to some of the recent, illuminating, experimental work on regulatory genes now being carried out in *Drosophila* embryos: specifically the 'segmentation' genes whose normal expression results in determination of blastoderm cells to organise into a repeating series of homologous, segment primordia and the 'homoeotic' genes which specify segment identity and position. He recalls too E. B. Lewis' idea that the mesothorax is the '*basic body segment*' or "segment grundgestalt" upon which products of the homoeotic genes work to generate the diverse insect segments we now see.

Schwalm's objectives in writing the book were to: "...present embryonic morphogenesis in a sequence of 'typical' events which interdigitate with earlier and later events as the embryo forms..." and to identify differences in development among insects that are worthy of further analysis. He is reasonably successful in achieving these goals.

His chapters on systematics and adult morphology were obviously written by one who has little knowledge of or interest in either since they are poorly done and are not referred to again. Chapter 1 includes two cladograms revised from the works of Hennig, Kastner and Kristensen that can be used by the reader to organise the observations presented elsewhere in the book within an evolutionary framework. He considers the entognathous apterygotes (Collembola, Protura, Diplura) to be monophyletic and to constitute the sister group of the remaining insects; not to be separate classes as many recent authors (e.g. Jamieson, Manton) have suggested. Chapter 2 contains some appropriate, though superficial, information on male and female reproductive systems and genitalia, but its brief summaries of distribution and behavioural adaptations seem totally out of place in a book on embryogenesis. He offers nothing about the role of sexual selection in shaping insect genitalia (see Eberhard, 1985. *Sexual Selection and Animal Genitalia*. Harvard).

In Chapter 3 are brief but reasonably up-to-date summaries of sex determination, hermaphroditism, parthenogenesis, heterogony and viviparity, oogenesis and egg membranes, spermatogenesis, sex ratios, life cycles and metamorphosis, neoteny, paedogenesis, caste formation in social insects, and quiescence and diapause. Coverage of comparative aspects is encyclopaedic and is presented in tables that include appropriate literature citations: Table I (6 pp.): oogenesis; II (2 pp.): synthetic activities of oocyte nuclei; III (2 pp.): types of parthenogenesis; IV (1 p.): sex ratios in Hymenoptera; and V (4 pp.): fecundity and duration of developmental stages.

Rearing and egg collecting methods are described in Chapter 4 for 69 species in 16 orders (Archaeognatha-2 spp., Zygentoma-2, Ephemeroptera-3, Odonata-10, Plecoptera-1, Phasmatodea-1, Orthoptera-6, Dictyoptera-2, Isoptera-2, Hemiptera-5, Coleoptera-11, Hymenoptera-6, Trichoptera-1, Lepidoptera-6, Mecoptera-1, and Diptera-11) and should be useful to investigators seeking for research beasts other than *Drosophila* upon which to work.

A straight, descriptive account of oviposition and egg masses in Chapter 5 informs us that Collembola "...deposit about 250 eggs in batches..." and that "... Psocoptera lay individual eggs or form cocoons with egg batches...". Schwalm seems not to realise that individual females, not taxa, deposit eggs. Generalizations such as these are of little value since they are based on detailed knowledge of a few species whose identities are only sporadically revealed.

Mating behaviour, and the size (Table VI: 3 pp.), shape, maturation, internal structure and fertilization of eggs are discussed in Chapter 6 while tables of embryogenic development comprise Chapter 7: Table VII (6 pp.): the literature of descriptive embryogenesis arranged by order and VIII (4 pp.): timetables for major morphogenetic events in the embryogenesis of 52 species in 18 orders (Collembola-1 sp., Archaeognatha-2, Zygentoma-1, Ephemeroptera-1, Odonata-1, Plecoptera-1, Phasmida-1, Orthoptera-5, Dictyoptera-3, Isoptera-1, Hemiptera-4, Coleoptera-6, Megaloptera-1, Neuroptera-1, Hymenoptera-6, Trichoptera-1, Lepidoptera-10 and Diptera-4) . Both tables are filled with information that would require much effort to extract from the primary literature.

The final chapter is a detailed, well illustrated summary of embryonic development beginning with cleavage and ending with hatching. Coverage is extensive and up-to-date and on insects selected from throughout the class. Only very recent discoveries are not mentioned (*e.g.,* Ball and Goodman's [1983, 1985] ingenious experimental work on muscle pioneers in locust embryos [Nature 301:

66-69; Dev. Biol. 111: 383-418], Campos-Ortega and Hartenstein's [1985] superb book on the embryogenesis of *Drosophila* and recent papers on the embryogenesis of Thysanoptera [Heming, 1979. J. Morph. 160: 323-344; 1980. *Ibid.* 164: 235-263; Haga, 1985. Rec. Adv. Ins. Embryol. Jap. 1: 45-106; and Moritz, 1988. Zool. Jb. Anat. 117: 1-64]). The book contains 1255 references of which 156 were published after 1980.

Much comparative information is, again, presented in tables: Table IX (4 pp.): duration of nuclear cycles during cleavage; X (1 p.): vitellophage fate; XI (1 p.): pole cell formation; XII (1 p.): intercalary appendages; XIII (1 p.): head segmentation; and XIV (1 p.): embryonic abdominal appendages and their fate.

The book is nicely printed on good quality paper and seems to be strongly bound but is exorbitantly priced and has numerous typographical errors and a substantial number of errors in interpretation. In his preface, Seidel hopes "...that the volume will find wide distribution and that it will generate new developmental concepts for experimental analysis" (p. xvi). At $ 261.00 (CAN) this is hardly possible since onl; the most pecunious of libraries and individuals will be able to afford it. Also, much of its content is better presented in other works that are readily available in most libraries (*e.g.,* Anderson, 1973. *Embryology and Phylogeny in Annelids and Arthropods,* Pergamon Press; Counce and Waddington [eds.], 1972, 1973. *Developmental Systems: Insects,* Vols. 1 & 2, Academic Press; Haget, 1977. *Traité de Zoologie*, Vol. 8, part 5Ba: 1-262; 279-387. Masson et Cie; and Sander, Gutzeit and Jackle, 1985. pp. 319-385 *In* Kerkut and Gilbert [eds.] *Comparative Insect Physiology, Biochemistry and Pharmacology.* Vol. 1. Pergamon Press).

Below I note some of the more obvious errors in interpretation:

p. viii: insects do *not* constitute a phylum;

p. 14: the Devonian formations he refers to are 375–400 million years old *not* 350;

p. 20: the Monarch Butterfly, *Danaus plexippus*, is a new world species;

p. 46: Thysanoptera are *not* known to have nonparthenogenetic paedogenesis. Rather males of the thripid, *Limothri, denticornis* develop more rapidly than females, are preferentially attracted to an ate with female pupae and lodge fully differentiated spermatozoa in their still un. ished spermathecae (Bournier, 1956. Arch. Zool. exp. gen. 93: 219-317);

Tables I, III, V, X: numerous misplacements of genera or the laboratory species of various authors into families and higher taxa;

p. 73: adult aphid macropterae usually develop in crowded conditions not the opposite;

p. 230: the pleuropodia of the phasmid, *Carausius* develop from modifications in the embryonic appendages of abdominal segment 1 (ectodermal), as in many other insects, *not* from secondary coelomic sacs (mesodermal) (Louvet. 1976. Int. J. Ins. Embryol. Morphol. 5: 35-49);

during larval development, eventually to generate large numbers of imaginal neurons which differentiate during metamorphosis (Heming [1982] J. Morphol. 172: 23-43; Booker and Truman [1987] J. Comp. Neurol. 255: 547-559; Truman and Bate [1988] Dev. Biol. 125: 145-157.);

p. 254: the description of mouthpart morphogenesis in thrips is derived from Risler's (1956) account of *adult* mouthparts in *Thrips physapus*. A full description of their *embryonic* development in *Haplothrips verbasci* is presented by Heming (1980. J. Morphol. 164: 235-263).

p. 255: labels for labial palpus and paraglossa are incorrect in Fig. 85c;

p. 257: salivary gland invaginations in *Drosophila* are here said to originate between the labial and prothoracic segments; in Fig. 86c, they are shown as being located between the maxillary and labial segments.

Finally, there are numerous inconsistencies in the use of subtitles and some of his paragraphs go on for pages. Considering the above, one is better advised to purchase one of the general references cited above.

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