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BOOK REVIEW

MATSUDA, R. 1976. Morphology and Evolution of the Insect Abdomen - with special reference to developmental patterns and their bearings upon systematics. International Series in Pure and Applied Biology. Volume 56. Pergamon Press, Oxford and New York. viii + 532 pp., 155 text-figures, 1 table, author, subject and taxonomic indices. Cloth $34.00 (U.S.).

In 1965, Matsuda published "Morphology and Evolution of the Insect Head" (Memoirs of the American Entomological Institute, Volume 4), the first of a series of works in which he proposed to review more recent studies on insect morphology. His second volume "Morphology and Evolution of the Insect Thorax" (Memoirs of the Entomological Society of Canada, Volume 76) appeared in 1970 (see review in Quaestiones Entomologicae 7(2): 284-286, 1971) while the third (and last?), the subject of this review, came out in 1976.

This book is larger (532 pp) than the first two (respectively 334 and 431 pp) and its coverage of the literature apparently more extensive (2173 vs. 586 and 744 refs.), although these differences could reflect the relative research activity directed towards each tagma of the insect body. As before, Matsuda's goal is to "determine the homologies of structures in the light of recently accumulated facts (p. 1, 1965) . . . using as many kinds of evidence as possible." (p. 2, 1965). The evidence he marshalls in this volume has its origin in descriptive and experimental embryology and postembryology, developmental genetics, comparative morphology, palaentology, and, to a lesser extent than in his previous works, phylogeny. He omits discussion of musculature (an important component of his previous volumes) because (p. vii) "homologies of the kinds of structures treated in this work can safely be established without reference to the associated musculature." This may be true but it results in this work being of less value than previous ones to biologists interested in how structures work. As before, his conclusions are based on his reading, interpretation and digestion of published work - not on the results of his own investigations.

The book is in three parts: the principles of structural evolution (45 pp), a general discussion of the abdomen (56 pp) and comprehensive treatments of the abdomen and its appendages in representatives of each order (318 pp).

In part I, Matsuda provides the theoretical and philosophical framework for his analyses of homology of structure which follow. *Homology* is the inheritence, through natural selection, of structures of descendants from those of a common ancestor. The development of these is often *heterochronic* in different insects, ie. the timing of morphogenesis of homologous structures has often become *retarded* or *accelerated* in different evolutionary lines. Metamorphosis, neoteny, caenogenesis, hypermorphosis, the "biogenetic law", and "law of deviation" are all manifestations of or generalities on heterochronic development. With *substitution*, one developmental process is replaced by another in producing a homologous structure in different animals.

Matsuda emphasizes that the concept of homology applies primarily to the end product of morphogenesis, ie. to the functioning, differentiated structure be it embryonic, larval, or imaginal, because it is on the finished structure that selection works. He also provides a list of criteria that one can use to establish homology between any two structures (eg. position of the structure relative to another, special features of the structure (often the only criterion used by palaentologists), developmental sequence of complex structures, development of muscles and exoskeleton and innervation) and discusses the various kinds of homology presently recognized.

Homology of a complex organ must be determined from study both at the level of the whole and at the level of its components. The penis and ovipositor, for example, have been largely maintained as homologous organs throughout insect evolution (complete homology) but their components, in different evolutionary lines, have undergone frequent modification due to reduction, loss, interiorization, fusion of preexisting components and addition of new components (incomplete homology). *Serial Homology*, the structural correspondence among repetitive or serial structures within a single individual, is a concept that features prominently in controversies concerning the sternal or appendicular origin of insect genitalia and larval abdominal legs; these are discussed by Matsuda in part II.

When considering homology, one must be aware of the havoc that convergent evolution can wreak on one's conclusions. *Convergence* is the development of similar structures separately in two or more lineages without a common ancestor but involving adaptation to similar ecological status. The *analogous* structures which result thus have functional similarity not related to common ancestry.

Part I is an original and valuable contribution because it expands upon numerous topics ignored by most recent students of insect structure. Unfortunately, it is sorely marred by foggy exposition. Matsuda's hope (expressed in his acknowledgements) that "I have a right amount of "the" in the manuscript." is - alas - not realized. Rather, he usually has "the's" where they shouldn't be and leaves them out where they should be. Here is Matsuda's definition of the biogenetic law: "The essence of the biogenetic law or Haeckel's law, is that ontogeny consists of the stage of development in which the adult structures of the ancestor are recapitulated by the function of heredity (palingenesis) and the stage in which the reconstruction of the adult structures of the ancestor does not take place (caenogenesis); the latter falsifies the aspect of palingenesis." This statement has a higher "fog index" than "ontogeny recapitulates phylogeny." There are numerous additional examples - all pointing to a lack of editorial attention to the manuscript by those having English as their native tongue. This is not a criticism of Matsuda but of the editorial board of Pergamon Press.

In part II, Matsuda summarizes the conclusions of his detailed, order-by-order-analysis of the insect abdomen (part III). He has chapters on segmentation, abdominal appendages, male and female external genitalia, efferent ducts and abdominal ganglia. He believes the ancestral number of segments in the insect abdomen to be 12 (including the telson) but shows how this number is reduced in members of most taxa through loss or fusion of segments during subsequent development. This reduction makes recognition of segment number in larval or adult abdomens difficult because of the possibility of originally non-adjacent segments becoming juxtaposed.

The criteria by which he defines a segment are the presence of paired 1) segmental ganglia, 2) coelomic sacs and 3) appendages in the embryo, of 4) intersegmental sutures, and of a segmental pattern of 5) chaetotaxy, 6) innervation, 7) musculature, and 8) spiracles. Based on presence of these, the telson is not a segment in spite of Matsuda's statement to the contrary (p. 52) because only 4 and 5, in a few insects hold true for it.

According to Matsuda, paired segmental appendages develop on abdominal segments 1-11 in embryos of most species in most, less-derived, evolutionary lines. In numerous groups one or more pairs of these develop directly into larval prolegs and/or into other larval appendages. Matsuda uses this developmental continuity to oppose Hinton's (1955. Transactions of the Royal Entomological Society of London 106: 455-545) widely-accepted theory of multiple, independent, secondary origin for these structures. However, Matsuda does not do this as convincingly as he could. If one plots the presence of embryonic appendages and larval prolegs on a dendogram showing the presently-accepted cladistic relationships of insect orders, one finds prolegs to be absent from members of many orders (eg. Orthoptera) whose embryos have appendages and present in members of other orders (eg. many Diptera) whose embryos do not. Even within lower monophyletic taxa, abdominal appendages are present in larvae of some groups, and are absent from larvae of other groups.

Because of this variation, prolegs can be considered homologous throughout the Insecta only if they can be traced directly to embryonic abdominal cells in appendage - less embryos having a latent potential to develop embryonic appendages in Scudder's sense (1964. Canadian Entomologist 96: 405-417). Matsuda implicitly accepts this idea to interpret data on prolegs. However, he does *not* accept Scudder's reasoning when considering the presence or absence of direct developmental continuity between embryonic abdominal appendages and imaginal male and female genitalia (pp. 90-91 - see below).

Experimental evidence is available to support the existence of latent homology. The "notched sternite" mutant of *Blattella germanica* which has many of the abdominal characteristics typical of Thysanura (pregenital styli, division of abdominal sterna into median and lateral sternites and paired abdominal membranous outgrowths comparable to the eversible sacs) reveals, in this species, the presence of relict genetic mechanisms which may have influenced or controlled development of abdominal segments in some Thysanura - like ancestral form (Ross, 1966. Annals of the Entomological Society of America 59: 473-484; 1160-1162). I see no reason why similar genetic mechanisms could not exist in most insects.

Matsuda also uses this evidence to support Berlese's theory in which larvae are claimed to be free-living embryos that hatch at earlier (protopod) or later (polypod, oligopod) stages of development.

The appendages of abdominal segment 1 develop into the purely embryonic *pleuropodia* in investigated representatives of orders other than Collembola, Ephemeroptera, Dermaptera, Psocoptera, Neuroptera, Hymenoptera, Mecoptera, Siphonaptera, Diptera and Strepsiptera. Their role in embryogenesis is mostly unknown but appears to vary greatly in different insects (their contributions to embryonic nutrition, hatching and electrolyte transport have been demonstrated experimentally in embryos of different insects).

In females of Acrididae and Tettigoniidae (Orthoptera) the ovipositor valves of segments 8 and 9 develop directly from the embryonic appendages of these segments and in males the external genitalia from those of segment 10. These structures have a proven appendicular origin only in members of these families. In most investigated representatives of other orders, the external genitalia of both sexes appear to arise *independent* of the embryonic appendages from *sternal* epidermis of the genital segments. This occurs either after the embryonic appendages have withdrawn into the abdominal epidermis (in members of those taxa having such appendages) or *de novo* (in members of those taxa lacking them). Matsuda thus refuses to accept a leg origin for insect genitalia and criticizes workers such as G.G.E. Scudder and E.L. Smith for using leg terms for genitalic structures.

As mentioned above, Matsuda uses the evidence of direct developmental continuity between embryonic abdominal appendages and larval prolegs to support homologizing the prolegs of all immature insects having them. If he accepted Scudder's (1964) thesis of latent homology between embryonic appendages or equivalent cells and insect genitalia, he could do the same for insect genitalia. He does, in fact, homologize the valvular ovipositor in female insects and the penis in males throughout the Insecta - but *not* on this basis. Instead, he considers the *apparent* appendicular origin of genitalia in acridids and tettigoniids to have arisen secondarily through acceleration and substitution in the cells determined to form these structures. Additional evidence of a sternal origin for genitalia exists in Thysanura where the ovipositor of females arises *between* the coxopodites of the eighth and ninth segments, only the latter developing from embryonic abdominal appendages of these segments.

Until further evidence is accumulated, I am inclined to agree with Matsuda on both counts even though the evidence for his concept of "homology through substitution" is not strong.

In most insects, Matsuda considers the penis (phallus of Snodgrass) and its accessory structures to arise postembryonically from a pair of primary phallic lobes in the sternal epidermis at the posterior margin of segment 9. In those insects (some species of Phthiraptera, Homoptera, Coleoptera and Diptera) in which they appear to arise on other segments (7, 8, or 10), one or more adjacent segments have probably been lost through segmental reduction or fusion. The later differentiation of these lobes into the diversity of structures so loved by insect systematists provides good examples of Matsuda's *law of deviation* (the developmental process whereby similar rudiments in different animals become increasingly dissimilar in later development) and of complete (the primary phallic lobes themselves) and incomplete (the diverse external genitalia they become) homology. Because deviation occurs, E.L. Smith's (1969. Annals of the Entomological Society of America 62: 1051-1079) piece-by-piece homologizing of each component of male and female external genitalia is unacceptable as is Snodgrass' (1957. Smithsonian Miscellaneous Collections 136(6): 1-60) of parts of the male genitalia.

The ovipositors of most females are considered by Matsuda to be gonapophyseal in origin (paired apophyses of the 8th and 9th abdominal sterna) but are formed secondarily by modification of posterior abdominal segments after the gonapophyseal ovipositor has been lost. Matsuda hence concludes that the valvular ovipositor is archaic and arose early in insect evolution. It has since become modified or lost independently in members of each evolutionary line. Therefore, although the ovipositor is completely homologous in most insects, its parts are incompletely homologous.

In chapter 11, Matsuda critically analyzes the 11 theories that have been developed to explain the evolutionary origin of insect external genitalia. These are grouped into three categories: 1) those based only on developmental information, 2) those based on comparison of adult structures, and 3) those based on consideration of both kinds of information. Insect genital appendages have not only been homologized with abdominal legs but with diplopod gonopods, crustacean biramous limbs and with the eversible sacs of thysanuran pregenital segments. Matsuda believes both male and female genitalia to be sternal.

The efferent ducts and associated structures of the reproductive systems of insects of both sexes in most species consist of primary and secondary parts. The primary exit system is paired and usually originates from posterior extensions of genital ridges of the mesodermal coelomic sacs during embryogenesis. The secondary exit system is not paired and usually takes form after hatching by invagination of sternal ectoderm of the genital segments (7, 8 and 9).

The primary exit system of males begins as a pair of rudimentary vasa deferentia each terminating anteriorly in a testicular rudiment and posteriorly, in segment 9, as a swollen genital ampulla. With subsequent differentiation, these primordia give rise to the vasa deferentia, seminal vesicles, and accessory glands (mesadenes) and to a greater or lesser part of the ejaculatory bulb. The primary exit system of females is similar but each primordial lateral oviduct terminates in segment 7 and, at most, differentiates into the imaginal lateral oviduct. Female embryos of some species of Phasmida and Orthoptera and male embryos and larvae of Diptera-Nematocera have rudiments of the primary exit system of *both* sexes, one or the other degenerating with subsequent development (a phenomena similar to the sexually indifferent period experienced by vertebrate embryos).

The secondary exit system of most male insects ultimately comprises the ejaculatory duct, ejaculatory bulb and additional accessory glands (ectadenes). These usually first appear as a single, forward invagination of ectoderm from between the bases of the primary phallic lobes shortly before or after hatching. In most females, the secondary exit system consists of a common oviduct, spermatheca, vagina and accessory glands. Most begin to develop post embryonically, the common oviduct as an invagination behind the 7th sternum (often continued to the back of the 8th as a longitudinal groove whose lips subsequently fuse), the spermatheca from sternum 8 and the accessory glands from sternum 9. The openings of the spermathecal duct and accessory glands are then carried in by invagination of what remains of the 8th and 9th sterna to form the vagina.

The above developmental sequence characterizes most insects (in females of investigated species of Ephemeroptera only the primary system develops to any extent, each lateral oviduct having its own opening at the back of the seventh sternum. In males of most investigated species of Ephemeroptera and Dermaptera, two ejaculatory ducts arise, each invaginating forward from the apex of a primary phallic lobe). In endopterygote lines, a greater or lesser number of steps have been omitted due to heterochrony and substitution. There has been a general tendency for the secondary efferent system to substitute for the primary one and for the imaginal discs of adjacent segments in the female abdomen to amalgamate. This trend culminates in members of the Diptera - Cyclorrhapha in which the genital disc(s) in a larva differentiate not only into the complete male or female reproductive system and external genitalia (except gonads) but also into part of the hindgut and into the terminal abdominal segments of adults.

Part III is an almost overwhelming detailed analysis of abdominal structure and development in representatives of 30 orders. The chapter on Diptera is the longest (28 pp) because of the vast amount known about abdomens of members of this order. In it are treated 1) embryonic and 2) larval abdominal segmentation; 3) female and 4) male imaginal segmentation; 5) theories of abdominal segmentation; 6) abdominal appendages; 7) postembryogenesis of male external genitalia; 8) torsion of the post-abdomen; 9) the male and 10) female terminalia; 11) germ cells; 12) postembryogenesis of the male efferent system; 13) male internal reproductive system; 14) postembryogenesis of the female efferent system, and 15) female internal reproductive system. One or more of these discussions is omitted from the treatments of other orders because of lack of information. For example, the chapter on Zoraptera is only 1 1/2 pages long and considers only 3, 4, 9, 10 and 13 above. Matsuda's book is thus not only an important source of information on abdominal characteristics for members of each order, but also a good place to find research problems.

Development of the ovary and testis and oogenesis and spermatogenesis are not covered because of the reviews of these subjects already available. Matsuda does, however, provide detailed access to these literature sources.

My principal criticism of this book concerns Matsuda's decision not to consider musculature (already alluded to), phylogeny, or Hennig's (1966. "Phylogenetic Systematics") principles of cladistic analysis. I am convinced that the best way to relate everything in a complicated work of this kind is through the use of phylogenetic diagrams and through knowledge and use of sister group relationships between higher taxa. Except for included taxa of the Orthopteromorpha

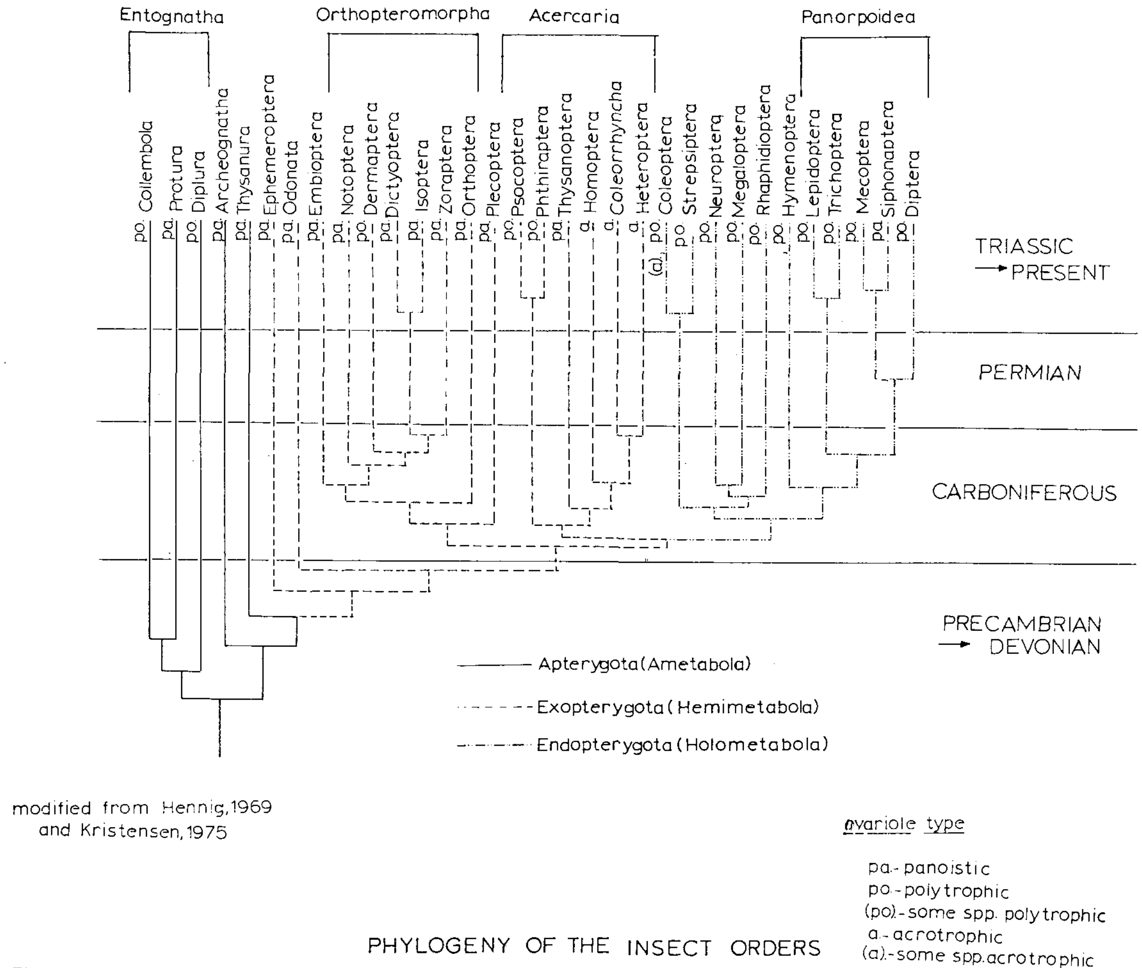

Fig. 1. Distribution of ovariole type in the Insecta.

(knowledge of whose relationships is still inadequate) accepted sister group relations of the insect orders are becoming stabilized (see Hennig, W. 1969. "Die Stammesgeschichte der Insekten" and Kristensen, N.P. 1975. Zeitschrift für zoologische Systematik und Evolutionsforschung 13: 1-44). If details of particular abdominal structures or developmental sequences are plotted on a phylogenetic dendrogram of the insect orders, one sees quickly whether they arose independently several times or only once in the common ancestor of monophyletic assemblages of orders. For example, if one does this for ovariole type (Fig. 1) one sees at a glance that the panoistic type is plesiomorphic but has been lost and secondarily regained either once (Siphonaptera) or twice (Thysanoptera and Siphonaptera), that the polytrophic type has independently arisen four times (in Collembola, Diplura, Dermaptera, and in the common ancestor of all remaining orders), and that the acrotrophic type has arisen independently twice (Hemiptera and Coleoptera) from ancestors having the polytrophic type. If such a plot is then superimposed on an identical diagram in which species diversity per order is indicated, one sees that the evolution of trophocytes (nurse cells) has probably contributed directly to the evolutionary success of those orders whose members' ovarioles are characterized by their presence. The selective advantage of meroistic (nurse cell-containing) ovarioles is that their oocytes grow faster and are produced in greater numbers than those of panoistic ovarioles because of the large amount of template DNA (up to 1024C) available for oogenesis in the polyploid nuclei of their nurse cells (only 4C amounts of DNA are available for RNA synthesis in the germinal vesicles of panoistic oocytes - see Mahowald, A.P. 1972 in Vol. Developmental Systems: Insects).

Use of Hennig's methods would add rigor to Matsuda's analysis and would make more obvious structural and developmental clines. This would result in Matsuda's book being of use to a larger number of workers than it is now. It would also enable readers to make conparisons more easily and to use the book in making predictions about structure of the abdominal appendages in unstudied taxa.

The volume is well-produced but there are many typographical errors and some of the print of my copy ended up on my fingers and on the pages of the first draft of this review. Some figures, though fully-labeled, are difficult to interpret because they were sloppily done or reproduced with too much reduction. They compare unfavourably with those of Anderson's recent treatise (1973. "Embryology and Phylogeny in Annelids and Arthropods") in the same series.

In spite of these criticisms, I consider Matsuda's book to be a major contribution because of its comprehensive bibliography and because of the vast amount of information it contains.

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B.S. Heming
Department of Entomology
University of Alberta
Edmonton, Alberta T6G 2E3