## BOOK REVIEW

JAMIESON, B. G. M. 1987. The Ultrastructure and Phylogeny of Insect Spermatozoa. Cambridge University Press, Cambridge. xv + 320 pp., 159 figs., author and subject indices. 30 pounds , U. K.

Most zoologists probably recall animal spermatozoa as resembling the miniature tadpoles figured in many introductory textbooks of biology or zoology (our own having a ghostly little bloke squeezing his knees inside). But, as emphasized by B. A. Afzelius in the foreword to this book, and as vividly illustrated on its pages, these cells are as diverse as the male animals from which they come. This comprehensive new book rigorously surveys the known ultrastructure of this diversity within a cladistic framework for members of the phylum 'Uniramia' (Onychophora, Myriapoda, Hexapoda) of Tiegs, Manton and Anderson but with particular emphasis on the sperm of insects.

The book is dedicated to Baccio Baccetti of the University of Siena in Italy, who, with his students and colleagues, has probably described the ultrastructure, physiology and behaviour of the sperm of more insect species than have all other workers combined. He, too, has written extensively about the phylogenetic significance of his findings, but not within a cladistic framework, and with little regard for previous phylogenies reconstructed on the basis of comparative morphology and life style.

Jamieson believes that information about spermatozoa can act as an "independent arbiter" for resolving contentious problems of relationship. He attempts to prove this by reviewing knowledge of hexapod sperm structure for known members of each order and by examining congruence between his cladograms, based on analysis of these character sequences, and Niels Kristensen's recent cladogram of hexapod relationships (1981-Phylogeny of Insect Orders. Ann. Rev. Ent. 26: 135-157) reconstructed on the basis of holomorphology (reproduced as Fig. 4.1 on page 81).

He 'sets the stage' for his attempt in the first three chapters of the book which provide comparative information about the sperm of other arthropods. In Chapter 1 (25 pp.), Jamieson defines the phylum Uniramia, summarizes the structural, physiological, biochemical, embryological and fossil evidence for and against its existence as a monophyletic taxon, and also for arthropod polyphyly vs. monophyly. He concludes that the Uniramia does form a monophyletic lineage, albeit of problematic position, but that the issue of arthropod polyphyly or monophyly cannot be settled yet (however, the emphasis of his words about the latter topic will convince any reader that he is an ardent polyphyleticist).

This chapter also contains brief, but rich and fully illustrated summaries of chelicerate and crustacean sperm diversity (incredible) wherein he concludes that the ground plan spermatozoan for both taxa is an "aquasperm" (an aquatic cell generally associated with external fertilization and, like the 'tadpole' mentioned

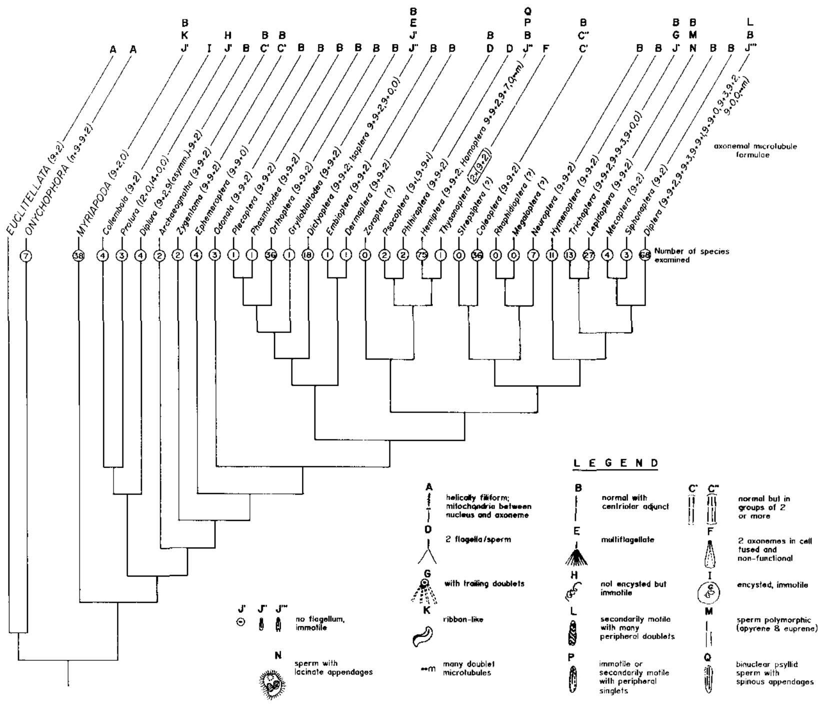

Fig. 1. Phylogeny of the Uniramia as interpreted by Jamieson showing some aspects of sperm diversity.

above, having a round nucleus, an apical acrosomal vesicle, a few large mitochondria surrounding the base of the axoneme, the latter with a 9+2 arrangement of 9 doublet microtubules and 2 central singlets; and 2 centrioles behind the head, of 9 triplet microtubules each, the distal one comprising the basal body of the axoneme). However, such a sperm is unknown for any extant crustacean, those of most species being aflagellate. He also emphasizes that sperm ultrastructure of neither taxon provides evidence for close relationship with Uniramia.

Sperm of onychophorans (Chapter 2 [13 pp.]– filiform, helically twisted cells; w ith midpiece mitochondria separating the nucleus from the single centriole; a flagellum containing a 9+2 axoneme + 9 peripheral accessory tubules and, external to these, a persistent sheath [=manchette] of microtubules [*i.e.*, n+9+9+2])– share several characters considered by Jamieson to be synapotypic with those of euclitellate annelids (Fig. 2.1). These, along with other, non spermatozoal, characters, suggest to him that these taxa are sister groups descended from a common, protoclitellate ancestor near the base of the Uniramia (Fig. 2.6, my Fig. 1). This, of course, and as he mentions, would result in these worms being included within the Uniramia; the remaining Annelida constituting a paraphyletic phylum.

At the end of this chapter, and seeming to this reviewer to have little to do with spermatozoa, Jamieson considers the odd possibility that the trochophore larva is not primitive to the annelids but was developed secondarily in the polychaete line as a mechanism for dispersal (Fig. 2.6). This causes problems for the origin of molluscs "as it would have to be postulated: (1), that molluscs developed a trochophore independently of annelids; or (2), that molluscs arose from an ancestor, shared with or ... referable to the polychaetes, which had a trochophore; or (3) that molluscs developed by neoteny of a trochophore and have retained this in their life cycle. . ." (p. 38). His Figure 2.6, which includes this possibility, will be difficult for many invertebrate zoologists to swallow, since it shows the zany (at least to this reader) phylogenetic relationship: [Chelicerata+[Crustacea+[Mollusca +[Polychaeta+ Uniramia]]]! I fear that many may not read his discussion which is intriguing, but will accept his figure at face value-perhaps even using it in a course-parish the thought!

Sperm ultrastructure in myriapods (Chapter 3-40 pp.) is characteristic for members of each class (Fig. 3.1). Jamieson believes the myriapod ground plan for sperm to resemble those of extant pauropods and chilopods and, to a lesser extent of symphylans, with adaptation for increased length and motility in those of most pauropods and chilopods and for immotility and a ribbon- or biscuit-shape in those of extant diplopods. The ground plans for both myriapod and hexapod sperm are synapotypic for a centriolar adjunct (a mass of material surrounding the remains of the centriole at the junction between nucleus and axoneme and perhaps holding the two together), a 9+2 axoneme with a tendency for addition of peripheral singlets, peripheral axonemal material, and loss of the peripheral manchette of onychophoran sperm (Fig. 2.6).

The next 16 chapters summarize information about sperm ultrastructure and function in investigated hexapods and indicate that Jamieson agrees with Kristensen in including each of the entognath (Collembola, Protura, Diplura), apterygote groups and Insecta as separate classes within a monophyletic superclass Hexapoda. His chapters mostly treat what he believes to be monophyletic assemblages of orders (Chapter 4-entognath apterygotes, 9 pp.; 5-ectognath apterygotes, 8 pp.; 6-summary of pterygote sperm, 8 pp.; 7-Palaeoptera, 5 pp.; 8-Blattodea and Isoptera, 11 pp.; 9-Orthoptera and Phasmatodea, 18 pp.; 10-Embioptera, Dermaptera, Plecoptera and Grylloblattodea, 6 pp.; 11-Psocoptera, Phthiraptera and Thysanoptera, 6 pp.; 12-Homoptera, 14 pp.; 13-Heteroptera, 9 pp.; 14-Holometabola-summary and Neuroptera, 4 pp.; 15-Coleoptera, 19 pp.; 16-Mecoptera and Siphonaptera, 5 pp.; 17-Diptera, 38 pp.; 18-Amphiesmenoptera (Trichoptera and Lepidoptera), 24 pp.; and 19-Hymenoptera, 6 pp.), many to the family level. References provided at the end of each chapter, or at the end of some orders, vary in number from 6 (chapter 7) to 132 (chapter 17).

From reading these chapters, one can see that knowledge of sperm ultrastructure varies tremendously among higher taxa: from 0 species investigated (Zoraptera, Mantodea, Megaloptera, Rhaphidioptera and Strepsiptera), through 1 (Phasmatodea, Embioptera, Dermaptera, Plecoptera, Grylloblattodea and Thysanoptera), 2 (Symphyla, Pauropoda, Archaeognatha, Zygentoma, Psocoptera and Phthiraptera), 3 (Protura, Odonata and Siphonaptera), 4 (Collembola, Diplura, Ephemeroptera and Mecoptera), 5 (Blattodea), 7 (Onychophora and Neuroptera), 10 (Hymenoptera), 11 (Chilopoda and Isoptera), 13 (Trichoptera), 18 (Heteroptera), 23 (Diplopoda), 27 (Lepidoptera), 33 (Orthoptera), 36 (Coleoptera), 57 (Homoptera), and 68 (Diptera). In some taxa (Chilopoda, Diplopoda, Isoptera, Homoptera, Coleoptera, Diptera and Lepidoptera), representatives have been selected from species occurring within most lineages of the taxon; in others, from only one or two (Orthoptera and Heteroptera). Such spotty coverage, as Jamieson states, makes phylogenetic reconstruction based on analysis of sperm ultrastructure alone (he coins the term 'spermiocladistics' for this enterprise) highly speculative. This is particularly so when one considers the remarkable diversity in sperm structure known to occur within some well-studied taxa such as Homoptera (*e.g.*,, some psylloids have binuclear sperm with spinose, acrosomal appendages; some aleyrodids, immotile sperm with mitochondria and axoneme vestigial; and coccoids, immotile or secondarily motile sperm with acrosomes, mitochondria, centrioles and axonemes absent, the latter replaced with circlets or spirals of 20 to >400 microtubules) and Diptera (*e.g.*,, Bibionidae– axoneme 9+9+0 or 9+0; Mycetophilidae– only one mitochondrial derivative, axoneme 9+2 or with variable number of outer singlets, rarely 9+9+3; Sciaridae– many axonemal doublets; Cecidomyiidae– acrosome lost; mitochondrial derivatives one or two, and cristate, crystalline or not; axonemes one or two of 9+0 microtubules, or doublets multiplied, some greatly, outer singlets lost but outer microtubules may be many; Simuliidae– axoneme 9+9+3; Culicidae– axoneme 9+9+l; Psychodidae– immotile, aflagellate, bifurcate sperm). Such diversity may, eventually, be found to be true of other, now inadequately known, taxa even though this seems not to be so of beetles.

In Chapter 20 (24 pp.), Jamieson integrates all this information together by first postulating a detailed ground plan for the hexapod spermatozoan and then summarizing evolution within member taxa of the Insecta. This ground plan gamete he postulates to have the following characteristics (p. 282): elongate, filamentous and motile; acrosome with bilayered or possibly trilayered perforatorium; nucleus elongate with condensed chromatin; centriole with doublets only and surrounded by a centriole adjunct; accessory bodies absent (2 elongate bodies typically flanking the axoneme in the flagellum); two elongate, at least partly cristate, non-crystalline mitochondrial derivatives; additional smaller mitochondria present in variable numbers; axoneme of the 9+9+2 type, with regularly arranged peripheral singlets; and peripheral 'coarse fibre' material present but ill defined.

In table 20.1, he lists the 57 derived character states he identified in the ground plans of the spermatozoa of each higher group of hexapods and, before summarizing the distribution of these on appropriate portions of Kristensen's cladogram, provides his own (Fig. 20.1) derived solely from consideration of these states. This tree bears some resemblance to Kristensen's tree but the relationships of many orders are inadequately discriminated.

In the rest of this chapter he derives the spermatozoal ground plans for each higher taxon treated in chapters 4 through l9, emphasizing in italics the character states he believes to be apotypic for that taxon. These apotypies he then superimposes on the appropriate portion of Kristensen's cladogram (Figs. 20. 2-20.8), in some instances (entognath and ectognath Apterygota, Polyneoptera, and Acercaria) supplying alternate hypotheses of relationship. These arguments are far too complex to detail in this review but I include some differences in the attached phylogenetic tree as Figure 1.

The book is well produced on good quality paper, is relatively free of typographical errors, and is profusely illustrated with fully labelled line drawings, and transmission (and a few scanning) electron micrographs, partly from others publications and partly from his own laboratory. Many of the figures are full page plates comprising many separate drawings or photomicrographs so that the book actually contains about 490 illustrations! The amount of information available about sperm of some species is mind-boggling (*e.g.*,, the summary of sperm structure in *Drosophila* spp. covers 11 pages and includes not only information about ultrastructure, but also about function of the mitochondrial derivatives, axonemal orientation during locomotion, developmental gradients in the axoneme, and genetic control of spermiogenesis).

My principal criticisms of the book are that Jamieson failed to provide: (1), a glossary to aid non-specialist readers in coping with the profusion of special terms for spermatozoal organelles; and (2), a general discussion of factors possibly influencing sperm structure and function, such as mode of transmission, duration of survival in male and female genital tract or within spermatophore or spermatheca, type of fluid they swim in and complexity of envelopes they must penetrate. The latter details are known for sperm of few species, but a general summary of possibilities such as that in Baccetti and Afzelius (1976, The Biology of the Sperm Cell. Karger) would surely result in readers having these ideas in mind as they plunge into the complex universe of spermatology.

Jamieson also missed a critical reference about thrips spermatozoa (Bode, W. 1983. Spermienstruktur und Spermatohistogenese bei *Thrips validus* Uzel [Insecta, Thysanoptera]. Zool. Jb. Anat. 109: 301-318.) showing the males of this species to produce sperm having an axoneme with 18 doublet intermixed with 9 singlet microtubules that is formed, during spermiogenesis, by development, alteration and fusion of three, separate, 9+0 cilia present in early spermatids. In addition, the Habilitationsschrift of this author (1986. Auswertung von Ultrastrukturmerkmalen für die Phylogenetische Systematik der Thysanopteren. Fakultat fur Biologie, Universitat Bielefeld-pp. 49-70) treats the ultrastructure of spermatozoa in 5 other species of thrips in 4 families suggesting a ground plan axoneme for Thysanoptera of 2x(9+2) or 2x(9+9+2) with those of the suborder Terebrantia 3x(9+0) and of Tubulifera 2x(9+2) or 2x(9+3).

The book is expensive but no more so than others its size now being published in Great Britain. It will enable the cell biologist interested in the function of cell organelles to select the best experimental material for his investigations and will help these and other process-oriented biologists to understand and appreciate evolutionary thinking–an understanding often seeming to be in short supply. It will provide systematic entomologists, and other invertebrate zoologists and comparative biologists entry to a valuable new source of taxonomic characters and will provide guidance as to which taxa to examine. Finally, it should open a door for some ecologists interested in sexual selection, since many seem to forget the little gametes that make it all work.

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