Preface

For simplicity, the title of this book is 'The Ultrastructure and Phylogeny of Insect Spermatozoa' but its subject is, in fact, the spermatozoa of the Uniramia: Onychophora; Myriapoda; and Hexapoda, including the Insecta. Some out-group comparison with the spermatozoa of the Crustacea and Chelicerata is also made. The primary aim of the work has been to make available in a single volume a critical resumé of all research reports on uniramian sperm, the literature of which is large and scattered, there being substantially more than one hundred works on the spermatozoa of the Diptera alone, as only one order. New data of the author on some groups are added. To keep the size of the volume within acceptable limits, only ultrastructure and only that of the mature spermatozoon is considered, with few exceptions. The intention has been to review the salient points of each publication within a taxonomic framework, insofar as these illuminate the ultrastructure of the spermatozoon, rather than to produce an overall synthesis in which details for each taxonomic entity might be obscured. Phylogenetic studies are also critically reviewed. A taxonomic and phylogenetic overview is, nevertheless, presented in the last chapter. While no other work attempts to review and cite the entire ultrastructural literature, this book complements and does not supplant excellent but briefer reviews by Professor Baccio Baccetti, Dr. David Phillips and the late Professor Odette Tuzet and others which are cited in the text.

The use of spermatozoal ultrastructure for taxonomy and phylogeny is now accepted in an ever-widening circle of *cognoscenti* and opposition to its use is usually dispelled when its effectiveness for resolving hitherto intractable problems of taxonomic placement and relationship is demonstrated. I here coin the term **spermiocladistics** and **spermiotaxonomy** for phylogenetic and taxonomic applications of sperm ultrastructure. To recognize as true cladistics the now numerous examples is appropriate because even where strict Hennigian procedures, the basis of true cladistics, have not been employed, or are employed independently of formal cladism by using well-established principles of **homology**, recognition of affinity on the basis of sperm structure has nevertheless obeyed a fundamental requirement of the Hennigian system. This requirement (Hennig, 1966) is that relationship be recognized on the basis of shared *advanced* (i.e. derived) characters. An advanced character is termed an **apomorphy** and an apomorphy shared between two or more taxa is a **synapomorphy**. Furthermore, each taxonomic or phylogenetic entity must be defined by at least one distinctive apomorphy, an **autapomorphy**. A corollary of the requirement is that relationship is not recognized on the basis of shared unmodified (i.e. primitive) characters. A primitive character is termed a **plesiomorphy** and when shared with another entity is termed a **symplesiomorphy**.

In very briefly mentioning some of the well-established examples of the utility of sperm ultrastructure for taxonomy and phylogeny, it is appropriate to first cite examples which formally employed, and acknowledged their debt to, the methodology established by Willi Hennig. The first was that of Schmidt and Zissler (1979) for anthozoan coelenterates, a particularly interesting example as it showed that even 'primitive' sperm (aquasperm in the author's terminology) have apomorphies distinctive of their various groups, a fact to which Afzelius (1979) had independently drawn our attention. The author (Jamieson, 1983), working on oligochaete sperm, related sperm structure to a holomorphological phylogram, later (Jamieson, 1984a) used numerical, computer procedures to model Hennig's methods, and recently (Jamieson, 1986; Jamieson *et al.* 1987) employed the excellent program of Swofford (1984) for phylogenetic analysis using parsimony. This Wagner program attains one of the chief aims of Hennigian phylogeny in minimizing homoplasy (homoiology or parallelism), for which the term **symparamorphy** has been introduced (Jamieson, 1984b). The only other use of computer techniques for spermiocladistics has been that of Harding *et al.* (1986) for the sperm of marsupials. But use of sperm ultrastructure reached its ultimate expression, appropriately in the school of Ax who has done so much to establish the value of Hennigian theory, with the definition and naming of a taxonomic group (and a major one), in an otherwise somatic analysis, on the basis of a spermatozoal apomorphy: recognition of the new taxon Trepaxonemata for platyhelminthes from the Polycladida through Cestoda on the autapomorphy of a single central element in the spermatozoal axoneme by Ehlers (1984). The classification obtained contrasted with that supported by Hendelberg (e.g. 1986) and demonstrated the wide gulf often seen between Hennigian systems and those obtained by other means. Numerous valuable non-Hennigian phylogenetic papers have been published by Justine and Mattei on monogeneans and by Swiderski on cestodes.

Spermiocladistics, with preparation of formal cladograms, has been painstakingly utilized by Wirth (1984), for a number of groups, of which his analysis of chelicerate phylogeny is particularly impressive; Alberti's meticulous studies of chelicerate sperm have laid the foundation for this and further cladistic analyses (see Chapter 1). In the Crustacea, Grygier (1982) has made a strict spermiocladistic analysis of flagellated, maxillopod sperm; Pochon-Masson and colleagues, Hinsch and others too numerous to mention have informally shown the value of sperm ultrastructure for phylogeny; and Wingstrand (1978) has left an example to all in thorough spermiocladistic analysis of a group, the Branchiopoda, though without reference to Hennigian methods (references in Chapter 1). Franzén (1977) has related sperm structure to a conventional phylogeny of the Metazoa. The author (Jamieson, 1985) has made a prelimnary spermiocladistic study of echinoderms. The taxonomy of gastropod molluscs is undergoing a valid revolution as a result of the far-reaching investigations by Healy of sperm ultrastructure though he has yet to apply formal cladistics. In the Nematoda, Anya (1976) and later, Baccetti and colleagues (1983), at Siena, have attempted spermatozoal phylogenies. The most prodigious investigations of sperm ultrastructure have been those of Baccetti and his team, chiefly on Uniramia, studies which they have frequently directed to development of phylogenies, again, however, not in an Hennigian framework. In the present work these and other insectan studies are reviewed and the congruence of spermatozoal characters, in Hennigian terms, to a pre-exisisting, chiefly somatic cladogram of Kristensen is examined for each order. The value of holomorphological cladistics, sampling the entire anatomy of the organism, is not to be disputed but spermatozoa offer an 'independent arbiter' capable in many cases of resolving contentious taxonomic and phylogenetic problems.

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REFERENCES CITED IN THE PREFACE
(See also Chapter 1)

Afzelius, B.A. 1979. Sperm structure in relation to phylogeny in lower Metazoa. In Fawcett, D.W. and Bedford, J.M. *The Spermatozoon.* Urban and Schwarzenberg, Baltimore. 243-251.

Anya, A.O. 1976. Physiological aspects of reproduction in nematodes. *Advances in Parasitology* **14**: 267-351.

Baccetti, B., Dallai, R., Grimaldi de Zio, S. and Marinari, A. 1983. The evolution of the nematode spermatozoon. *Gamete Research* **8**: 309-323.

Ehlers, U. 1984. Phylogenetisches System der Platyhelminthes. *Verhandlungen der Naturwissenschaftlichen Vereins in Hamburg* **27**: 291-294.

Franzén, A. 1977. Sperm structure with regard to fertilization biology and phylogenetics. *Verhandlungen der deutschen zoologischen Gessellschaft* **1977**: 123-138.

Harding, H.R., Aplin, K. and Shorey, C.D. 1986. Cladistic analysis of marsupial sperm structure: methodological perspectives. *Development, Growth and Differentiation* **28** Supplement: 62 (Abstract only).

Hendelberg, J. 1986. The phylogenetic significance of sperm morphology in the Platyhleminthes. *Hydrobiologia* **132**: 53-58.

Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana.

Jamieson, B.G.M. 1983. Spermatozoal ultrastructure: evolution and congruence with a holomorphological phylogeny of the Oligochaeta (Annelida). *Zoologica Scripta* **12**: 107-114.

Jamieson, B.G.M. 1984a. A phenetic and cladistic study of spermatozoal ultrastructure in the Oligochaeta (Annelida). *Hydrobiologia* **115**: 3-13.

Jamieson, B.G.M. 1984b. Spermatozoal ultrastructure in *Branchiostoma moretonensis* Kelly, a comparison with *B. lanceolatum* (Cephalochordata) and with other deuterostomes. *Zoologica Scripta* **13**: 223-229.

Jamieson, B.G.M. 1985. The spermatozoa of the Holothuroidea (Echinodermata): an ultrastructural review with data on two Australian species and phylogenetic discussion. *Zoologica Scripta* **14**: 123-135.

Jamieson, B.G.M. 1986. Some recent studies on the ultrastructure and phylogeny of annelid and uniramian spermatozoa. *Development, Growth and Differentiation* **28** Supplement: 25-26.

Jamieson, B.G.M., Erséus, C. and Ferraguti, M. 1987. Parsimony analysis of the phylogeny of some Oligochaeta (Annelida) using spermatozoal ultrastructure. *Cladistics* (In press).

Schmidt, H. and Zissler, D. 1979. The sperm of the Anthozoa and their phylogenetic significance. *Zoologica (Stuttgart)* **44**: 1-98.

Swofford, D.L. 1984. *Phylogenetic analysis using parsimony*. Version 2.2. User's Manual. D.L. Swofford, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820.