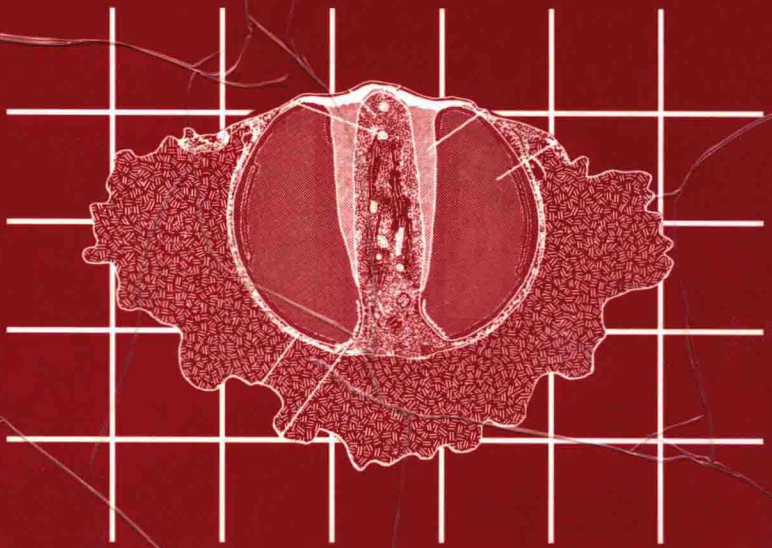


Reproductive Biology of Invertebrates

VOLUME IX • PART C

**Progress in Male Gamete
Ultrastructure and Phylogeny**



**Series Edited by
K.G. Adiyodi and
R.G. Adiyodi**

**Volume Edited by
B.G.M. Jamieson**

REPRODUCTIVE BIOLOGY OF INVERTEBRATES

Series edited by

K.G. and RITA G. ADIYODI

*Cochin University of Science & Technology, Kochi 682022,
Vatsyayana Centre of Invertebrate Reproduction
Calicut University, Kerala 673635, India*

Volume edited by

B.G.M. JAMIESON

*Department of Zoology and Entomology, University of Queensland
Brisbane 4072, Queensland, Australia*

VOLUME IX, PART C

Progress in Male Gamete Ultrastructure and Phylogeny

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**REPRODUCTIVE BIOLOGY
OF INVERTEBRATES**

REPRODUCTIVE BIOLOGY OF INVERTEBRATES

<i>Volume I</i>	OOGENESIS, OVIPOSITION, AND OOSORPTION
<i>Volume II</i>	SPERMATOGENESIS AND SPERM FUNCTION
<i>Volume III</i>	ACCESSORY SEX GLANDS
<i>Volume IV</i>	FERTILIZATION, DEVELOPMENT, AND PARENTAL CARE (PARTS A AND B)
<i>Volume V</i>	SEXUAL DIFFERENTIATION AND BEHAVIOUR
<i>Volume VI</i>	ASEXUAL PROPAGATION AND REPRODUCTIVE STRATEGIES (PARTS A AND B)
<i>Volume VII</i>	PROGRESS IN DEVELOPMENTAL BIOLOGY
<i>Volume VIII</i>	PROGRESS IN REPRODUCTIVE ENDOCRINOLOGY

PREFACE TO THE PROGRESS SERIES

With the release of Volume VI, Part B in 1994, we completed all the projected six volumes (eight books) in the series, "Reproductive Biology of Invertebrates". Going by the reviews, the series has been, on the whole, extremely well received: as one reviewer put it, "it is difficult to imagine any institution with a serious research or teaching involvement in invertebrate reproductive biology finding the series anything but indispensable."

Strengths apart, we find (and this has been pointed out by us in the Series Preface appearing in Volumes I-VI) serious gaps exist in the series as chapters could not be commissioned on some of the phyla and groups, for various reasons, a task we were forced to leave to the future. Another drawback of the series, we think, is that contributions analysing sexuality, reproduction and development from a strictly comparative and evolutionary point of view do not form a part of it as treatment has been phyletic within a thematic framework, though some observations from a comparative point of view do find a place here and there in some contributions. It may also be pointed out this is a difficult class of contributions to commission in as much as comparative gametologists, physiologists, biochemists, endocrinologists, sexologists, and developmental biologists with on-hand experience in different phyletic groups and an overall view of the animal kingdom are becoming rarer and rarer, most investigators confining their observations and comparisons to species or to the phyletic group in question at the most. Third, because of delays in production schedule some contributions were dated even as they appeared in print. The volume of new material that has come to light since Volume I was published in 1983 is formidably large, calling for updating on an extensive scale to ensure the topicality, encyclopaedic nature, and continued utility of this well-established series.

This task is by no means easy, as in some areas such as developmental biology, because of its association with the use of techniques and procedures of molecular biology, genetics and cell physiology, advances at the cutting edge are being made so fast parts of contributions become dated even as they are being hurriedly printed. The scenario is one of the scientist who is hotly chasing the truth in turn being chased even more hotly by the editors as well as the publisher, and all becoming helpless before the great master and leveller, time, with all its philosophical dimensions and manifestations!

Each volume in the "Progress Series" in "Reproductive Biology of Invertebrates" is being organized and guest-edited by a scientist of international repute who is active, has substantial work in the area to his credit, and can impart the necessary degree of authoritativeness and incisiveness to the volume. This has brought to each volume in the series contributions from a wider range of leading authors and laboratories actively pursuing research in the field. Furthermore, as all freedom was given to the guest-editors to organize the volumes departing from the usual phyletic format followed in Volumes I–VI, we ended up refreshingly with bouquets of some of the choicest flowers which we are happy to pass on to the readers.

K.G. ADIYODI
R.G. ADIYODI

PREFACE TO VOLUME IX, PART C

This is the third of three volumes which record progress in our knowledge of the ultrastructure and phylogeny of spermatozoa of the invertebrates since publication of a previous volume in this series, edited by K.G. and R.G. Adiyodi (1983), on spermatogenesis and sperm function. Spermatozoal ultrastructure of some of the included taxa has recently been treated in Jamieson *et al.* (1995), but all chapters in the new volumes represent significant, and often very major, advances in knowledge. Although the chapters are intended as reviews of progress, most list the entire ultrastructural literature on the spermatozoa of the phylum concerned, and much new information is provided. Aspects of fertilization biology are usually included. This volume is devoted to the sperm of non-chelicerate arthropod groups: the Decapoda, Pentastomida, and Myriapoda. The sperm of non-decapod Crustacea have been reviewed elsewhere by Jamieson (1991). Insecta are treated in another book (Jamieson *et al.*, 1999). The present volume also includes the Lophophorata, and the unequivocally deuterostome groups, Echinodermata, Chordata, Urochordata, and Cephalochordata.

For considerations of space, the lengthy chapter on Decapoda by Jamieson and Tudge is restricted to sperm ultrastructure with some functional considerations. Brief reference is also made to the Euphausiacea. One or more species have now been examined for sperm ultrastructure in all major decapod groups except the Polychelida. Particular attention is paid to the Anomura and Brachyura which the authors have extensively investigated. These groups exemplify the great utility of sperm ultrastructure for phylogeny and taxonomy.

The chapter on Pentastomida by Jamieson and Storch confirms the sister-group relationship of pentastomes to branchiuran Crustacea which is unequivocally indicated by sperm ultrastructure. Molecular evidence for and against this relationship, and objections by Walossek and Muller to its recognition are discussed.

Mazzini, Carcupino and Fausto review and provide new information on the spermatozoa of the Myriapoda, reviewed earlier by Jamieson (1987). They preface the account with an introduction to the group. This is followed by an account for the Chilopoda, commencing with the male genital system. A review of sperm ultrastructure reports sperm dimorphism for the Scolopendromorpha, Scutigleromorpha and Lithobiomorpha, but not for the Geophilomorpha. Spermiogenesis and spermatophore formation are reviewed. New scanning electron micrographs are provided for five chilopod genera. Similarly structured accounts are given for the

Diplopoda, Symphyla and Pauropoda. In a discussion of myriapod sperm evolution, they suggest that Chilopoda may be the plesiomorph sister-group of Pauropoda and that the two lines of myriapod sperm may therefore be derived from a basic sperm model closer to the chilopod model.

There has been remarkably little recent work on the sperm of the Lophophorata, which contain the Phoronida, Bryozoa (=Ectoprocta) and Brachiopoda but the chapter by Jamieson adds some new data to the accounts of Bryozoa and Brachiopoda in Adiyodi and Adiyodi (1983) and Jamieson (1991).

The chapter on Echinodermata by Jamieson comprehensively reviews the large volume of literature on spermatozoal ultrastructure in the phylum and adds some previously unpublished data. As noted in Jamieson (1991), a round-headed 'echniosperm' is general for the Crinoidea, Asteroidea, Ophiuroidea and Holothuroidea. The Echinoidea is seen as advanced in elongation of the nucleus and loss of the satellite apparatus in the sperm. However, the possibility is very tentatively raised that an elongated sperm of a 'modified' type, resembling that in *Rhabdopleura*, *Phoronis* and *Xyloplax*, was primitive for their common ancestor and that the round-headed sperm (echinosperm) in most echinoderm classes is a secondary simplification for broadcast spawning in these secondarily radial animals. Sections are also devoted to gamete interactions at the egg plasma membrane, including the acrosome reaction, and to sperm dimorphism recently reported for an echinoid.

There have been no descriptions of hemichordate spermatozoa since the review of Jamieson (1991), from which the chapter on this group is therefore drawn. Knowledge of sperm ultrastructure is limited to one species each of *Saccoglossus*, *Saxipendium* (Enteropneusta) and *Rhabdopleura* (Rhabdopleurida). It is noteworthy that the sperm of *Cephalodiscus*, so central to discussion of the origin of echinoderms, is undescribed.

The highly original and authoritative chapter on Urochordata by Burighel and Martinucci commences with an introduction to the morphology, taxonomy and fertilization biology of the group and contains sections on morphology of male genital organs; the origin of germ cells; spermatogenesis; sperm morphology; phylogenetic implications of the latter; spawning and sperm biology; the acrosome and sperm reactions; sperm in the female tract and storage; and concluding remarks. It adds very substantially to the review by Jamieson (1991).

The chapter on Cephalochordata, included for completeness, is again drawn largely from Jamieson (1991). Recent work on gonadal hormones and fertilization is added.

The generosity of authors and publishers who have allowed illustrations to be reproduced is most gratefully acknowledged. The assistance of David M. Scheltinga (my Australian Research Council Research Assistant), and the support of the Department of Zoology and Entomology, University of Queensland, has greatly facilitated preparation of these volumes. The kind collaboration of all the authors, who have borne uncomplainingly the delays inevitable in gestation of a work of this

type, has been greatly appreciated. Finally, the efficient and courteous participation of the publishers, and of Dr. K.G. Adiyodi, who conceived the series, was indispensable to production of these volumes.

BARRIE JAMIESON

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CONTRIBUTORS

PAOLO BURIGHEL, *Dipartimento di Biologia, Università di Padova, Via Trieste 75, 35121 Padova, Italy*

MARCELLA CARCUPINO, *Department of Zoology and Anthropology, University of Sassari, 07100 Sassari, Italy*

ANNA MARIA FAUSTO, *Department of Environmental Sciences, University of Tuscia, 01100 Viterbo, Italy*

BARRIE G.M. JAMIESON, *Department of Zoology and Entomology, University of Queensland, Brisbane Q4072, Queensland, Australia*

GIAN BRUNO MARTINUCCI, *Dipartimento di Biologia, Università di Padova, Via Trieste 75, 35121 Padova, Italy*

MASSIMO MAZZINI, *Department of Environmental Sciences, University of Tuscia, 01100 Viterbo, Italy*

VOLKER STORCH, *Zoologisches Institut, Im-Neuerteimer-Feld-230, D-69120-Heidelberg, Germany*

CHRISTOPHER C. TUDGE, *Zoology Department, The University of Queensland, Brisbane Q4072, Australia*

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1. CRUSTACEA-DECAPODA

BARRIE G. M. JAMIESON AND CHRISTOPHER C. TUDGE

*Zoology Department, The University of Queensland, Brisbane Q4072
Australia*

I. ORDER EUPHAUSIACEA

Euphausiid sperm give little indication of the eucarid ground plan. They are ovoidal, lack appendages and have irregular central material which is considered to be chromatin (Jamieson, 1991b). This structure has been confirmed in a detailed description of the sperm of *Meganyctiphanes norvegica* (Fig.1) by Medina *et al.* (1998). If absence of arms were plesiomorphic for eucarids, the arms of most decapods would have to be regarded as having developed independently of those of phyllopods. This is further suggested by their absence from non-eucarid malacostracans. A proposed spermatological phylogeny of the Euphausiacea and other Eucarida by Medina *et al.* (1998) is shown in Fig. 1.

II. ORDER DECAPODA

A. Suborder Dendrobranchiata

Spermatozoal ultrastructure has been described for some members of six families of the superfamily Penaeoidea: Penaeidae, Sicyonidae, Atyidae, Aristeidae and Solenoceridae (see Table 1 for list of species investigated). A brief ultrastructural description of the sperm of *Sergestes arcticus* was also provided by Medina (1995a) to exemplify the superfamily Sergestoidea in support of general phylogenetic considerations.

1. Penaeoidea

The Penaeoidea, which, with the Sergestoidea, form the Dendrobranchiata, were at one time grouped with the crangonid and palaemonid shrimps within the Natantia as opposed to the Reptantia which contained, *inter alia*, hermit crabs,

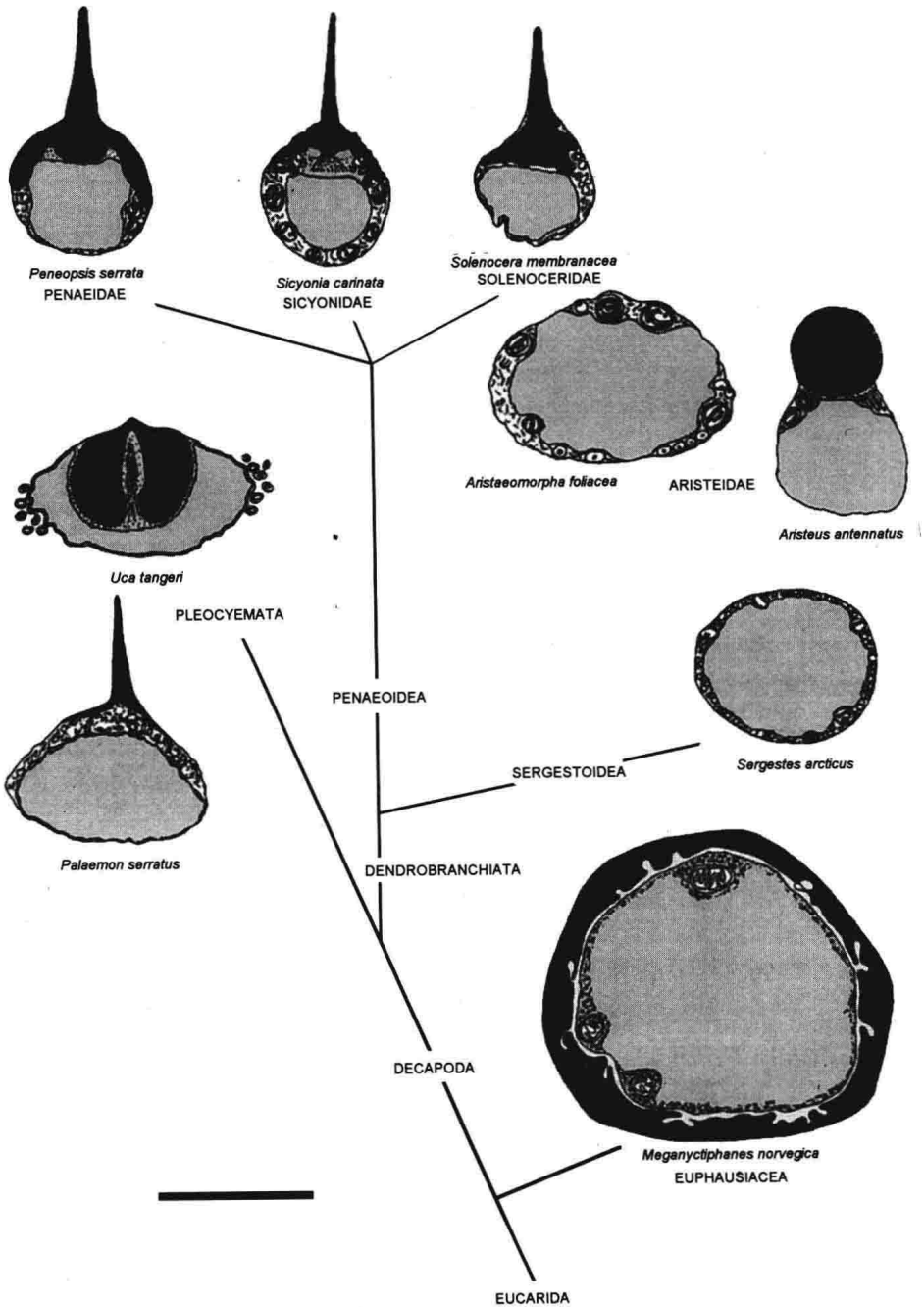


Fig. 1. A proposed spermatological phylogeny of the Euphausiacea and other Eucarida. From Medina *et al.* (1998). *Invertebrate Reproduction and Development*, **34**, 65–68, fig. 2.

Table 1

List of Dendrobranchiata for which sperm ultrastructure is known. (Slightly modified from Medina, 1995a)

Superfamily and family	Species	Reference
Penaeoidea		
PENAEIDAE	<i>Parapeneus longirostris</i> (Lucas, 1846)	Medina, 1994
	<i>Peneopsis serrata</i> Bate, 1881	Medina <i>et al.</i> , 1994a
	<i>Penaeus aztecus</i> Ives, 1891	Clark <i>et al.</i> , 1973
	<i>Penaeus japonicus</i> Bate, 1888	Medina <i>et al.</i> , 1994b; Ogawa and Kakuda, 1987
	<i>Penaeus kerathurus</i> (Forskål, 1775)	Medina, <i>et al.</i> , 1994b
	<i>Penaeus setiferus</i> (Linnaeus, 1767)	Felgenhauer <i>et al.</i> , 1988; Krol <i>et al.</i> , 1992; Lu <i>et al.</i> , 1973
	<i>Penaeus vannamei</i> Boone, 1931	Dougherty and Dougherty, 1989; Krol <i>et al.</i> , 1992
	<i>Trachypeneus similis</i> (Smith, 1885)	Krol <i>et al.</i> , 1992
	<i>Sicyonia brevirostris</i> Stimpson, 1874	Brown <i>et al.</i> , 1977
	<i>Sicyonia carinata</i> (Brünnich, 1768)	Medina <i>et al.</i> , 1994a
SICYONIDAE	<i>Sicyonia ingentis</i> (Burkenroad, 1938)	Kleve, <i>et al.</i> , 1980; Shigekawa and Clark, 1986
		Medina, 1995b
ARISTEIDAE	<i>Aristaeomorpha foliacea</i> (Risso, 1827)	
	<i>Aristeus antennatus</i> (Risso, 1816)	Demestre <i>et al.</i> , 1993, 1997; Demestre and Fortuno, 1992; Medina, 1995b
SOLENCERIDAE	<i>Solenocera membranacea</i> (Risso, 1816)	Medina, 1995a
Sergestoidea		
SERGESTIDAE	<i>Sergestes arcticus</i> Kroyer, 1855	Medina, 1995a

crayfish, lobsters and crabs. Penaeoids are now regarded as distinct from the suborder Eukyphida, containing the Procarididea and the Caridea, and the Euzygida, containing the Stenopodidea (Schram, 1986). Paraphyly of penaeid and eukyphid shrimps, as opposed to monophyly of the Natantia, appears to be indicated from rRNA studies (Abele, 1991). These authors, with considerable justification, retain the names Caridea for Eukyphida, and Stenopodidea for Euzygida and are followed here.

(a) *Penaeidae*

Within the Dendrobranchiata, penaeid sperm have been the most extensively studied in terms of the number of species examined. These include five *Penaeus* species (*P. setiferus*, *P. vannamei*, *P. aztecus*, *P. japonicus* and *P. kerathurus*), *Trachypeneus similis*, *Parapeneus longirostris* and *Peneopsis serrata* (Table 1). In gross

morphology, the penaeid spermatozoon basically consists of a subspheroidal or ovoid main body and a spike. The main body comprises the central nuclear region, a cytoplasmic band surrounding it posterolaterally, and the acrosomal cap, which overlies the nuclear region anteriorly and is prolonged into a tapering spike (Fig. 1). Both spike and acrosomal cap make up a membrane-bound acrosomal vesicle, with heterogeneous contents, which is directly invested by the plasma membrane. In particular, the spike morphology and substructure vary markedly from species to species. The whole acrosomal complex is completed with the subacrosomal region, which is quite simple in this family, merely containing a sparse flocculent material between the chromatin and acrosomal cap.

The sperm of *Parapeneus longirostris* and *Peneopsis serrata* (Fig. 1) have a central protuberance at the concave side of the acrosomal cap immediately opposite the spike. This supposed synapomorphy is consistent with the close phylogenetic proximity of the genera *Parapeneus* and *Peneopsis*, both grouped together by Burkenroad (1983) within the tribe Parapeneini, which also includes *Artemesia* and *Metapeneopsis*. Confirmation of such a structure in the latter genera would strengthen phylogenetic unity of this taxon.

As in all dendrobranchiate species whose spermatozoon has been ultrastructurally studied, the nuclear region of penaeid sperm consists of a non-membrane-bound, filamentous chromatin mass. Posterolaterally, the chromatin is surrounded by a band of cytoplasm which contains membrane lamellae, vesicles and mitochondria-like bodies, but lacks centrioles and microtubules. Within the Dendrobranchiata, the sperm of *Penaeus japonicus* are exceptional in that they exhibit several microtubule bundles in the cytoplasm (Medina *et al.*, 1994b). The microtubules appear in primary spermatocytes of *P. japonicus* and are retained through spermiogenesis to the mature spermatozoon. In other penaeid species (e.g. *Penaeus kerathurus*, *Parapeneus longirostris*), microtubules are absent from all spermatogenetic stages.

Recent molecular studies (Palumbi and Benzie, 1991) have revealed extensive genetic differences between species of *Penaeus* which have not been accompanied by substantial evolutionary morphological changes. As noted by Medina (1995a), this is congruent with the occurrence of diverse species-specific dissimilarities leading to different ultrastructure of sperm in the genus *Penaeus* and in general in the Penaeidae, and confirms the taxonomic validity of sperm morphology in the Dendrobranchiata.

(b) *Sicyonidae*

Ultrastructural data have been reported for three *Sicyonia* species: *S. brevirostris*, *S. carinata* (Fig. 1) and *S. ingentis* (Table 1). The ultrastructure of the spermatozoon is very similar in *S. ingentis* (Kleve *et al.*, 1980; Wikramanayake *et al.*, 1992) and *S. carinata* (Medina *et al.*, 1994a). In general, as in Penaeidae, the sperm consist of an acrosomal vesicle (formed by the spike and acrosomal cap), subacrosomal

region, and nuclear region surrounded by a cytoplasmic band. Anteriorly, the acrosome and plasma membranes are closely joined. As a taxonomically significant difference, the spike of *S. ingentis* is spiralled, whereas that of *S. carinata* is smooth. The plesiomorphies (1) absence of nuclear envelope and (2) perinuclear cytoplasmic band (containing small and large vesicles and lacking microtubules) are also found in this sperm type. Nevertheless, the highly elaborate subacrosomal region (comprising diverse distinct structures) (Kleve *et al.*, 1980; Medina *et al.*, 1994a) appear to be a clear synapomorphy and autapomorphy of the family Sicyonidae. Compared with the spermatozoa of the other dendrobranchiate families, the acrosomal vesicle shows the apomorphic character that the posterior membrane of the acrosomal cap is intricately folded in a ring of convoluted membrane pouches or digitations (Kleve *et al.*, 1980; Medina, 1995a; Medina *et al.*, 1994a).

Clark and co-workers have described morphological details and biochemical events of the acrosome reaction and penetration of the vitelline envelope in *Sicyonia ingentis* (Chen *et al.*, 1994; Clark *et al.*, 1981, 1984; Clark and Griffin, 1988; Griffin *et al.*, 1988; Griffin and Clark, 1990; Hertzler and Clark, 1993; Lindsay and Clark, 1992a, b; Wikramanayake *et al.*, 1992; Yudin *et al.*, 1979). These accounts investigate the role played by each of the spermatozoal components during fertilization and the biological significance of the acrosomal structures in dendrobranchiates.

(c) *Aristeidae*

The relatively high ultrastructural homogeneity found within the Penaeidae and Sicyonidae is not seen in the Aristeidae. Studies of *Aristeus antennatus* (Demestre *et al.*, 1993, 1997; Demestre and Fortuno, 1992; Medina, 1995b) and *Aristaeomorpha foliacea* (Medina, 1995b) indicate the existence in the family of at least two different ultrastructural sperm plans that are in turn discordant with the penaeid-sicyoniid assemblage. The *A. antennatus* (Fig. 1) sperm type exhibits diverse peculiarities in comparison with the other Dendrobranchiata. First, its spherical acrosome does not cap the nuclear region and lacks both spike and subacrosomal region; the inner arrangement of the acrosomal contents is complex and different from that of any other known dendrobranchiate spermatozoon. Secondly, the cytoplasm does not constitute a band around the filamentous chromatin mass but is accumulated in a collar between the acrosome and nuclear region, enclosing mitochondria-like vesicles and membrane lamellae. Consequently, most of the chromatin is bounded directly by the plasma membrane because the nuclear region is, as in all dendrobranchiates, not membrane-bound. Changes in the structure of the acrosome in the final stages of spermiogenesis are described by Demestre *et al.* (1997).

Medina (1995a) concurs with Demestre and Fortuno (1992) that the basic sperm structure of *Aristeus antennatus* resembles that of spiny lobsters, *Panulirus* spp. (Talbot and Summers, 1978), although with the highly significant absence of