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ORIGINAL ARTICLE

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Ultrastructure of the spermatozoa of *Aristaeopsis edwardsiana* and *Aristeus varidens* (Crustacea, Dendrobranchiata, Aristeidae)

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Abstract The acrosome-less spermatozoon of *Aristaeopsis edwardsiana* (Crustacea, Aristeidae), which consists of a central non-membrane bound nuclear region surrounded by a thin peripheral cytoplasm, much resembles that of the previously studied aristeid *Aristaeomorpha foliacea*. The marked spermatozoal similarities between these two species appear to indicate a close phylogenetic proximity. A considerably different spermatozoal pattern is observed in aristeids from the genus *Aristeus* (*A. varidens* and *A. antennatus*), whose spermatozoa possess an anterior spherical acrosome, lacking a spike, and partially embedded in (instead of capping) the main sperm body. The two distinct sperm types found in the Aristeidae differ significantly from the spiked sperm typically found in most penaeoids (Penaeidae, Solenoceridae and Sicyoniidae), thus suggesting a phylogenetic separation of the Aristeidae from the remaining Penaeoidea.

Keywords Decapoda · Crustacea · Dendrobranchiata · Spermatozoa · Aristeidae · *Aristaeopsis edwardsiana* · *Aristeus varidens* · Phylogeny

Introduction

The sperm ultrastructure has been successfully employed in studies on taxonomy and phylogeny in different animal taxa, including the Crustacea (Felgenhauer and Abele 1991; Jamieson 1991; Jamieson et al. 1995a, b; Medina 1995a, b; Tudge 1995; Jamieson and Tudge 2000; Martin and Davis 2001). Although the sperm ultrastructure has been investigated in numerous species from the Pleocyemata, several groups of Dendrobranchiata still remain poorly studied. In particular, the available information on spermatozoal ultrastructure in the Aristeidae, which comprises nine genera and 27 species (Pérez-Farfante and Kensley 1997), is very limited, since only two species have been described thus far, *Aristeus antennatus* (Risso, 1816) (Demestre and Fortuño 1992; Demestre et al. 1993, 1997; Medina 1995b) and *Aristaeomorpha foliacea* (Risso, 1827) (Medina 1995b). The taxon Dendrobranchiata is traditionally divided into two subgroups, the Penaeoidea and Sergestoidea. Recently, Pérez-Farfante and Kensley (1997) have reviewed the taxonomy of the group, but they have not provided phylogenetic analyses. Perhaps, studies on inner phylogenetic relationships in dendrobranchiates are scarce because their classification is fairly stable (Martin and Davis 2001).

The 'unistellate' spermatozoon of dendrobranchiates, which occurs in the majority of the representatives of the Penaeoidea (Penaeidae, Solenoceridae and Sicyoniidae), is primarily characterized by the presence of an acrosomal cap that projects forward into a pointed appendage referred to as the spike (Kleve et al. 1980; Dougherty and Dougherty 1989; Medina 1994, 1995a; Medina et al. 1994a, b; Jamieson and Tudge 2000; Scelzo and Medina 2003; Medina et al. 2005). However, previous studies (Demestre and Fortuño 1992; Demestre et al. 1993, 1997; Medina 1995b) described spike-less spermatozoa in two species of Aristeidae (*A. antennatus* and *A. foliacea*) that represent remarkable exceptions to the spermatozoal uniformity found in the other dendrobranchiate species. In addition, the spermatozoal organization was shown to be highly dissimilar between both aristeid species, thus posing interesting questions in terms of sperm phylogeny within the group. It was thus proposed that the Aristeidae encompasses two distinct sperm types that constitute separate evolutionary trends diverging from the spermatozoal configuration present

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in the remaining Penaeoidea (Medina 1995b). In order to test this hypothesis, we examined the sperm ultrastructure in two other aristeid species, *Aristaeopsis edwardsiana* (Johnson, 1867) and *Aristeus varidens* (Holthuis, 1952) with a view to determine whether such unique spermatozoal patterns are consistent within the group. The present observations might help to draw an overall picture of the spermatozoal evolutionary trends in decapod crustaceans, thus contributing to improvement of our understanding of their phylogenetic relationships.

Materials and methods

Adult specimens of *Aristaeopsis edwardsiana* (Johnson, 1867) and *Aristeus varidens* (Holthuis, 1952) were caught by trawl in waters off Angola in November 2003. After dissection of the male reproductive system, small fragments of vasa deferentia including ampullae were immediately fixed in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.2, for 12–24 h. Then the samples were washed and stored at 4°C in the buffer for several days until use. Once in the laboratory, the tissue samples were postfixed in 1% cacodylate-buffered osmium tetroxide. Following several short washes in buffer, they were dehydrated through ascending concentrations of acetone and finally embedded in epoxy resin (Epon 812). Thin sections (˜80 nm thick) picked up on copper grids were stained with uranyl acetate and lead citrate and examined in a JEOL JEM 1200 EX transmission electron microscope operated at 80 kV. Sperm dimensions were measured from electron micrographs of midsagittal sections and are expressed as means ± SD.

Results

Ultrastructure of the spermatozoon in *Aristaeopsis edwardsiana*

Sperm clusters found in the vasa deferentia of *Aristaeopsis edwardsiana* are surrounded by an extracellular material that extends between sperm cells (Fig. 1a). The spermatozoa are rounded or slightly ovoid in shape (Fig. 1a), measuring 1.93 ± 0.24 µm at their widest diameter ($n = 11$). The sperm cell lacks any recognizable acrosome and is also devoid of microtubular (either flagellar or centriolar) structures, whereby it constitutes a quite simple cell that consists of a central nuclear region surrounded by a rather reduced cytoplasm (Fig. 1a–c, e and Table 1). As the thickness of the cytoplasmic band is variable throughout the cell, discontinuities become evident where the nucleoplasm is in direct contact with the plasma membrane (Fig. 1b). The most conspicuous cytoplasmic elements are the mitochondria, which occur in a number of 1–7 in sections through the equatorial plane of the spermatozoon. They frequently appear grouped together on one side of the cytoplasm (Fig. 1c, d). The scarce cristae are distributed randomly in the electron-clear mitochondrial matrix (Fig. 1d). Other components of the cytoplasm are hardly recognized from the background. Vesicular structures and amorphous membrane remnants can be identified (Fig. 1e).

Most of the cell volume is occupied by the nucleoplasm, which, as is common in decapods, is not enclosed by a membranous nuclear envelope (Fig. 1b–e). The uncondensed chromatin assumes the typical fibrillar structure of the dendrobranchiate sperm, exhibiting a reticulate pattern of filaments with conspicuous nodules at points of entwining of chromatin fibres (Fig. 1d, e). Osmiophilic bodies are occasionally observed in the extracellular medium between spermatozoa.

Ultrastructure of the spermatozoon of *Aristeus varidens*

Spermatozoa stored in the *vas deferens* of *Aristeus varidens* are surrounded by an amorphous extracellular matrix (Fig. 2a). The aflagellate sperm cell comprises a conspicuous anterior acrosome, the posterior nuclear region and the cytoplasmic mass, which is concentrated to form a collar between the acrosome and the nuclear region (Fig. 2a, b and Table 1). The spermatozoon is 5.33 ± 0.42 µm in length and 3.55 ± 0.20 µm in width ($n = 15$). The acrosome, which is 2.25 ± 0.19 µm in diameter ($n = 15$), consists of a spherical or ovoid vesicle bounded by a smooth membrane that encloses structurally complex contents. Sagittal and transverse sections show small vesicles, which are arranged in a single row at the periphery of the acrosome vesicle and contain an electron-lucent matrix and a dense central core (Fig. 2c, d). Oblique and tangential sections show these vesicular structures to be numerous at the base of the acrosome, forming several layers and displaying an elongate or tubular shape (Fig. 2d). Such images suggest that these membranous tubules extend radially from the base through the remainder of the acrosome vesicle periphery. The greater part of the acrosome is filled with a moderately electron-dense, finely granular material (Fig. 2a–g). At the innermost region of the acrosome, there is an electron-lucent area containing granular elements, which usually appear associated with a dense material (Fig. 2e, f). Depending on the angle of the sections, the granules exhibit a random (Fig. 2d, g), parallel (Fig. 2e) or concentric (Fig. 2f) arrangement.

The cytoplasm is confined to a collar intervening between the acrosome and nuclear region. It lodges the acrosome base and extends laterally over the anterior portion of the nuclear region (Fig. 2a, b). The cytoplasmic mass contains parallel membrane arrays, which sometimes show an osmiophilic content, electron-clear vesicles and mitochondria (Fig. 2b, g, h). In transverse sections of the cytoplasmic collar the membranous lamellae appear arranged in concentric circles (Fig. 2h);

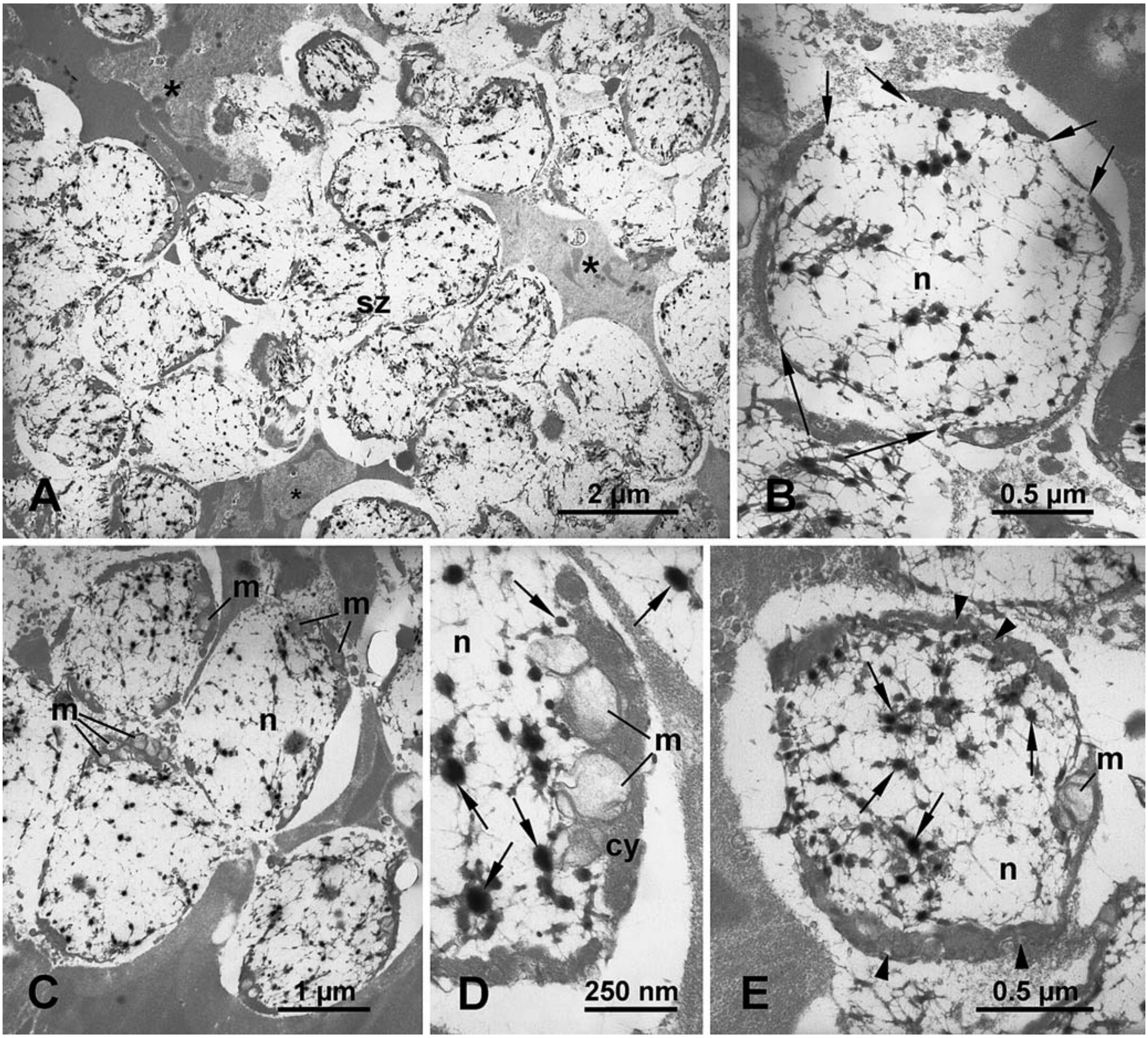


Fig. 1 *Aristaeopsis edwardsiana*. Transmission electron micrographs of spermatozoa. **a** Spermatozoal clusters (*sz*) in the vas deferens appear surrounded by an amorphous extracellular material (*asterisks*). **b** The spermatozoon consists of a central nuclear region (*n*) surrounded by reduced peripheral cytoplasm (*cy*) that shows discontinuities (*arrows*). **c** Mitochondria (*m*) are often grouped in certain areas of the cytoplasm. **d** Group of mitochondria located in the inner part of the cytoplasm (*cy*) are in contact with the nucleoplasm (*n*); they show a homogeneous, electron-clear matrix and very scarce cristae. The chromatin network forms dense nodules at points where the fibres converge (*arrows*). **e** Apart from mitochondria, the cytoplasm includes vesicular structures and other amorphous membrane remnants (*arrowheads*). Numerous chromatin nodules (*arrows*) are visible in the nuclear region

whereas longitudinal sections show them to be orientated in the direction of the lateral expansion of the cytoplasmic mass (Fig. 2g).

Like in *Aristaeopsis edwardsiana*, the non-membrane bound nucleoplasm consists of a network of thick chromatin fibres (Fig. 2a, b). Some fibres are apparently inserted in the cytoplasmic mass and arranged longitudinally (Fig. 2d). Nodules are visible at points where chromatin filaments converge. Membranous vesicles can be observed within the nucleoplasm (Fig. 2b).

Discussion

Dendrobranchiate sperm ultrastructure—general considerations

Dendrobranchiate crustaceans show a diverse range of sperm morphologies. Most penaeoid species investigated so far possess a spermatozoon of the ‘unistellate’ type, which is characterized by the presence of a pointed

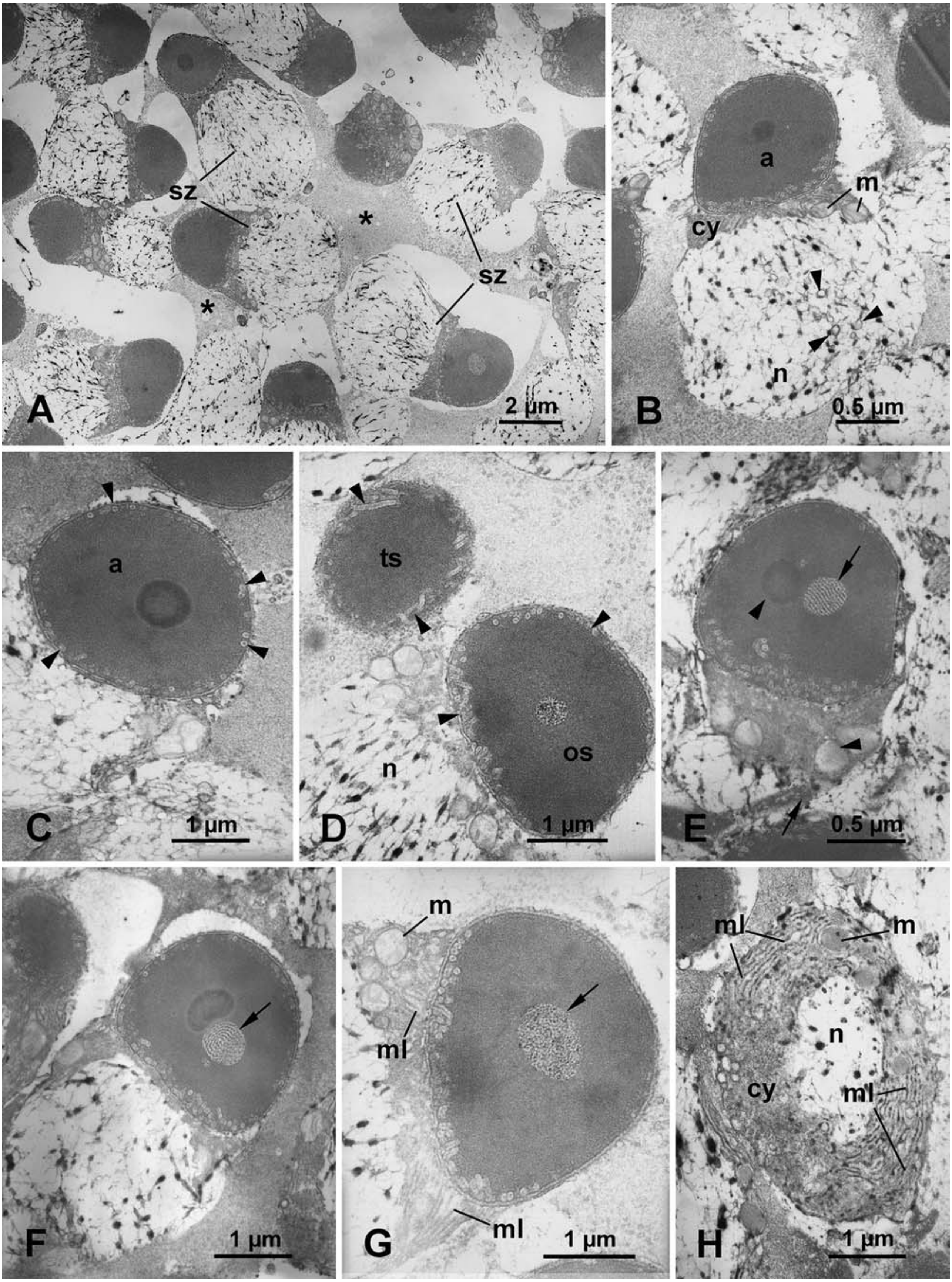
Table 1 Key features of the sperm ultrastructure that define differences among the different dendrobranchiate taxa investigated so far

	Taxon	Nucleus location	Cytoplasm distribution	Acrosomal vesicle	Spike	Intra-acrosomal peripheral vesicles	Centrioles (diplosome)	Chromatin	Bibliographic source
Penaeoidea									
Aristeidae	*Aristeus varidens*	Eccentric	Subacrosomal collar	+	–	+	–	Filamentous	This study
	Aristeus antennatus	Eccentric	Subacrosomal collar	+	–	+	–	Filamentous	Demestre et al. (1993, 1997) and Medina (1995b)
	Aristaeopsis edwardsiana	Central	Perinuclear band	–	–	–	–	Filamentous	This study
	Aristaeomorpha foliacea	Central	Perinuclear band	–	–	–	–	Filamentous	Medina (1995b)
Penaeidae, Solenoceridae, Sicyoniidae		Central	Perinuclear band	+	+	–	–	Filamentous	Medina (1995[a])
Sergestoidea									
Sergestidae		Central, eccentric	Perinuclear band, subacrosomal layer	–, +	–	–	–, +	Filamentous and granular	Medina (1995) and Scelzo and Medina (2004)

Fig. 2 *Aristeus varidens*. Transmission electron micrographs of spermatozoa. **a** Spermatozoa in the vas deferens (*sz*) are embedded in a homogeneous extracellular matrix (*asterisks*). **b** Sagittal section of a spermatozoon showing the anterior acrosome (*a*), the posterior nuclear region (*n*) containing small membranous vesicles (*arrowheads*), and the cytoplasmic collar (*cy*) including conspicuous mitochondria (*m*). **c** Longitudinal section of the acrosome (*a*) where small vesicles are seen arranged in a single row at the acrosome periphery (*arrowheads*). **d** Oblique (*os*) and tangential (*ts*) sections of the acrosome show the peripheral vesicles to have a tubular profile (*arrowheads*), at least on the side close to the nuclear region. **e** Oblique section of an acrosome in which the central electron-clear area (*arrow*) and its associated dense material (*arrowhead*) are visible; the granular material of the electron-lucent area displays a parallel arrangement. In other sections, the granules exhibit concentric (**f**) or (more commonly) random (**g**) arrangements (*arrows*). **g** Longitudinal sections through the cytoplasm show parallel membrane arrays (*ml*), electron-clear vesicles and mitochondria. **h** Those elements appear here sectioned transversally; the membrane lamellae (*ml*) are arranged concentrically conforming to the shape of the cytoplasmic collar (*cy*), which encloses the anteriormost portion of the nucleoplasm

prolongation of the acrosome vesicle that is termed spike (Felgenhauer and Abele 1991; Jamieson 1991; Krol et al. 1992; Medina 1995a; Jamieson and Tudge 2000). However, an earlier study (Medina 1995b) revealed that two representatives of the Aristeidae have spike-less spermatozoa (Fig. 3), either because the spermatozoon lacks an acrosome (*Aristaeomorpha foliacea*) or because the acrosome vesicle develops no projecting structure (*Aristeus antennatus*). Like in aristeids, the only two Sergestoidea species whose spermatozoal ultrastructure is known to show spike-less spermatozoa. One of these species has a well-developed acrosome (Scelzo and Medina 2004), while the other species possesses acrosome-less spermatozoa (Medina 1995a) (Fig. 3). Table 1 summarizes key features of the spermatozoal ultrastructure in Dendrobranchiata that may be useful in comparative studies.

Within Decapoda, close relationship between various acrosome-less sperm taxa and groups endowed with highly elaborate acrosomal structures is a puzzling phenomenon. It hints at multiple convergent reduction of the acrosome to which our current knowledge cannot yet give a satisfactory functional explanation. In Pleocyemata (Brown 1966; Pochon-Masson 1968; Hinsch 1971; Talbot and Chanmanon 1980; Goudeau 1982; Talbot et al. 1991; Medina 1992; Medina and Rodríguez 1992) and Dendrobranchiata (Yudin et al. 1979; Clark et al. 1981; Clark and Griffin 1988; Griffin et al. 1988; Griffin and Clark 1990; Hertzler and Clark 1993) an extremely complicated acrosomal reaction is a crucial step in the fertilization process that facilitates penetration of the sperm nucleoplasm into the ooplasm through the egg envelopes. The fact that spermatozoa of some decapods do not need an acrosome to fertilize the oocyte implies that they must have evolved particular mechanisms of fertilization that probably involve also the female gamete (e.g. structural and/or chemical modifications of the egg coat to make it easily penetrable by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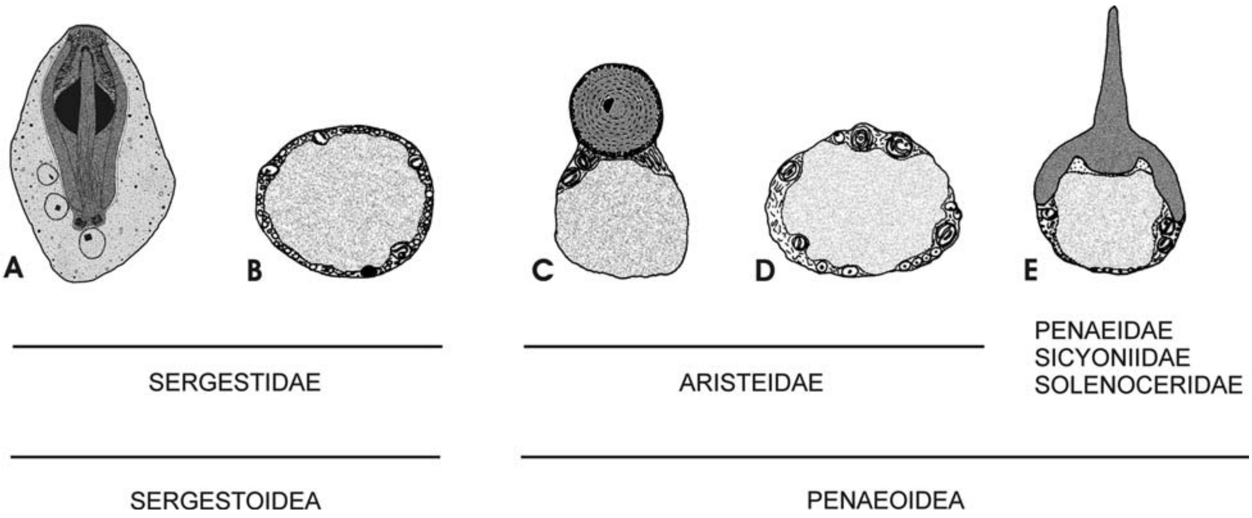

Fig. 3 Schematic drawing illustrating the diverse spermatozoal morphologies present in Dendrobranchiata (not at scale). **A** *Peisos petrunkevitchi* spermatozoon (redrawn from Scelzo and Medina 2004). **b** *Sergestes arcticus* spermatozoon (redrawn from Medina 1995a). **c** Sperm type found in *Aristeus* species (redrawn from Medina 1995b). **d** Sperm type found in *Aristaeomorpha* species and *Aristaeopsis* species (redrawn from Medina 1995a). **e** Spiked spermatozoon of *Penaeopsis serrata* (Penaeidae) (redrawn from Medina et al. 1994a)

the spermatozoon). To answer this question, detailed studies on the fertilization process in species with acrosome-less spermatozoa will be needed.

Sperm ultrastructure in *Aristaeopsis* and *Aristaeomorpha*

The spermatozoon of *Aristaeopsis edwardsiana*, characterized by the central reticulate chromatin, perinuclear cytoplasm, and absence of acrosome, is quite similar in fine structure to that of *A. foliacea* (Medina 1995b), with the only difference that in the former, the cytoplasm is less vesiculate, and it appears to contain a larger number of mitochondria and lacks myelin-like structures. The high spermatozoal similarity between these species suggests phylogenetic proximity between both aristeid genera. An acrosome-less sperm pattern resembling that of *Aristaeopsis* and *Aristaeomorpha* is also found in the dendrobranchiate sergestid *Sergestes arcticus* Krøyer, 1855 (Medina 1995a), two euphausiids, *Euphausia* sp. (Jamieson 1991) and *Meganyctiphanes norvegica* (Sars, 1857) (Medina et al. 1998), and the pleocyemate stenopid *Stenopus hispidus* (Olivier, 1811) (Felgenhauer and Abele 1991). The loss of the acrosome is a repeated event that has occurred several times independently throughout evolution of the crustacean sperm (Jamieson 1991). Whether the acrosome-less condition of the aristeids is apomorphic or otherwise, it represents a plesiomorphy, is a controversial issue that requires further comparative investigation.

Sperm ultrastructure in *Aristeus*

Strong resemblances in the spermatozoal ultrastructure of *Aristeus varidens* and *Aristeus antennatus* unequivocally denote a phylogenetic proximity between both species and suggest the occurrence of spermatozoal uniformity in the genus *Aristeus*. The only clear structural difference between the two species is that the main acrosomal content is homogeneous in *A. varidens*, while it is composed of hollow particles arranged concentrically in *A. antennatus* (Medina 1995b). Apart from three features that concur in all known dendrobranchiate sperm (non-membrane bound nuclear region, filamentous chromatin, and absence of radial arms), the widespread perinuclear distribution of the cytoplasm and the spiked acrosome have been postulated to represent penaeoid plesiomorphies (Medina 1995a). Should this be true, then the subacrosomal (instead of perinuclear) cytoplasm and the spherical (not capping) acrosome, with unique internal organization and lacking the projecting spike, should be viewed as autapomorphies of the genus *Aristeus*. However, the finding in the sergestid *Peisos petrunkevitchi* of a spermatozoon possessing a pear-shaped acrosome without spike and non-perinuclear cytoplasm (Scelzo and Medina 2004) poses serious doubts as to the reliability of this assumption. The unique sperm pattern of *Aristeus*, characterized by the spherical acrosome devoid of basal invagination or perforatorium, and the lamellar cytoplasm located between it and the nucleoplasm, recall that of palinurid reptants (Talbot and Summers 1978; Tudge et al. 1998). However, some remarkable disparities (absence of radial arms and microtubules) also occur between these groups (Medina 1995b).

Conclusion

The present study confirms the occurrence within the Aristeidae of two independent lineages of spermatozoal evolution, which are in turn divergent from the presumed spermatozoon structure in the ground pattern of Penaeoidea. Thus, the Aristeidae include at least two distinct sperm types that are quite different from the unistellate spermatozoon found in the remaining Penaeoidea. One of such sperm types is shared by the genera *Aristaeomorpha* and *Aristaeopsis*, and the other occurs in *Aristeus*. The question now is to find out which of these two sperm patterns is derived and which is ancestral. Unfortunately, the scarce number of studies made on the spermatozoal ultrastructure in Dendrobranchiata does not allow constructing consistent phylogenetic analyses from sperm characters alone. Therefore, a more reliable assessment of spermatozoal relationships in the Dendrobranchiata, in general, and the Aristeidae, in particular, will be possible only when more aristeid species are investigated.

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