

13. G. Yasuzumi Memorial Lecture

Some Recent Studies on the Ultrastructure and Phylogeny of Annelid and Uniramian Spermatozoa

B. G. M. JAMIESON, Department of Zoology, University of Queensland, Brisbane 4067, Australia

Primitive sperm, seen in many polychaetes, have recently been termed aquasperm. Further new terms are now proposed (with G. W. Rouse): ect-aquasperm, and ent-aquasperm and, for 'non-aquatic' sperm, the term introsperm (Fig. 1).

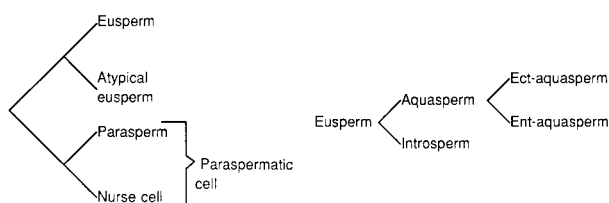


Fig. 1. Types of spermatozoa in the Eumetazoa.

The ect-aquasperm is an aquasperm which is liberated freely into the ambient water in which it (potentially at least) fertilizes the similarly free egg. Ect-aquasperm are characterized, in 'anterior-posterior' sequence, by a caplike acrosome (sometimes absent, as in Cnidaria), a subspherical nucleus, a small number of rounded, cristate mitochondria and a free axoneme with the 9+2 arrangement of microtubules. In its most basic form two centrioles are retained, the distal (posterior) of which forms the basal body of the axoneme, and a satellite- or anchoring-apparatus arises from this centriole. In polychaetes, ect-aquasperm are probably the most common type of sperm. Examples are *Eurythoe complanata* (Amphinomidae), *Galeolaria caespitosa* (Serpulidae), *Idanthyrsus pennatus* (Sabellariidae) and *Chaetopterus variopedatus* (Chaetopteridae).

The ent-aquasperm is also shed into the ambient water but differs from the ect-aquasperm in that it is drawn in by the inhalent or feeding current of the female (sometimes hermaphrodite), or otherwise reaches it, and may be stored, for instance in spermathecae, as in *Spirorbis*. Fertilization may occur in water within the female, for instance in the mantle cavity (bivalves) or in the tube (sedentary polychaetes). The ent-aquasperm mode of fertilization appears to be related chiefly to female retention of large-yolked eggs in animals which are not motile. They may be profoundly modified from the basic aquasperm type. Modifications relate to features of the egg and to sperm storage. Annelid examples are *Fabricia*, *Oriopsis* (Sabellidae), and *Micromaldane* (Maldanidae) spp.

The introsperm never enters the water in aquatic species and is general for terrestrial metazoans. It is transferred from the male to the female by some form of copulation or by uptake of free spermatophores by the female. In annelids it is transferred by true copulation, via female pores, as in some hesionid and saccocirrid polychaetes and some leeches; by 'pseudo-copulation', in which the apposed male and female shed gametes directly into a 'cocoon', as in the aflagellate sperm of *Ophryotrocha* species (Dorvilleidae), or sperm received from a partner into spermathecae are subsequently shed onto the eggs within a cocoon as in questid polychaetes and most oligochaetes; or transfer may be by hypodermic impregnation, as in the histriobdellid polychaetes, in which the male stabs the female with the penis and injects sperm into the female

coelomic cavity. Spermatophores may be involved in these processes; alternatively spermatophores may be transferred directly to the body surface of the partner, the sperm later penetrating the body wall to reach the eggs, as in some hesionids and leeches, or may be shed into the water and gathered by the female, as in some spionids. A series in development of internal fertilization with true copulation is seen in eudrilid earthworms. Sperm penetrate the wall of the spermatheca in *Stuhlmannia variabilis* to reach the eggs internally. In *S. asymmetrica* an open connection exists between the spermatheca (now effectively a vagina) and the ovarian apparatus.

Further categories of sperm exist. Sperm dimorphism occurs in tubificid Oligochaeta, Rotifera, Pogonophora, internally fertilizing prosobranch molluscs, Symphyla, Lepidoptera, Hymenoptera (*Dahlbominus*, with transient polymorphism) and is here demonstrated ultrastructurally for the first time in chilopods in the scolopendromorph *Ethmostigmus rubripes*. In *Ethmostigmus* macrosperm and microsperm are present, the structure of which, especially that of the nuclear-axonemal junction (connecting piece), has taxonomic value at the ordinal level. Whether each chilopod sperm can contribute to a zygote genome is not known; the dimorphism does not appear to be concerned with sex-determination.

In the spermatophore of *Tubifex tubifex* the fertilizing sperm lie mutually parallel to form an axial cylinder enclosed in a sheath by cortical sperm which are held together by septate junctions between adjacent flagella and have reduced acrosomes. In the terminology of Healy and Jamieson, sperm which contribute to the zygote genome are eusperm, those of the non-fertilizing lineage, which may aid but do not contribute genetically to fertilization are termed parasperm (Fig. 1). The term paraspermatic cell of other authors is an appropriate collective term for nurse cells associated with the eusperm (in, for instance, molluscs), and parasperm. Nurse cells, in molluscs at least, appear to be sterilized male gonocytes. The cortical parasperm of the tubificid spermatophore are presumably a product of selection of peripheral eusperm in the simple spermatozeugmata seen in other tubificids. What may be termed atypical eusperm occur in some prosobranchs, in addition to eu- and parasperm but if found not to contribute to the zygote genome should be relegated to the parasperm category.

The taxonomic and phylogenetic value of spermatozoal ultrastructure is well exemplified by the Annelida, especially the Euclitellata. Even in polychaetes, where a single family may show both ect- and ent-aquasperm (e.g. sabellids), or ect-aquasperm and introsperm (e.g. spionids), the second sperm type in each case may show morphological affinities across included species; the structure of spionid introsperm, especially, is distinctive of the family. In oligochaetes, sperm ultrastructure shows a close congruence to phylogeny derived from somatic characters and it has recently been shown that highly heuristic dendrograms are produced by using spermatozoal characters alone in parsimony, phenetic, and other forms of numerical analysis. The structure of the acrosome has proved particularly valuable. An acrosome tube is restricted to euclitellates, though an approach to this structure occurs in nematomorphs and possibly, with interesting phylogenetic implications, in vestimentiferan Pogonophora. Similarities between the sperm of oligochaetes and Onychophora have led to the proposition of a special phylogenetic relationship between these two groups, supported independently from studies on leech somatic anatomy and biology. Striking oligochaete-onychophoran spermatozoal shared apomorphies include the highly distinctive interpolation of mitochondria between nucleus and axoneme, with no penetration of the mitochondria by the axoneme, and the presence of a basal cylinder at the anterior end of the two central axonemal singlets.

Use of a combination of somatic and gametological characters is advocated in future phylogenetic studies.