

Franzén Å. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zool. Bidr. Uppsala* 31:355-482, 1956.
[Zoological Institute, University of Uppsala, Sweden]

This paper showed that sperm morphology in metazoans has a definite relation to fertilization biology. The primitive sperm is found only in animals that have retained external fertilization. Spermatozoa of animals with direct sperm transfer to the female are more or less modified. [Cited in over 165 publications, this is one of the most-cited papers published in this journal.]

Åke Franzén
Department of Invertebrate Zoology
Swedish Museum of Natural History
S-104 05 Stockholm
Sweden

August 19, 1985

In 1951 I commenced my PhD studies at Uppsala University and, not unlike other graduate students, was confronted with the problem of selecting a suitable research topic and securing a graduate adviser. During my undergraduate years I had been especially interested in invertebrate zoology, phylogeny, and marine biology. This led to Gösta Jägersten suggesting that I should study spermiogenesis and sperm structure of invertebrates. I gladly accepted this project even though numerous colleagues were skeptical of my choice. The project gave me the splendid opportunity to study and examine living marine animals from the west coast of Sweden.

At that time I had no access to an electron microscope, and most of the difficulties I encountered were concerned with the low resolution of the light microscope. Using a phase-contrast microscope and variable dyes, I attempted to reveal homologies between sperm-cell organelles from numerous invertebrate groups.

After reviewing the literature it appeared to me that acrosome, nucleus, and the mitochondrial midpiece should be most carefully considered. It soon became apparent that sperm morphology is a sensitive indicator of fertilization biology in most groups. Collecting and identifying more than 120 species from 16 different phyla for this investigation was an exciting challenge.

I found that the primitive sperm was common in most invertebrate groups with external fertilization. This sperm is a small cell with three regions: head, midpiece, and tail. The head consists of a rounded, condensed nucleus surmounted by the acrosome. The midpiece contains mitochondria and centrioles, and the tail is a flagellum about 50 μ m long. When released in water, this sperm swims vigorously with the head directed forward. Modified sperms show a pronounced similarity to the primitive type and have evolved from the primitive sperm through changes following a common pattern: nucleus and midpiece are elongated, and the entire sperm is enlarged. Modified sperms appear in animals with some type of direct sperm transfer. Aberrant sperms occur in many groups with internal fertilization or an otherwise specialized biology of fertilization. After this paper was published, the common utilization of the electron microscope confirmed and supported my results and added new facts.^{1,2}

The response to this paper has brought me in contact with numerous invertebrate zoologists from all corners of the world, which has been most gratifying and stimulating.

I suppose that my paper has been widely cited for three reasons. First, it explained in a simple way the striking difference in sperm morphology that sometimes occurs between closely related species. Second, it showed that knowledge of sperm structure is of great value from a phylogenetic and taxonomic point of view. And third, it still appears to provide basic information and definitions useful in research on spermatozoa. The original paper developed a general view on the evolution of spermatozoa and fertilization biology in metazoans. A more recent, updated review will appear shortly.³

1. Franzén Å. Ultrastructure of spermatids and spermatozoa in three polychaetes with modified biology of reproduction: *Autolytus* sp., *Chitinopoma serrula*, and *Capitella capitata*. *Int. J. Inver. Repr. Devel.* 5:185-200, 1982.
2. Ultrastructural studies of spermatozoa in three bivalve species with notes on evolution of elongated sperm nucleus in primitive spermatozoa. *Gamete Res.* 7:199-214, 1983.
3. Spermatogenesis. (Giess A C & Pearse J S, eds.) *Reproduction of marine invertebrates*. New York: Academic Press, Vol. 9. In press.