jections appeared fused. Associated with the dense projections were electron-dense strands lying deeper in the presynaptic terminal that sometimes appeared to form direct contacts with the plasma membrane. This structural aggregation, which resembled the finger-like processes observed in synapses of *Dugesia dorotocephala*[8,9], is similar to the presynaptic network of vertebrate synapses[10]. In oblique sections through the synapses of *H. microstoma*, the dense projections appeared few in number, and did not show a regular arrangement. This is in contrast to the situation observed in vertebrate synapses[4,10,11].

The presynaptic terminals were filled with numerous synaptic vesicles (200–450 Å diam.), interspersed with the occasional small dense-cored vesicles (450–750 Å diam.). Complex vesicles, from which dense projections are believed to be derived[12], were observed in the presynaptic terminal (Figure 3).

Post-synaptic densities, emanating from the inner thickened leaflet of the postsynaptic membranes (Figure 1), were a constant feature of the synapses. These structures, which were up to 300 Å wide, usually extended the length of the synaptic cleft. Whispy projections were observed, extending from the postsynaptic density into the postsynaptic space. Thus the postsynaptic densities are similar to those observed in vertebrate synapses. While the variation in width of the postsynaptic density of vertebrates is usually associated with excitatory or inhibitory synapses[4], such correlation was not possible in the present study where flattened synaptic vesicles have not been observed.

The present results therefore show that the synapses of *H. microstoma* possess almost all those features found in many higher invertebrate and vertebrate synapses, and attest to an early phylogenetic origin of this type of synapse. Several of these features, however, have not been observed in other platyhelminths or in coelenterates. For example, while small presynaptic dense projections and postsynaptic thickenings have been observed in several coelenterates[13,14], neither complex vesicles nor presynaptic networks have been described. Many of these features observed, however, may apply only to certain types of synapses where mechanical strength is of importance[15]. Such may be the case with the present material, where ,under differing experimental conditions, the extracellular space between neurites may be variable, the synaptic cleft is of constant dimensions[16]. Further research is required to allow differentiation between those structures associated with synaptic membrane adhesion, and those structures associated with chemical transmission at synapses.

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The Fine Structure of the Conical-Headed Sperm of the Crinoid *Antedon bifida*

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Summary. Scanning- and transmission electron microscopy show that the sperm head of *Antedon bifida* is conical and thus different from the spherical sperm head that is typical of crinoids. The head consists of the acrosome and the nucleus. The posterior fibrogranular component of the acrosome is housed in a tubular, axial invagination running from the anterior pole almost to the posterior pole of the nucleus. The middle piece includes a mitochondrion and a pair of centrioles. One of the centrioles is a basal body, which gives rise to the tail flagellum.

In the echinoderm class Crinoidea, the sperm is divisible into a head, a middle piece and a tail. The sperm head is approximately spherical in many species of stalked and unstalked crinoids[1–5]. By contrast, a conical sperm head was reported for the crinoid *Antedon bifida* by Chadwick[6] in 1907. I once suspected[5] that Chadwick had mistaken a spherical head for a conical head. However, my recent electron microscopy has shown that Chadwick was correct and that I have been the mistaken one, since the sperm head of *Antedon bifida* is indeed conical. The present report describes the fine structure of sperm from ripe male specimens of *Antedon bifida* collected at Plymouth, England[7]. The methods for the scanning- and transmission electron microscopy have already been published elsewhere[8].

The scanning electron micrograph (Figure 1) shows the sperm head, the middle piece and the proximal part of the tail. The conical sperm head is 2 μm in length by 1.1 μm in maximum width. The middle piece is 0.7 μm long by 1.3 μm wide. The tail, as measured from whole mounts of freshly killed sperm, is roughly 50 μm long.

Transmission electron micrographs (Figure 2, a and b) show that the sperm head is made up of an acrosome and a nucleus. The acrosome consists of a spherical acrosomal granule and the surrounding fibrogranular material. The acrosomal granule is about 0.5 μm in diameter, and the posterior pole of the granule has a small concavity 0.05 μm deep (Figure 2b). The granule is filled with amorphous contents of moderate electron density. The fibro-granular acrosomal material outside of the granule is divided into

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2 portions. The first portion (Figure 2b, single arrow) encircles the meridian of the granule; the second portion (Figure 2b, twin arrows) is located just posterior to the granule in a deep, tubular invagination of the nucleus. This invagination runs axially from the anterior pole of the nucleus and ends blindly just short of the posterior pole of the nucleus (Figure 2a). The nuclear chromatin is everywhere condensed and appears as compacted granules, each about 300 Å in diameter.

The middle piece of the sperm contains a crescent-shaped or annular mitochondrion (Figure 2, c and d). Also present in the middle piece are a dense body and a pair of centrioles. The dense body, which is not visible in the figures, may possibly be a lysosome. One of the two centrioles gives rise to the tail flagellum and thus is the basal body (Figure 2a). The basal body and the other centriole are usually oriented parallel to each other (Figure 2c). The wall of the basal body contains 9 typical triplet fibrils; by contrast, the wall of the other centriole (Figure 2c, arrow) contains 9 twin fibrils. The basal body, but not the other centriole, is associated with a centriolar satellite complex (Figure 2d) resembling that seen in sperm of other echinoderms[9].

The sperm tail, for most of its length, is a typical flagellum, which consists of an axial filament complex of 2 central fibrils and 9 surrounding double fibrils (Figure 2e). Scanning electron microscopy shows that the posterior 2 or 3 μm of the tail is a terminal piece with a diameter roughly half that of the unmodified flagellum. Within the terminal piece, the fibrils of the axial filament complex become disorganized and reduced in number (Figure 2e, lower right).

It is reasonable to assume that *Antedon bifida* with its conical sperm heads evolved from crinoid ancestors with spherical sperm heads. However, the adaptive significance of this change from spherical to conical is not clear. FRAZÉN[10] has argued that the evolutionary change from spherical to elongated sperm heads is correlated with a change from external to internal fertilization. Yet this explanation can not hold for *Antedon bifida*, a species with external fertilization. Alternatively, the egg investments of *Antedon bifida* might differ from those of other crinoids and thus require a specialized sperm for penetration. This possibility should be tested by a comparative study of egg investments, acrosome reactions and other sperm-egg interactions in *Antedon bifida* and in crinoids with typical, spherical sperm heads.

For the sake of completeness, it should be added that FIELD[11] mistakenly reported that *Antedon mediterranea* has a conical sperm head. My own observations have shown that this species has a spherical sperm head[5]. Finally, a recent compilation of sperm shapes in echinoderms[5] gives me credit for claiming that the sperm head of *Antedon adriatica* is shperical. In truth, I have never seen the sperm of this species, and I have never communicated any such information to anyone.

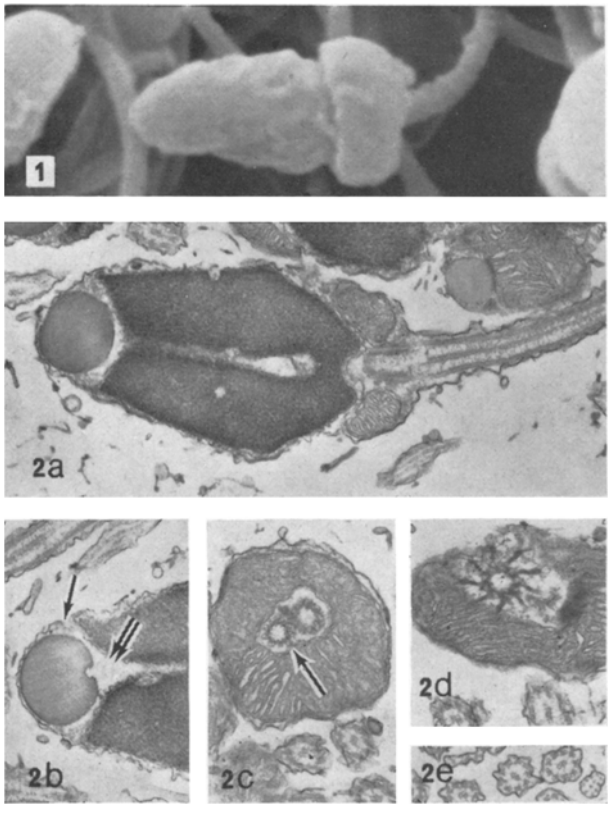

Fig. 1. A scanning electron micrograph of the head, middle piece and part of the tail of a sperm of *Antedon bifida*. The anterior end of the head is pointing toward the left. × 15,500.

Fig. 2. Transmission electron micrographs of sperm of *Antedon bifida*. × 19,000. a) Transverse section of the head, middle piece and part of the tail oriented as in Figure 1. Conspicuous features from left to right are the following: acrosomal granule; nucleus with tabular invagination; middle piece with mitochondrion and basal body; and flagellar tail. b) Transverse section of antertior third of the sperm head showing the following acrosomal components: granule with small posterior concavity; meridional fibrogranular component (single arrow); and posterior, axial fibrogranular component (twin arrows). c) Cross section of the middle piece showing the annular mitochondrion and the pair of centrioles. The centriole which is not the basal body is indicated by the arrow. d) Cross section of the middle piece slightly posterior to Figure 2c. The centriolar satellite complex radiates from the basal body. e) Cross sections of several sperm tails. A cross section of a terminal piece is at the lower right.

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