

the value measured in December by Dalrymple (7). The calculated average daily total radiation ($\sigma_v = 0.05 \text{ km}^{-1}$) reaching the surface at 85°S is $\sim 0.62 \text{ cal cm}^{-2} \text{ min}^{-1}$, compared with a measured value in January over the South Pole of $0.64 \text{ cal cm}^{-2} \text{ min}^{-1}$ (7). Also, the calculated solar heating rate of the aerosol particles at 630 and 674 mbar is $\sim 0.96^\circ\text{K}$ per 24-hour day, compared with the value of 0.5°K per 12-hour day that has been quoted by Hobbs *et al.* (11).

For an assumed present background aerosol σ_v of ~ 0.065 to 0.1 km^{-1} (12), the surface temperature change at 85°N due to these aerosol particles ($+0.05^\circ\text{K}$) is within measured temperature uncertainties. At 85°S the comparable value is slightly under $+0.2^\circ\text{K}$, and averaged over the year this difference would also probably be undetectable.

There is a striking difference between the effect of aerosols over 85°N and that of aerosols over 85°S . In the north polar region, a tenfold increase in the background aerosol density would yield a surface temperature rise of $\sim 0.5^\circ\text{K}$. In the south a similar increase in particle density would give a rise of $\sim 5.25^\circ\text{K}$. Additional calculations have been made to determine the reason for this high sensitivity at 85°S . It appears that the relative importance of the factors is as follows: thinness of atmosphere $>$ increased surface albedo $\gg$ increased solar radiation. Of course the atmospheric system is highly nonlinear and all variations must be considered jointly to obtain the high temperature sensitivity reported here.

I conclude that aerosol particles over the polar regions have not been responsible for the ice mass increase in the Arctic, since they always have a heating effect. Of course, aerosol-induced changes in the general circulation have not been considered here.

Fletcher (13) has indicated that the Southern Hemisphere is the controlling factor in determining the vigor of the global atmospheric circulation. In December both the potential energy and the poleward gradients are equal between the hemispheres, while in June the kinetic energy of the circulation in the south is 3.5 times that in the north. Therefore, an increase of the particle content of south polar atmosphere may have a considerable effect on the air circulation. It may well be that a decrease in the poleward advection (which is not included in these calculations) is responsible for the reduction in the observed polar temperatures.

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Uniflagellate Spermatozoa in Nemertoderma (Turbellaria) and Their Phylogenetic Significance

Abstract. *An ultrastructural study of Nemertoderma (Turbellaria, Nemertodermatida) has revealed that its spermatozoa have only a single flagellum. This is the first uniflagellate spermatozoon known in the Turbellaria; it is indicative of the primitiveness of Nemertoderma and is evidence in support of the view that the Turbellaria as a whole are among the most primitive living Bilateria.*

Many theories on the origin and evolution of the Metazoa consider the Turbellaria to be the most primitive of all Bilateria (1). The finding in recent years, however, that all Platyhelminthes, including the Turbellaria, have biflagellate, or occasionally aflagellate, spermatids and spermatozoa (2), has been a serious obstacle to the acceptance of these theories. Since the occurrence in most metazoan phyla of uniflagellate sperm indicates that the primitive spermatozoon type was uniflagellate (3), the turbellarians, with their biflagellate spermatozoa, seem to be well removed from the metazoan ancestor. We have found, however, that the spermatozoa of *Nemertoderma*, a primitive marine turbellarian (4, 5), are uniflagellate and sufficiently similar to the hypothetical primitive spermatozoon to establish the Turbellaria again near the base of the phylogenetic tree of the Bilateria.

Specimens of an undescribed species of *Nemertoderma* [*Nemertoderma* sp. A (6)] from the shallow subtidal off Bogue Bank, N.C., were fixed in phosphate-buffered 2.5 percent glutaraldehyde plus 2 percent tannic acid, postfixed in phosphate-buffered 2 percent OsO_4 , and embedded in a mixture of Epon and Araldite. Thin sections from the embedment blocks were stained with uranyl acetate and lead citrate and examined with a Zeiss electron microscope.

The spermatozoa in *Nemertoderma* sp. A are grouped in bundles in the testis. In transverse sections of these bundles (Figs. 1 to 3), the spermatozoa can be seen to have three easily distinguished regions: a head, with the nucleus; a middle piece, with what are presumed to be mitochondrial de-

rivatives partially enwrapping the single flagellar axoneme; and a tail, with the continuation of the flagellar axoneme. The spermatozoa are uniflagellate and the axoneme of the flagellum has a regular $9 + 2$ pattern of microtubules. No centriole, in the sense of a $9 + 0$ triplet microtubule structure, is to be seen in the mature sperm. Instead, the $9 + 2$ axoneme inserts directly into a small fossa in the posterior end of the nucleus, and the central pair of singlets is continuous all the way into the base of this fossa. The only character that differentiates this basal part from the rest of the axoneme is the presence of a set of $0.3\text{-}\mu\text{m}$ -long peripheral dense fibers contiguous with the outer edge of each doublet (Figs. 2 and 4).

The axoneme is the only organelle to be seen through most of the sperm tail; it is not present, however, in the extreme tail tip where instead numerous loosely packed singlet microtubules are seen (Fig. 3).

The nucleus of the mature spermatozoon is a highly condensed structure approximately $6.5\text{ }\mu\text{m}$ long and $0.25\text{ }\mu\text{m}$ wide, with a deep longitudinal spiral groove (Fig. 1). At its tip is a simple vesicle, $0.3\text{ }\mu\text{m}$ long, evidently an acrosome. Such an organelle has not been identified in any other turbellarian spermatozoa (7).

The middle piece of the spermatozoon (Figs. 2 and 4) is as long as the nucleus ($6.5\text{ }\mu\text{m}$). Its cytoplasm is homogeneous and finely granular. A row of six to eight dense crescent-shaped bodies embedded in this cytoplasm, each with one, two, or occasionally three vesicular structures, are presumably mitochondrial derivatives.

According to Franzén (3), who has con-

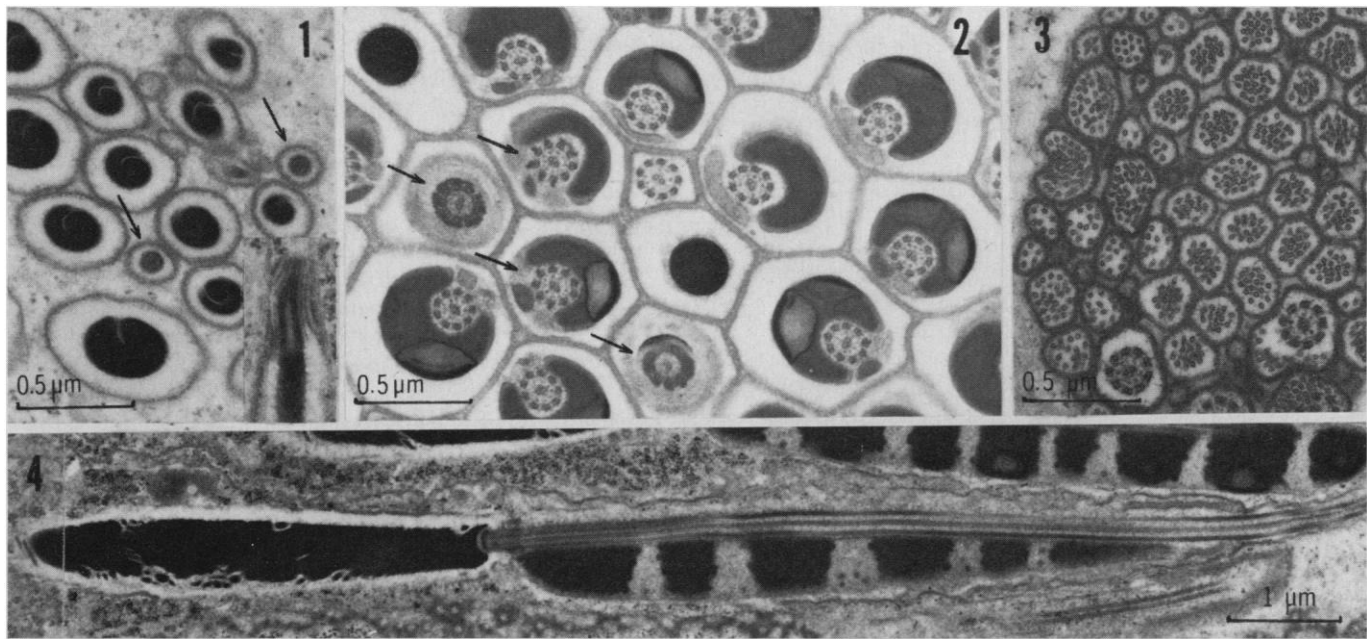


Fig. 1. Heads of mature spermatozoa of *Nemertoderma* sp. A in transverse section. The larger profiles show the deep groove in the nucleus; the smaller profiles (arrows) are acrosomes. Inset: Acrosome in longitudinal section. Fig. 2. Middle pieces of spermatozoa in transverse section. The single flagellar axoneme of each spermatozoon has a typical $9 + 2$ array of microtubules. Axonemes at the arrows are sectioned through the basal region near the nucleus; note the peripheral fibers just to the outside of each of the microtubule doublets. Two nuclei and a tail are also visible. Fig. 3. Tips of tails of spermatozoa in transverse section. Two tails are sectioned through a portion where the $9 + 2$ axoneme is present; the other tails are sectioned more posteriorly and show instead microtubule singlets. Fig. 4. An immature spermatozoon in longitudinal section. The nucleus, toward the left, is not completely condensed. The axoneme inserts in a small fossa of the nucleus, extends through the middle piece, and emerges on the right as the tail. Both the tail and the tip of the nucleus with the acrosome are bent out of the plane of the section.

ducted a comparative study of spermiogenesis and fertilization in metazoan phyla, the type of spermatozoon that one would expect to find in the primitive metazoan with external fertilization has a rounded or oval head with an acrosome, and a short middle piece with four to five mitochondrial spheres in a ring around a $9 + 2$ axial filament that issues from a centriole and extends posteriorly from the middle piece as a tail. Though *Nemertoderma*'s spermatozoon does not fit this description completely, it is closer to this hypothetical primitive metazoan sperm than is any other turbellarian sperm. The deviations from Franzén's hypothetical primitive sperm that are seen in *Nemertoderma*'s sperm—the relatively elongate shape of the head and middle piece and the absence of a centriole—could arise, according to Franzén's reasoning, as modification for specialized internal fertilization.

Another older theory on the nature of turbellarian sperm proposes that the biflagellate turbellarian sperm is primitive, persisting from a premetazoan stage of evolution (8). By this reasoning *Nemertoderma*'s unflagellate sperm would be viewed as more advanced than other turbellarian sperm, and *Nemertoderma* then would provide a link between the turbellaria and all other metazoans with unflagellate sperm. Unless the Turbellaria are to be regarded as the most primitive of all Metazoa, that is, even more primitive

than the Porifera, Cnidaria, and Ctenophora all of which have unflagellate sperm, then this theory cannot be supported. Similarly, the unflagellate nature of *Nemertoderma*'s spermatozoon might be considered a case of retrograde evolution, derived from a loss of one of the two flagella in a turbellarian ancestor's sperm (9). Again, this does not seem likely, however, since *Nemertoderma*'s unflagellate spermatozoon is symmetrical about the single flagellar axoneme with no indication that a second axoneme has been lost.

The systematic position of *Nemertoderma* has been an issue of long and bitter debate. Steinböck, who described the first *Nemertoderma* species, placed the genus in the order Acoela and considered it the most primitive of all turbellarians (4). His interpretation has been challenged by other turbellarian systematists who have denied *Nemertoderma*'s primitiveness on the basis of more recent findings and have placed it in its own separate taxon on equal rank with the Acoela (10). Yet other systematists have recognized the primitiveness of *Nemertoderma* but still have insisted that it be regarded as distinct from the Acoela (5).

Our finding of unflagellate spermatozoa in *Nemertoderma* supports the view that *Nemertoderma* should be split from the Acoela. In fact, the unique spermatozoon sets *Nemertoderma* apart from all other platyhelminths, although there is no doubt

that *Nemertoderma* is a turbellarian (5, 10). Still, of all the turbellarians, it is the Acoela to which *Nemertoderma* is the most closely related, and we are reluctant to endorse the separation of *Nemertoderma* from the Acoela without leaving some recognition of the close systematic ties between these groups. There are many characters discernible by light microscopy which link *Nemertoderma* with the Acoela (11); and, in regard to sperm ultrastructure, even though the spermatozoa of acoels are highly aberrant, it is only in acoel spermatozoa, of all turbellarian spermatozoa, that a $9 + 2$ flagellar axoneme can be seen, as has been described here for *Nemertoderma* (2, 12).

Therefore, although we support the systematic separation of *Nemertoderma* from the Acoela, at the same time, we feel that for considerations of the phylogenetic position of the Turbellaria, it is important to recognize that *Nemertoderma*, probably the most primitive turbellarian, is most closely related to the Acoela. By virtue of *Nemertoderma*'s evident primitiveness and its ties with the Acoela, the Turbellaria as a whole can be more easily accepted as among the most primitive of living Bilateria.

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Human Lymphocytes: Similarity of B and T Cell Surface Morphology

Abstract. When viewed by scanning electron microscopy, human lymphocytes fixed in suspension and processed with minimal cell loss appear uniformly covered with short microvilli. Contrary to previous reports, lymphocytes from subpopulations selectively enriched for T cells are villous and indistinguishable from B lymphocytes. Whereas lymphocyte surface architecture can change rapidly and substantially in response to environmental modifications, such as contact with an underlying surface, these alterations are similar for both B and T cells and do not serve to distinguish these subpopulations.

Despite differences in function, surface receptors, and membrane properties B (bursa-equivalent, or thymus-independent) lymphocytes and T (thymus-dependent) lymphocytes have proved indistinguishable by light and transmission electron microscopy (1). With the recent application

of scanning electron microscopy (SEM) to cellular immunology, attempts have been made to delineate differences in lymphocyte surface morphology which might provide a definitive means of identifying B and T cell prototypes. Previous investigators (2-5) have reported that human B and T

lymphocytes can be distinguished by differences in their surface architecture. The B lymphocyte has been described as "villous," replete with microvilli, whereas the T lymphocyte has been represented as "relatively smooth" with few surface irregularities. However, in our experience, when human peripheral blood lymphocytes have been fixed in suspension and processed for SEM with minimal cell loss, no such dichotomy in cell surface morphology has been observed (6).

Mononuclear cells were obtained from the peripheral blood of seven normal human donors by Ficoll-Hypaque density gradient centrifugation (7). Lymphocyte yields by this procedure were greater than 80 percent. Subpopulations enriched for T lymphocytes were obtained by passing washed mononuclear cells over nylon columns (8). Nonadherent cells were eluted from the column, and adherent cells were displaced from the fibers by gentle mechanical agitation (9). Approximately 45 percent of the cells placed on the column were recovered in the nonadherent subpopulations and 10 percent in the adherent subpopulations. Surface markers were studied by standard methods (10). The percentage of cells with surface immunoglobulin and of phagocytic cells for each fraction is shown in Table 1. Cell viability, as estimated by the exclusion of trypan blue, was greater than 98 percent for all populations under consideration. After they were washed, cells from the Ficoll-Hypaque and column preparations were resuspended in Eagle's minimum essential medium with 10 percent fetal calf serum and fixed in suspension for 90 minutes at 23°C by the addition of an equal volume of 3.0 percent glutaraldehyde in 0.1M phosphate buffer (pH 7.2). Parallel samples were allowed to settle live onto silver filters for varying time periods before fixation. Fixed cells were sampled for SEM by trapping them on filters in a thin film of water, freezing them quickly, and vacuum-coating them with carbon and gold-palladium. By this procedure approximately 90 percent of fixed cells were retained for viewing by SEM (6). Duplicate samples were also processed by the critical point drying method (11). In some samples, individual cells examined by SEM were identified by their characteristic nuclear morphology as revealed by subsequent light microscopy. The samples were examined and micrographed in an Etec Autoscan microscope at 20 kv and 45° tilt.

As shown in Table 1, in nine experiments the surface architecture of 200 cells was analyzed in micrographs of each of three preparations—the unseparated Ficoll-Hypaque population and the non-

Table 1. Surface morphology of human lymphocytes. Values are means $\pm$ standard deviations. The total number of cells in each category = (200 per experiment) $\times$ (9 experiments) = 1800.

Property	Percentage of total cells in		
	Unseparated Ficoll-Hypaque population	Nonadherent population	Adherent population
Cell marker			
Latex ingestion	24.17 $\pm$ 9.29	1.12 $\pm$ 0.76	3.03 $\pm$ 2.42
Surface immunoglobulin	13.56 $\pm$ 6.40	1.72 $\pm$ 1.35	51.51 $\pm$ 21.82
SEM category			
(0) Devoid of microvilli; smooth or with slight surface irregularity	0	0	0
(1) Relatively smooth with occasional short microvilli	0.17 $\pm$ 0.50	0.28 $\pm$ 0.57	0
(2) Moderate number of microvilli	5.33 $\pm$ 2.06	5.06 $\pm$ 2.05	5.90 $\pm$ 1.41
(3) Large number of microvilli	82.83 $\pm$ 3.96	93.56 $\pm$ 1.93	88.11 $\pm$ 3.21
(4) Extensive number of surface microvilli or long, tortuous microvilli, or both	2.28 $\pm$ 2.17	0.56 $\pm$ 1.21	1.83 $\pm$ 2.03
(5) Ruffled cells	9.39 $\pm$ 4.24	0.56 $\pm$ 0.47	4.06 $\pm$ 3.05