The Nephridia of *Geonemertes dendyi*  

**BY**  
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With five Text-figures

*Geonemertes dendyi* (Dakin) is a terrestrial nemertine. The genus has a predominantly Australian distribution, but in recent years this species has been recorded from the western parts of England and Wales (Waterston and Quick, 1937; Pantin, 1944). In this genus the nephridial system is highly developed, and its structure in several species has been described by Hett (1924), Coe (1929), and others. Stammer (1934) mentioned the existence of a nephridial system in *G. dendyi* but did not describe it. The present work arose from a study of this species collected in South Devon, in all stages from the newly hatched young to the adult. The nephridial system proves to be at least as highly developed in this as in other species, and there are points of some interest regarding its function.

**METHODS**

The flame-cells and the proximal part of the tubule system into which they open are easily detected in living worms owing to their ciliary activity, particularly in newly hatched larvae (about 1 mm. long) and immature specimens of about 3–4 mm. in length. The distal parts of the tubule system show no signs of ciliary activity and have not yet been observed in life.

The system is best seen if the worms are immersed in tap-water and slightly compressed with a large coverslip, or held by a small square of wet cellophane covering a shallow hanging drop on the underside of a coverslip above a moist chamber. For prolonged observation under a powerful light, absorption of heat-radiation entering the condenser is essential.

For micro-anatomical studies the best fixatives were found to be Susa, and Zenker in which formic acid is substituted for acetic. Brief preliminary anaesthetization with 5–10 per cent. ethyl alcohol had no apparent ill effects and enabled the specimen to be fixed without distortion. This was done by arranging the animal on a waxed coverslip, covering it with a piece of moist cigarette paper, and dropping it face down on the fixative. Convenient stains were Mallory's Triple Stain, 'Azan', and Heidenhain's Iron-Haematoxylin with or without Masson’s Ponceau-Light Green used as counterstain. Paraffin sections 4μ–10μ were cut, commonly after Peterfi’s celloidin-paraffin method.
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**STRUCTURE**

In general the nephridia of *G. dendyi* conform to the plan described by Hett (1924) in *G. hillii*, and by Coe (1929) in *G. agricola*. The flame-cells are exceedingly numerous beneath the dermal musculature. The terminal ducts from groups of them unite in a common canal, the ‘end-canal’, which passes to a glandular tubule from whence goes a final efferent duct to one of a very large number of external openings of the system, scattered all over the body.

Text-figs. 1 A, B, and C illustrate living and fixed flame-cells of *G. dendyi*. In fixed material the terminal chamber is 12-17μ long by 3.5μ broad, thus being slightly smaller than those of *G. agricola*, but decidedly larger than those in *G. hillii*. Active living flame-cells are considerably broader than fixed ones, averaging about 17μ by 4.5μ. Though it is difficult to measure them alive except during activity, their size seems to diminish somewhat when the ciliary flame stops moving, and their smaller size when fixed may not therefore be entirely an artifact of fixation.
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The head of the cell is occupied by a mass of protoplasm which in fixed material appears to be attached to neighbouring structures in the parenchyma by two or three fine strands. As in G. hillii, but unlike G. agricola, there is only one nucleus in the head of the cell and none in the wall of the terminal chamber. Indications of two or three thickened bands may be seen encircling the terminal chamber, but they do not seem to be as evident as those in G. agricola.

In life the terminal chamber is somewhat flattened in a plane parallel to the surface of the worm. Within this tube and lying in the same plane is the powerful tongue-like ciliary flame. Like the flame itself, the sides of the chamber are roughly parallel until near the tip, where they converge to its end-canal.

A clearly defined cushion of protoplasm caps the head of the chamber. Along this cap is a row of basal granules from whence arise the long individual cilia which compose the flame (Text-fig. 1 B). In life the cilia are fused together, though they gradually separate under adverse conditions, a ragged separation first appearing at the tip. The living 'flame' is highly refractile and easily seen.

During activity, sinusoidal waves of contraction pass down the tongue-like flame with a frequency which varies from just above the flicker rate (c. 10 per sec.) down to about two a second. At any moment, two to three complete waves are in progress along the flame, their amplitude being about half a wavelength. Under conditions to be described later, the flame may gradually stop. As it does so, the frequency falls off without any change in wave-length or at first in amplitude. On cessation of the beat, the waves may be left for a moment 'standing' and then disappear, leaving the flame extended. As this condition is approached, waves may cease to be propagated along the whole length of the flame.

The active flame almost fills the terminal chamber when viewed in breadth. Viewed sideways, the flame does not fill the chamber when at rest, but during activity the crests of the waves seem to do so, a fact of importance in considering the mechanical efficiency of the flame-cell. At rest, the flame extends straight down the chamber, as it often does after fixation in 70 per cent. ethyl alcohol. Fixation in Susa and Zenker leaves the flame in wave form, often exaggerated.

The staining reactions of the flame in some ways resemble those of the nearby muscle-cells rather than those of the cilia of the ectoderm. It has a strong affinity for acid fuchsin, and the dark colour of iron haematoxylin is retained nearly as long as in the muscle during differentiation.

Text-fig. 2 shows the relation of the flame-cells to the rest of the nephridium. The flame-cells are usually in pairs, the terminal ducts of which join after a short distance (Text-fig. 1). A branched end-canal receives the ducts of several pairs and ultimately passes into a glandular duct. Terminal ducts and end-canals have moderately thin walls with scattered nuclei but without apparent cell-boundaries. In G. agricola the end-canals open directly into
the glandular part of the nephridial duct, which is convoluted (Coe, 1929). In \textit{G. hillii} they are in addition frequently coiled (Hett, 1924). In \textit{G. dendyi} the end-canals appear to be more highly organized. Branches from the terminal ducts of the flame-cells unite to form a canal which commonly runs fairly straight for a considerable distance. As it does so the canal widens from about 2 \( \mu \) to 4 \( \mu \) in diameter, and the walls thicken slightly. The canal then undergoes two or three convolutions, after which it passes into a thick-walled glandular part of larger cross-section but of rather smaller lumen. This glandular part generally continues the convolution (Text-fig. 2 \textit{A}). The convoluted portions of both end-canal and glandular duct are contained in well-defined spaces in the parenchyma. During life the end-canal is easily seen owing to the ciliary movement. This is absent in the terminal ducts. The movement begins in the branches of the end-canal and becomes stronger as
The convolution is approached. Ciliary movement in the convolution presents a striking appearance. It seems to finish abruptly at about the point where sections show the glandular region to begin. Fixed material shows that the lumen of the end-canal carries long fine helical fibrils, apparently cilia (Text-fig. 3 A).

The action of the cilia gives the appearance of helical waves running rapidly down the end-canal and round its convoluted portion. That the motion is helical, and not a plane wave as in an undulating membrane, is apparent from the fact that it can be seen from whatever angle the canal is viewed. The appearance (Text-fig. 1 A) resembles that seen in the nephridial ducts of Lumbricus.

No cilia can be seen beyond the convoluted end-canal in life, and none can be detected in sections of the glandular canal or efferent duct to the exterior. The walls of the glandular canal are thick and granular and have the well-marked radial structure recorded by authors in other species (Text-fig. 3 B).

In poorly fixed material the radial fibres actually separate, giving the tubule the appearance of a contorted bottle-brush. As in other species, there are scattered nuclei, but no cell boundaries are evident. Evidence will be presented later that the end-canal with its convolution and the glandular canal are physiologically distinct.

The glandular canal finally leaves the lacuna of the parenchyma occupied by the convolution, and may run some distance in a fairly straight path.
Pantin—The Nephridia of Geonemertes dendyi (Text-fig. 2 A and B). The histology of the duct then changes again to that of a thin-walled tube. This, after running just beneath the basement membrane, abruptly enters one of the numerous excretory pores. These consist of a hollow flask-shaped cell resting on the basement membrane and opening to the exterior by a minute pore (Text-fig. 2 B). How numerous these pores are is shown in Text-fig. 4, taken from a tangential section through the dorsal surface and basement membrane. Over much of the surface they are only 50–100 $\mu$ apart.

**ANATOMICAL RELATIONS**

The body of *G. dendyi* differs from that of most marine metanemertines in the thinness of the muscular body-wall and the voluminous parenchyma. The latter consists largely of connective tissue divided into well-defined lacunae and channels containing structures such as the convoluted tubules of the nephridia and the blood-vessels. It is this tissue which varies most clearly in volume according to the water content of the animal.

The thin muscular layer lies immediately below the basement membrane, and among and immediately below the innermost muscle-fibres, the longitudinal ones, lie the flame-cells. In *G. dendyi* they are confined to this plane and do not seem to occur in other situations, such as below the surface of the rhynchocoel. They are most numerous over the head and along the sides of the body. They are fewer along the mid-ventral line, and fewest along the mid-dorsal line, above the rhynchocoel. Text-fig. 5 A shows the distribution...
of flame-cells on the upper surface of a newly hatched (1 mm.) larva. As the animals grow, the relative number of flame-cells increases even more rapidly, so that over the head and sides no point on the surface of the animal is more than 10–20 μ from one of these structures. Water entering or leaving the body must pass near one or more of them.

Below the muscular layer and among the nephridia there ramifies a network of fine contractile blood-vessels, derived from the lateral vessels. As Coe (1929) points out in other species of Geonemertes, so also in *G. dendyi* the flame-cells are not in intimate contact with the vessels, as they are in some marine nemertines; they are, however, always near them and occupy the same stratum below the muscle layer.

The convoluted tubules in their lacunae of the parenchyma lie distinctly deeper than the flame-cell-vascular layer. The efferent ducts running out from these ultimately make their way again to the surface.

**FUNCTION OF THE PROTONEPHRIDIA**

Since the time when Goodrich (1899) made the suggestion that the solenocytes of *Glycera* are functionally analogous to the Malpighian corpuscles of...
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the vertebrate kidney and excrete fluid, the analogy has been extended to other protonephridia, particularly in Platyhelminthes (Reisinger, 1922; Westblad, 1922). Apart from the fact that the flame-cell system of freshwater Turbellaria is much better developed than that of their marine relatives, there is direct evidence in various acoelomates that water is excreted by such systems. Water can be seen to accumulate in the contractile bladders of some Rhabdocoela, Trematoda, and Rotifera, and to be periodically emptied. Herfs (1922) showed that in certain cercariae the rate of water secretion decreased as the osmotic pressure of the external medium was increased.

In *G. dendyi* there is no doubt that the upper part of the protonephridial system secretes fluid. If a relatively transparent individual is left for a time in fresh water and then compressed under a coverslip, the flame-cells and the ducts leading immediately from them can sometimes be seen to swell during the course of 10–15 minutes (Text-fig. 5 B). This is most often to be seen in the flame-cells that are farthest from the edge of the animal, and are therefore the most subject to compression.

Observation shows that there is a relation between excretion of water and the activity of flame-cells. During life this is often intermittent, or the cells may even be inactive for long periods. No swelling of the tubule system has so far been seen except when the ciliary flame is active. Moreover, the activity seems to be related to the water-content of the internal medium. It is absent in animals that have been allowed partly to dry, but is resumed if the animal is immersed for a time in tap-water. If an animal showing intermittent activity of the flame-cells is examined under a coverslip, it is seen that local groups of the cells begin to be active more or less simultaneously. Later, all gradually stop, though some continue to beat many minutes longer than others. Renewed activity often promptly follows local movements in the worm, either contraction of the body or the peristalsis of a blood-vessel in the neighbourhood of the flame-cell. Immobility of the worm is always followed sooner or later by inactivity of the ciliary flames, except those on the edge where the body is in contact with water under the coverslip. Activity of the flames can often be engendered by slightly raising and lowering the coverslip—as when focusing an oil-immersion lens when the coverslip is unsupported. Thus anything which tends to stir the internal medium round the flame-cells leads to the activity of the flame, while stagnation of the medium is correlated with inactivity.

If an animal with active flames is carefully squashed under a coverslip, it is possible to reach almost complete disintegration of the tissues while the individual flame-cells still beat for a time. If when they cease to be active, tap-water is allowed to run under the coverslip, the flames restart—even though they sometimes appear to be more or less isolated from neighbouring cells and detritus. It is possible to revive the activity of the flame-cells in the squashed mass by irrigation several times in succession. It is even possible sometimes to revive them by lifting the coverslip with some adhering cell debris and flame-cells and remounting it in a fresh drop of tap-water. It is
remarkable that the flame-cells should be able to resume or to continue their activity after breakdown and removal of much of the surrounding tissue.

**DISCUSSION**

It is difficult to avoid the conclusion that dilution of the internal medium of the parenchyma is a stimulus to the activity of the flame-cells. And since under conditions of activity water appears to pass into the nephridial system, it is natural to suggest, in conformity with common opinion, that the ciliary flame actually drives water into the system. But Carter (1940) has pointed out a difficulty in assuming the mechanism is powerful enough for this purpose. Ciliary and flagellar mechanisms elsewhere in the animal kingdom have not been shown to be able to produce large differences of pressure. Parker (1919) found the oscular pressure of the sponge *Stylotella* to be 3.5-4 mm. of water. Such pressures would be wholly inadequate for the separation of water from the salts in the body fluid. But they might suffice to overcome a very low colloidal osmotic pressure (cf. Picken, 1937), and Reisinger (1922) suggested that in the excretion of water by flame-cells the colloids of the body fluid might be kept back. The mechanical plan of a flame-cell seems to be far more efficient than that of the flagellate chamber of a sponge for the creation of a pressure-difference.

It has been suggested (Carter, 1940) that the cilia of flame-cells may not function as a pump, but rather as a stirring mechanism to prevent accumulation of substances which would hinder a process of active secretion. But since fluid is passing into the tubule system it seems unlikely that there could be such an accumulation on the inner boundary of the terminal chamber.

While it has not been possible to obtain a direct demonstration that the ciliary flame in *G. dendyi* is responsible for the flow of fluid into the tubule system, the observations recorded here certainly suggest this. Due weight must be given to the fact that if a ciliary mechanism can exert the necessary pressure-difference at all, the mechanical design of a flame-cell, as seen in operation, seems admirably adapted for such a purpose. Further, there is evidence that some pressure at least is set up by the action of the flame. If the tissues of an animal are gently squashed under a coverslip so as partly to separate the flame-cells from the surrounding tissues, the action of the flame sometimes causes visible oscillations of the base of the cell. Since the flame is apparently free inside the terminal chamber, the oscillation is presumably due to pressure-differences set up within the chamber.

Whatever the part played by the ciliary flame in the process, the evidence suggests that the nephridia of *G. dendyi* excrete water. But though it is easy to relate the development of the nephridia of freshwater acoelomates to an inevitable osmotic intake of water from the medium, the existence of a mechanism for excreting water in a terrestrial animal is remarkable. Such an animal might be expected to provide against loss of water rather than for its excretion. Loss of fluid in *G. dendyi* may certainly be great. The worms normally range from 1 to 20 mm. in length by 0.5 to 3 mm. in breadth. They
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continually secrete a tube of mucus in which the animal moves forward during locomotion, through the action of cilia which completely cover the body. Loss of mucus and evaporation cause the body visibly to diminish in size when exposed to an unsaturated atmosphere. When unable to escape to a moister place the animal ceases to move and the outer mucus hardens to a transparent cocoon in which water loss appears to diminish. Such cocoons, however, are sometimes formed to provide an aqueous medium for the eggs which are shed into them, together with a quantity of fluid. This is a further tax on water reserves, though the eggs are normally laid in very damp situations, where there may even be a film of running water. But the most rapid loss of water takes place when the proboscis of the worm is everted. This is primarily a flight response in this species, and when it occurs so much mucus is lost that after three or four eversions the animal becomes visibly smaller.

But while water loss may sometimes be considerable, it is incorrect to suppose that desiccation operates continuously. The worms live under damp stones and logs, particularly in woods where low vegetation impedes the drying action of the wind. They possess strongly developed responses, particularly positive geotaxis and negative phototaxis, which remove them from exposed situations. In a gradually drying vivarium they can be seen to bury themselves. Though sometimes to be found far from fresh water, they may be taken from under a log, of which the other end lies in a film of water sufficient to support Planaria vitta. They are often found in contact with dew or rain-water, and survive immersion in fresh water for some days, though not indefinitely. The worms are, in fact, frequently exposed to pure water: a situation more exacting than that to be met by many freshwater organisms. Their natural conditions of existence are thus not those of continuous desiccation, but may vary between this and excessive hydration. Hence any regulating mechanism must be able to deal with extremes of water conditions. The evidence presented here shows that the nephridial system can eliminate excessive water, and that under conditions of water loss the ciliary flames become inactive. What part is played by the highly differentiated portions of the nephridial canal remains to be seen.

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SUMMARY

1. The nephridia of the terrestrial nemertine Geonemertes dendyi are described. The flame-cells are in groups, each of which communicates with the exterior by its own duct. The flame-cells open into the branches of a ciliated end-canal. Distally this end-canal executes a number of convolutions and then passes into a non-ciliated glandular canal. The first part of the glandular canal is also convoluted, and the distal part of it passes to the efferent duct.

2. The nephridia are distributed over most of the surface of the animal immediately below the muscular layer. The convolutions of the end-canals
and glandular canals lie somewhat deeper, in well-defined lacunae in the parenchyma.

3. Evidence is presented that fluid can be excreted into the nephridia. The activity of the flame-cells varies with the degree of hydration of the animal and may cease on desiccation. The flame-cells can be stimulated to activity by dilution of the body fluid of crushed animals with tap-water. The relation of water excretion to the mechanical activity of the flame-cells is discussed.

4. Some features of the natural habitat and the water relations of the animal under natural conditions are described. It is pointed out that the animal may have to contend not only with desiccation but with excessive hydration. The physiological consequences of hydration appear to be met by the flame-cell mechanism.

REFERENCES