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Tell-tail Adaptations for Respiration and Rapid Escape in a Freshwater Oligochaete (*Lumbriculus variegatus* Müll.)

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The aquatic oligochaete, *Lumbriculus variegatus* (Order Lumbriculida; Family Lumbriculidae), utilizes a combination of postural and anatomical specializations that enhance gas exchange across the dorsal surface of posterior segments as these segments lay exposed at the air-water interface. Predator avoidance by exposed posterior segments is enhanced by neurobehavioral mechanisms involving a well-developed lateral giant nerve fiber system that mediates rapid escape withdrawal of the worm's tail in response to shadow or mechanosensory stimuli.

INDEX DESCRIPTORS: *Lumbriculus variegatus*, oligochaete, respiration, giant nerve fibers, rapid escape reflex.

Many aquatic oligochaetes occupy ecological niches deficient in dissolved oxygen and therefore utilize a variety of anatomical, behavioral, or physiological specializations to facilitate gas exchange. In some tubificid worms (Order Tubificida), for example, rhythmic undulatory movements of the worms' posterior ends circulate water and enhance gas exchange across the epidermis (Alsterberg, 1922; Stephenson, 1930). Since this behavior increases vulnerability to predation, posterior segments are appropriately endowed with a variety of neurobehavioral specializations that ensure rapid escape when a threatening stimulus is detected (Zoran and Drewes, 1987; Drewes and Zoran, 1989).

Here, I provide an integrated description of an unusual combination of adaptations for posterior respiration and rapid escape in the aquatic oligochaete, *Lumbriculus variegatus* Müll. This worm is a member of the aquatic Order Lumbriculida, a much less extensively studied group than the Order Tubificida. My observations derive from both field-collected and laboratory-reared colonies of *L. variegatus* obtained from two North American sites: West Lake Okoboji (Gull Point), Iowa and Swan Lake, Victoria, British Columbia, Canada. The worms are especially abundant in organic bottom debris comprising the very shallow margins of the marshes and ponds that lie adjacent to these lakes.

ADAPTATIONS FOR RESPIRATION

The combination of anatomical and behavioral specializations of the worm's posterior end that facilitate gas exchange include the following:

1. Tail Posture

When occupying their natural habitat or when placed in nonaerated aquaria containing natural sediments, these worms habitually protrude their tail ends vertically above the sediments. Unlike many tubificid worms, however, there are no rhythmic undulatory movements of the worm's posterior end. Rather, when the tail tip extends to a sufficient height that it contacts the air-water interface, the tail flexes ventrally, at a right angle, so that the most posterior 10-20 segments lie parallel to the water surface (Fig. 1).

2. Surface Tension Interactions

Based on laboratory observations, it is evident that this unusual posture involves a characteristic surface tension interaction in which the flexed tail emerges from a crater-like depression in the water surface, while the dorsal surface of the exposed segments clearly interrupts the surface tension and is directly exposed to the air (Fig. 2). Such interactions suggest that the tail surface may be endowed with specialized hydrophobic or surfactant properties (Hills, 1988) that facilitate gas exchange via the dorsal surface of the tail.

3. Dorsal Body Wall Configuration

Associated with these external and behavioral adaptations, there are also obvious internal specializations for gas exchange in posterior segments. One of these involves a body wall configuration in which the dorsal blood vessel is juxtaposed to the overlying epidermis (Fig. 3), without intervening layers of circular and longitudinal muscle. This contrasts with the conventional oligochaete design (characteristically seen in more anterior segments of *L. variegatus*) in which the circular and longitudinal muscles are interposed, as continuous layers, between the dorsal blood vessel and overlying epidermis.

As in other oligochaetes, anterograde pulsations of the dorsal blood vessel, originating at the tail tip, represent the primary mechanism for circulating blood (Fig. 1). Observations of dorsal blood vessel pulsations, originally made by Haffner (1927), indicated that very high pulsation rates (up to 80/min at 18°C) are possible in the most posterior segments and that pulsation waves are augmented by the synchronized contraction of segmentally arranged lateral diverticula along the dorsal vessel.

4. Dorsal Blood Vessel

As in other oligochaetes, anterograde pulsations of the dorsal blood vessel, originating at the tail tip, represent the primary mechanism for circulating blood (Fig. 1). Observations of dorsal blood vessel pulsations, originally made by Haffner (1927), indicated that very high pulsation rates (up to 80/min at 18°C) are possible in the most posterior segments and that pulsation waves are augmented by the synchronized contraction of segmentally arranged lateral diverticula along the dorsal vessel.

ADAPTATIONS FOR RAPID ESCAPE

Neurobehavioral adaptations in *L. variegatus* that permit rapid escape withdrawal of posterior segments and avoidance of potential predators include the following:

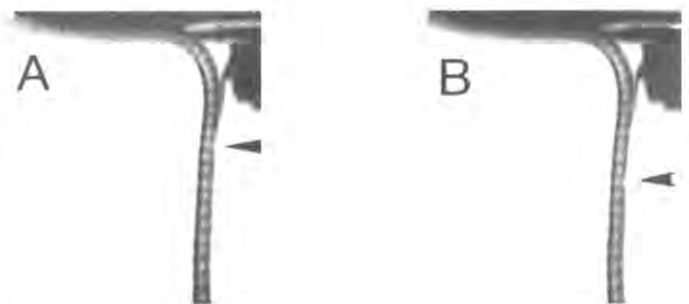


Fig. 1. Lateral view (video recording) of the stereotyped respiratory posture of tail segments in *L. variegatus*. The tip of the tail is flexed to the left at a 90° angle and laid horizontally at the air-water interface (indicated by dotted line). The arrow in A shows the site of dorsal blood vessel constriction as a pulsation wave, originating in the tail tip, passes along the worm. The arrow in B shows the constriction site after the wave has progressed three segments (about 1 mm) more anteriorly. The elapsed time between frames A and B is 0.5 s.

1. Sensitivity to Shadow Stimuli

Rapid withdrawal of the exposed tail is readily triggered by a moving shadow or abrupt decrease in background illumination; such a "shadow reflex" appears unique among the oligochaetes and probably represents a means of avoiding attack from surface or aerial predators. Sensitivity to shadow stimuli apparently derives from sparsely distributed photoreceptor cells (phaosomal type) in the epidermis of the tail (Drewes and Fournier, 1989).

A key component of the shadow reflex pathway is the pair of lateral giant nerve fibers (LGFs) in the ventral nerve cord (Fig. 3). *In situ* electrophysiological recordings indicate that repetitive impulse activity of the LGFs is initiated by a shadow stimulus and that this activity is requisite for excitation of motor pathways leading to rapid withdrawal (longitudinal shortening) of posterior segments (Drewes and Fournier, 1989).

Results from studies of a sexually reproducing population of *L. variegatus* (from British Columbia) demonstrate that shadow reflex capabilities are present when worms hatch from cocoons (Drewes and Brinkhurst, 1990). This suggests that, regardless of age, the shadow reflex may have an adaptive significance for avoiding surface predators (e.g. birds).

2. Sensitivity to Mechanical Stimuli

LGF-mediated escape withdrawal of the tail is also readily triggered by tactile stimulation, or water displacement. Sensitivity to these stimuli, perhaps important in avoiding subsurface predators, may arise from widely distributed, ciliated epithelial cells (Drewes and Fournier, 1989). Except for a substantial difference in the onset latency of tactile-evoked escape responses (latency = 3–12 ms) versus shadow-evoked responses (latency ≈ 300 ms), the reflex behaviors (i.e. withdrawal) evoked by these two stimulus modalities appear indistinguishable.

3. Interneuronal Features

In most aquatic oligochaetes, including *L. variegatus*, the caliber of the lateral giant nerve fibers is greater in posterior than anterior segments (Zoran and Drewes, 1987). Large LGF diameter (Fig. 3), together with a well developed glial sheath that surrounds each LGF (Drewes and Brinkhurst, 1990), likely contribute to the relatively rapid LGF conduction velocity in posterior segments (approximately 8–9 m/s; Drewes and Fournier, 1990). Assuming this conduction velocity, and that 2–3 cm of the worm's posterior end is exposed above the sediments, then the estimated conduction time over this distance is only 2–4 ms. The consequence of minimizing intersegmental conduction time is a nearly synchronous excitation, by the LGF pathway, of segmental motor pathways throughout the posterior end of the worm.

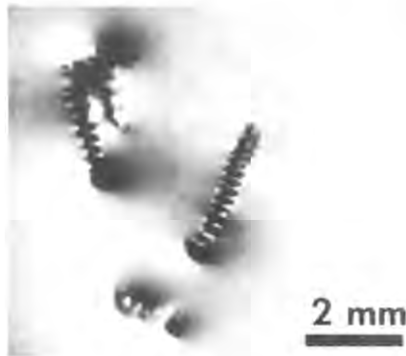


Fig. 2. Surface view (video recording) of several tails lying horizontally at the air-water surface. Note that tails emerge from crater-like depressions in the water.

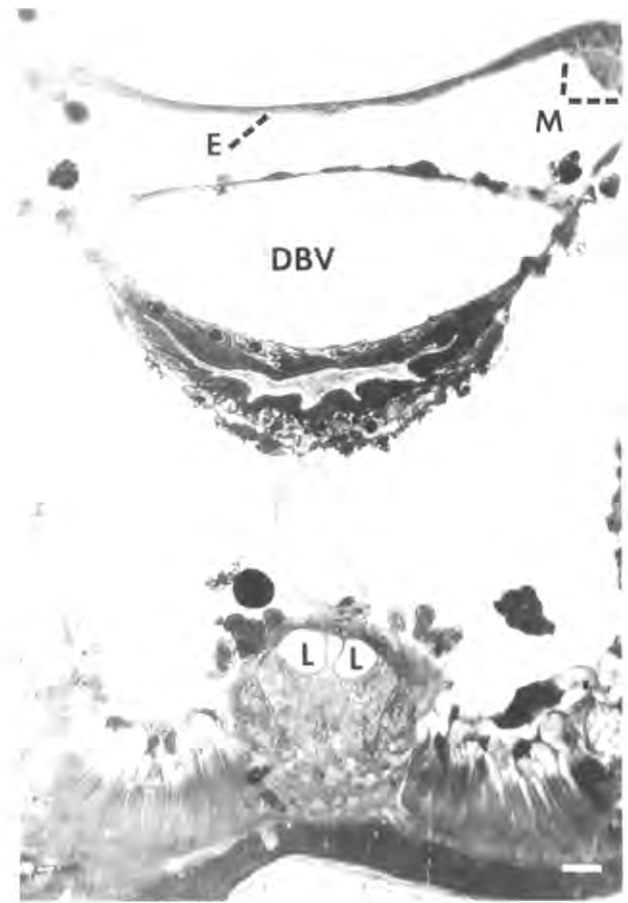


Fig. 3. Cross-section of the worm's posterior end. The middorsal epidermis (E) lies directly above the dorsal blood vessel (DBV). The body wall musculature (M) is evident at the lateral margins of the dorsal surface. Note the lateral giant nerve fibers (L and L) within the ventral nerve cord. (1 μm thick plastic section; stained with toluidine blue; scale bar = 25 μm).

SYNOPSIS

The aquatic oligochaete, *L. variegatus*, utilizes a combination of postural and anatomical specializations, involving the dorsal body wall in extremely posterior segments, to facilitate gas exchange at the air-water interface. Adoption of this lifestyle, however, undoubtedly involves increased vulnerability of the worm's tail to both surface and subsurface predation. Hence, natural selection would favor (1) neurosensory mechanisms that reliably detect relevant cues indicating the approach of a predator (i.e. moving shadow or abrupt water displacement), (2) central nervous and motor reflex mechanisms that ensure rapid escape withdrawal of the worm's tail at all ages, and (3) developmental mechanisms that permit rapid and complete regeneration of posterior segments following amputation (cf. Morgulis, 1907; Hyman, 1916).

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