Lumbriculus variegatus: A Biology Profile

(by C. Drewes -- document last updated 9-04)
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The freshwater oligochaete, *Lumbriculus variegatus* is not widely known to biologists but may be used to vividly illustrate a wide variety of biological phenomena such as: patterned regeneration of lost body parts, blood vessel pulsations, swimming reflex, peristaltic crawling behavior, giant nerve fiber action potentials, and sublethal sensitivity to pharmacological agents or environmental toxicants. This brief document provides general background information about *Lumbriculus* biology that is not generally available in biology or invertebrate zoology texts.

Classification and Evolution

Although superficially resembling tubifex worms, *Lumbriculus* is placed in the Order Lumbriculida, a group that is separate from both tubifex worms and earthworms, which are in the orders Tubificida and Haplotaxida, respectively (Jamieson, 1981):

Phylum: Annelida
Class: Oligochaeta
Order: Lumbriculida
Family: Lumbriculidae
Genus sp: *Lumbriculus variegatus*
Common names: California blackworms; blackworms; mudworms

Evolutionary relationships between this group and other annelids are not well understood or agreed upon. Some biologists suggest that the Order Lumbriculida may be an early stem group in the oligochaete branch of annelid evolution. But interpretations are complicated by variability in the number and location of gonads in the Lumbriculidae, a feature common in worms that reproduce asexually by fragmentation.

Lumbriculus Habitat, Lifestyle and Reproduction

Lumbriculus is found throughout North America and Europe. It prefers shallow habitats at the edges of ponds, lakes, or marshes where it feeds on decaying vegetation and microorganisms. Favorite microhabitats include layers of decomposing leaves, submerged rotting logs, or sediments at the base of emergent vegetation, such as cattails. *Lumbriculus* may also occupy silty sediments from deeper water, but other oligochaetes such as tubificids (tubifex worms) are more common in these habitats.

In nature, *Lumbriculus* uses its head to forage in sediments and debris, while its tail end, specialized for gas exchange, often projects upwards. When possible, the worm stretches its tail vertically to the water surface where it forms a right angle bend and breaks the water surface tension. This posture facilitates gas exchange between the air and the pulsating dorsal blood vessel lying just beneath the worm's epidermis. This respiratory behavior markedly contrasts with that of tubificid worms, which often undulate their tail ends as they protrude from burrows in sediments well below the water surface.

Field-collected *Lumbriculus* are often larger than laboratory-reared worms. Maximal body size is about 10 cm in length (approximately 200-250 segments) and 1.5 mm in diameter. Such specimens appear as sexually mature hermaphrodites. Although never documented, sexual reproduction in mature worms probably involves copulation and sperm exchange, as seen in many earthworms. Then, worms produce transparent cocoons, each containing 4-11 fertilized eggs that undergo direct embryonic development with no larval stage (Drewes and Brinkhurst, 1990). Small worms, about 1 cm in length, emerge from cocoons in about two weeks.

Worms cultured under standard laboratory conditions are usually small (4-6 cm in length) compared to field-collected ones, and never reach sexual maturity or produce cocoons. Reproduction under laboratory conditions is always by asexual fragmentation, during which a worm spontaneously divides into two or more body fragments.

Each surviving fragment then undergoes rapid regeneration of body segments to form a new head end, tail end, or both ends. Eventually each fragment grows into a normal sized worm comprising a combination of older and newer segments, representing two or more "generations" of development.

A worm’s capacity for asexual reproduction by fragmentation is matched by its ability to self-amputate in response to injury or other types of noxious stimulation. This protective reflex response is referred to as “autotomy.” One stimulus which causes worms to readily autotomize is body compression (Lesiuk and Drewes, 1999a). A sudden compression stimulus, which presumably simulates a predatory attack, induces rapid and clean division of the body in less than 1/5 of a second.

Anatomical and Physiological Gradient

Distinguishing head and tail ends of these worms is not difficult because head segments are more darkly pigmented, wider, and more maneuverable than tail segments. Specialized structures in the first 8-10 anterior segments include a conical prostomium, muscular pharynx, as well as male and female sex organs (hermaphroditism).

Although more posterior segments appear very similar to each other, there are important differences in their structure and function along the body. These differences are subtle and gradual, usually appearing as anterior-to-posterior gradients that affect nearly every organ system.

Unlike oligochaetes, such as leeches and most earthworms, the regional and numerical identity of segments in *Lumbriculus* is not finalized once segments have matured. For example, body segments in middle and posterior regions retain an ability to dramatically transform their identity to that of much more anterior segments. This transformation is closely tied to the worm's remarkable ability to reproduce copies of itself by a combination of self-fragmentation and segment regeneration (Drewes and Fourtner, 1990; Lesiuk and Drewes, 2001b).

Muscular and "Skeletal" Systems

Muscles in the body wall of *Lumbriculus*, as in most oligochaete worms, are arranged into two distinct layers - the circular and longitudinal muscle layers. These form more or less continuous and cylindrical sheets which wrap around each body segment. Muscle fibers in these layers are classified as obliquely striated fibers (Jamieson, 1981). Because there are no hard skeletal elements to which these muscles attach, the forces produced when they contract simply act upon the inner, fluid-filled body compartments - specifically, the coelomic cavity and gut. The result is that segments change shape but not volume, since fluids are not compressible. This design, referred to as a "hydrostatic skeleton," is typical of many burrowing invertebrates which lack appendages.

The circular and longitudinal muscle layers act in opposition to one another. When muscle fibers contract in the outer, circular muscle layer, segments constrict in diameter and lengthen. When fibers contract in the longitudinal muscle layer, which is just inside the circular layer, segments shorten and increase in diameter. Very little is known about the electrical, biochemical, or physiological properties of muscle cells in *Lumbriculus.*

In addition to the circular and longitudinal muscle layers, there are a few other accessory muscles in the worm's body, including small muscles that cause protrusion and retraction of the chaetae (= setae, or bristles) in each segment. There are four pairs of chaetae in a typical body segment of *Lumbriculus* and these are positioned laterally and ventrally, very similar to the pattern seen in the common earthworm, *Lumbricus terrestris*. When the worm is crawling, chaetae are protruded in those segments that are undergoing shortening and thickening due to longitudinal muscle contraction. This helps to anchor these segments to the substrate on which the worm is crawling. In contrast, chaetae are retracted in segments that are undergoing elongation and thinning due to circular muscle contraction.

Blood and Circulation

As in earthworms, *Lumbriculus* blood is red, due to a hemoglobin-like blood pigment, erythrocruorin, dissolved in the plasma. Blood circulates in a closed system of vessels and capillaries. It is pumped by rhythmic contractions of the dorsal blood vessel which moves the blood, segment by segment, from the posterior end (the main site of gas exchange) toward the head.

A diagnostic feature of *Lumbriculus* and related species is the presence of paired pulsatile lateral vessels that branch off the dorsal blood vessel in most body segments. Pulsations in these lateral vessels are coordinated with pulsations of the dorsal vessel and appear to serve an auxiliary pumping function (Stephenson, 1930).

Blood vessel pulsations and patterns of circulation are readily observed in whole worms because the body wall of *Lumbriculus* is transparent. At any time, numerous pulsation waves may be seen moving blood forward along the dorsal blood vessel. The large ventral blood vessel that carries blood back to the tail is also easily seen but is not contractile. Pulsation rate is sensitive to pharmacological agents and is significantly accelerated by both caffeine and nicotine (Lesiuk and Drewes, 1999b).

Nervous System, Reflexes, and Locomotion

The worm's central nervous system consists of a fused cerebral (supra-esophageal) ganglion in segment #1 and a ventral nerve cord that extends continuously along the entire body. In a typical segment, the ventral nerve cord has four pairs of segmental nerves that extend laterally and dorsally around the body wall (Stephenson, 1930). Some segmental nerve fibers are sensory in function and detect stimulation of the body surface; others are motor fibers that innervate body wall muscle or gland cells.

Sensory structures in the body wall of *Lumbriculus* include simple photoreceptor cells that sense shadow (Drewes and Fourtner, 1989), mechanosensory neurons that detect touch, vibration, or pressure, as well as chemosensory cells (Jamieson, 1981). Though their function has not been studied, chemosensory cell might be useful in detecting water-borne chemicals, such as nutrients from food sources or possibly dissolved oxygen.

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As a worm's tail lies at the water surface, an approaching shadow above, or sudden vibration below, may signal a life-threatening attack by a predator (e.g., bird, amphibian, aquatic insect larva, leech, crayfish, or small fish). As a defense, the worm senses these stimuli and initiates a rapid escape (or startle) response, in which it reflexively withdraws its tail by sudden contraction of longitudinal muscles (Drewes and Fourtner, 1989). A similar head withdrawal occurs in response to an abrupt touch of the head.

Both of these reflex responses are mediated by *giant nerve fibers* located within the worm's ventral nerve cord along the entire body. These giant fibers function as “conduits” for rapid conduction of nerve impulses that, in turn, trigger activity in motor neurons and longitudinal muscle, thus causing body shortening (Drewes and Fourtner, 1989; Drewes and Brinkhurst, 1990). Recent research (Lesiuk and Drewes, 2001a,b) has shown that giant nerve fibers in *Lumbriculus* have a remarkable capacity for rapid restoration of function following ventral nerve cord transection or ablation. Functional reconnection of severed giant fibers can occur within 10 hours!

Other reflex responses in *Lumbriculus* are also possible and these depend on the environmental surroundings of the worm and the type of the stimulus. For example, when a worm is lying on a rough surface and tail segments are touched, it reflexively responds by forward peristaltic crawling. During forward crawling, alternating waves of circular and longitudinal muscle contraction are produced. These waves begin in anterior segments and move rearward along the body, resulting in forward propulsion. When a worm is lying on rough substrate and head segments are touched, it responds by backward crawling movements in which peristaltic waves of body contraction move from the tail toward the head. The term “retrograde” is used to describe waves of muscle contraction that move in a direction opposite to the actual direction of body propulsion (see Drewes and Cain, 1999).

In addition to rapid escape and crawling movements, worms are capable of two other rather unique locomotor responses that occur only when they are submerged in an open area with no shelter around them and little traction beneath. One of these responses is an unusual undulatory swimming behavior, initiated by sudden touch to tail segments (Drewes, 1999; Drewes and Cain, 1999). During such swimming, worms rapidly twist their body into a helical coil that moves backward, in wave-like fashion, along the body. Rhythmic passage of such waves along the body provides propulsive thrust that moves the body forward. Although it happens too quickly to detect with the naked eye, each successive wave alternates between a clockwise and counter-clockwise helical twisting shape. Typically, one swim episode lasts only a few cycles and propels the worm about one or two body lengths away from the threatening stimulus.

A second type of reflex response, also seen when worms are in submerged in open areas with little traction, is body reversal (Drewes, 1999; Drewes and Cain, 1999). Reversal, evoked by suddenly touching head segments, occurs in a fraction of a second. During this time, the worm rapidly coils and then uncoils its body, often resulting in an approximate 180° reversal of the long axis of its body. By reversing, the worm is better positioned to swim away if and when another stimulus occurs near the first.

Opportunity

Until recently, *Lumbriculus* worms had been completely over-looked for purposes of both biology research and education. Nevertheless, they offer great promise for new, inexpensive, and user-friendly experiments for student laboratory activities. They also offer opportunity for basic research studies of physiology, development, behavior, environmental biology and toxicology (Drewes, 1997). For further clarification, please feel free to contact: C. Drewes, Science II Bldg (EEOB), Iowa State University, Ames, 50011. For complete listing of educational and research references about this worm, see:
http://www.eeob.iastate.edu/faculty/DrewesC/htdocs

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