Clive A. Edwards
Norman Q. Arancon

Biology and Ecology of Earthworms

Fourth Edition

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This 4th edition of the Biology and Ecology and Earthworms is lovingly dedicated to Clive A. Edwards, whose legacy left an indelible mark in the field of earthworm studies and sustainable agriculture. He passed peacefully in sleep on July 20, 2021. Clive was born on June 16, 1925, in Worcester, England, passed peacefully in his sleep on July 20, 2021, at Friendship Village of Dublin, Ohio. Clive was born to parents David Edwards and Rose Edwards (Evans) and completed his bachelor's, master's, and doctoral degrees at Bristol University, England, followed by master's and doctoral degrees at the University of Wisconsin, Madison. He served his home country proudly in the British armed forces following the Second World War. Clive worked for 25 years as Principal Scientific Officer at Rothamsted Experimental Station in Harpenden, England, and then another 23 years as Professor in the Department of Entomology at The Ohio State University, serving as Department Chair for 5 years.

He published more than 450 scientific papers and book chapters during his career. Clive traveled to more than two-dozen countries during his life, both for work and traveling with his wife Elvira. He received numerous awards for his professional accomplishments, including the prestigious Pollution Abatement Award from the Royal Society of Arts and Confederation of British Industry, presented to him by His Royal Highness the Duke of Edinburgh. This 4th edition would not have been possible without Clive's characteristic persistence toward a masterfully nuanced understanding of earthworms. It is an understatement that this edition has met many challenges over the last 10 years of its production, but Clive's persistence and determination were the driving force and inspiration behind its completion.

Preface

In the 26 years since the third edition of the *Biology and Ecology of Earthworms* was published, there has been an enormous expansion of interest and research in earthworms internationally. There has been a progressive appreciation by scientists and the general public of the key role of earthworms in the promotion of soil fertility, productivity, and environmental improvement. This has resulted not only from the very considerable increase in published research into the ecology and biology of earthworms, but also from the application of the results of this research into the management of earthworm populations in the field and the use of earthworms in organic waste management and ecotoxicology.

This progress in research and publications on earthworms exceeded even the optimistic forecasts that Dr. J. E. Satchell made in the Foreword to the First Edition (1972). In the First Edition, 565 references were cited, and these were a fairly exhaustive coverage of most of the existing scientific literature on earthworms at that time. Based on an analysis of the frequency of appearance of new publications in time, up to 1972, Dr. Satchell forecasted that by 1992 a further 640 papers would have to be reviewed to update the first edition. By the time the second edition appeared, in 1977, the number of references quoted was already 674. These updated references probably represented less than half of the available literature at the time and concentrated only on the more important publications but by the time the third edition was published in 1996 nearly 1500 references were cited, and this was a small fraction of the total publications on earthworms.

Another important book on earthworm ecology, by Dr. K.E. Lee published in 1985, *Earthworms: Their Ecology and Relationships with Soils and Land Use* (Academic Press, 1986), cited 814 references relevant to the more limited scope of this book, which did not address research into earthworm morphology, taxonomy, diversity, biology, or physiology. It seems reasonable to assume that more than twice the number of references quoted in that book had been published by that time. In support of this conclusion, Satchell and Martin (1985) published an exhaustive review of the available literature on earthworms up to 1985, with about 1360 references quoted.

In this fourth edition, nearly 1700 references are cited and it is the authors' impression that this represents less than a quarter of the references available in the scientific literature. Those quoted specifically in this edition focus on the more significant and important publications on earthworms. The rate of expansion of research on earthworms is so rapid that it is becoming increasingly difficult to cover the entire subject in a single volume; indeed, it seems possible that any future revisions of this book may involve more than one volume.

In the years since the second edition was published, there have been a number of major International Symposia on Earthworm Ecology (ISEEs), including the first (ISEE1) held in Grange-over-Sands, England (Satchell, 1983); the second (ISEE2) held in Bologna, Italy (Bonvicini-Pagliai & Omodeo, 1987); the third in Hamburg, Germany in 1987 (ISEE3); the fourth in Avignon, France (ISEE4) in 1990 (Kretzschmar, 1992); the fifth (ISEE5) in Columbus, Ohio, USA in 1994 (Edwards, 1996); the sixth (ISEE6) in Vigo, Spain in 1998 (D.J. Diaz Cosin, J.B. Jesus, D. Trigo, M.H. Garvín); the seventh (ISEE7) in Cardiff, Wales in 2002; the eighth (ISEE8) in Krakow, Poland in 2004; and the ninth (ISEE9) in Xalapa, Mexico in 2010 (G.G. Brown, E. Cooper, J. Dominguez, C. Fragoso, E. Huerta, S. James, A.J. Morgan, M. Pulleman, O. Schmidt, I. Barois). A Workshop on the Role of Earthworms in the Stabilization of Organic Residues was held in Kalamazoo, Michigan in 1979 (Appelhof, 1981). There was also a Symposium on *Earthworms in Waste and Environmental Management* held in Cambridge, England (Edwards & Neuhauser, 1988) and one on *Earthworm Ecology in Forest, Rangeland and Crop Ecosystems in North America* held in Georgia, USA, in 1993 (Hendrix, 1995). The first conference on the use of earthworms in ecotoxicology of earthworms was held at Sheffield University, UK, in 1991 (Greig-Smith et al., 1992). A second SETAC Earthworm Ecotoxicology Workshop was held in Amsterdam in 1997 (Sheppard et al., 1997)

We thank Paul Hendrix for being a huge part of updating this edition, especially in Chaps. 3, 5, 6, and 9. His contributions reflect his boundless expertise that enriches these chapters with carefully chosen significant sources. We thank Dr. Sam James for reading Chap. 2 critically and providing extremely valuable suggestions and comments. We thank Joseph Reid Carroll, an environmental science student at the University of Hawaii at Hilo, for relentlessly and passionately assisting in assembling and reviewing relevant literature for the book.

We should also bring your attention to several recent books: "Earthworm Ecology" 1st and 2nd Edition (ed. C. A. Edwards. 2004, CRC Press), "Vermiculture Technology: Earthworms: Organic Wastes, and Environmental Management" (eds. C.A Edwards, N.Q. Arancon, R.L. Sherman. 2010, CRC Press/Taylor and Francis Group), "Soil Ecology" (eds. P. Lavelle, A. V. Spain. 2001, Kluwer Academic Publishing/Springer Press). The Worm Farmer's Handbook (Sherman, 2018, Chelsea Green Publishing), We believe that we have reached a wide audience, ranging from high school and college students, teachers, university faculty, zoologists, biologists, ecologists, soil scientists, agriculturalists, and farmers. We have attempted to combine a straightforward and integrative approach to reviewing as much of the earthworm literature as possible in the available space with scientific accuracy and appropriate acknowledgments. We hope that the book continues to arouse worldwide interest in these widely distributed and important animals and contributes to promoting critical research in the field of earthworm ecology and biology.

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Hilo, HI, USA Norman Q. Arancon
August 2021

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Introduction

This is the fourth edition of this reference text which reviews all aspects of earthworm biology and ecology. The book has been fully updated throughout from the third edition and extensive additions made. The revisions include an update of earthworm diversity distribution taking into account new genetic taxonomic techniques, expanded discussion on interactions between earthworms and other organisms, the use of earthworms in ecotoxicology and bioremediation, and the use of earthworms in organic waste management and vermiculture. A straightforward and integrative approach has been taken to reviewing the literature of this important subject (more than 1700 references are cited).

This book will continue to be an invaluable text for students of agriculture, soil science, ecology, and invertebrate zoology as well as all soil scientists.

Clive A. Edwards was an Emeritus Professor of Entomology and Environmental Science at the Ohio State University, Columbus, Ohio, USA. Norman Q. Arancon is a Professor of Horticulture at the University of Hawaii at Hilo.

SPRINGER ENVIRONMENTAL SCIENCE
MA. U.S.A.

Columbus, OH, USA — Clive A. Edwards
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Contents

Chapter 1
Earthworm Morphology

Earthworms are bilaterally symmetrical, externally segmented, with a corresponding internal segmentation. They have no skeleton and a thinly pigmented cuticle bearing setae on all segments except the first two, with an outer layer of circular muscles and an inner layer of longitudinal muscles. Earthworms are hermaphrodite and have relatively few gonads, situated in consistent segmental positions. When mature, and after fertilization of the eggs, a swollen area of the epidermis termed a clitellum, located in particular segments, forms a cocoon in which the eggs or ova are deposited, and this is then passed over the anterior segment. The eggs are usually fertilized as the clitellum passes along the body and is extruded over the head as a cocoon and the young develop within the eggs without a pre-larval stage, the newly hatched worms resembling adults. A few species can reproduce occasionally or consistently parthenogenetically.

Structurally, earthworms have large coelomic cavities containing coelomocytes, a closed vascular system with at least a dorsal and a ventral trunk and a ventral nerve cord. The alimentary canal is basically an anterior–posterior tube with excretion through the anus or specialized organs called nephridia; respiration is mainly cuticular. These systems were discussed further by Wallwork (1983).

1.1 Segmentation

Earthworms are divided externally into bands or segments along the length of the body by furrows or intersegmental grooves, which coincide with the positions of the septa dividing the body internally. The segments vary in width, usually being widest in the anterior and clitellar regions of the body. Segments are numbered arbitrarily from the front to the rear, and the grooves are designated by the numbers of the segments on either side, e.g., 3/4, 10/11, etc. Often the external segments are

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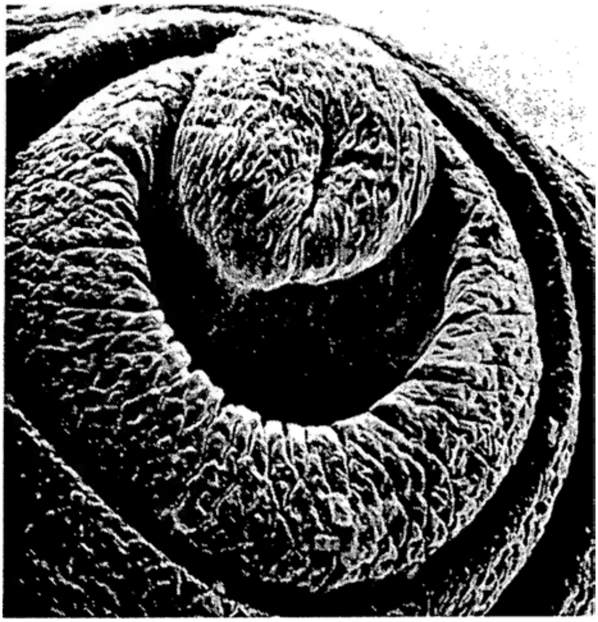

Plate 1.1 Prostomium of *Aporrectodea caliginosa*

subdivided by one or two secondary grooves, particularly in the anterior part, but these are superficial divisions which are not reflected in the internal anatomy. The mouth opens on the first segment, or peristomium, which bears on its dorsal surface the prostomium, a lobe overhanging the mouth (Plate 1.1). The prostomium varies in size, and in some worms, it may be so small that it cannot be distinguished. The way in which the peristomium and prostomium are joined differs between species and is a useful systemic character. The connection is termed zygolobous, prolobous, epilobous, or tanylobous depending on the demarcation of the prostomium (Fig. 1.1). The morphology of the segmentation of earthworms can change in response to soil contaminants such as antimony (Sb), becoming "broken" in appearance (Huang et al., 2021; Xu et al., 2021). More information regarding the effects of chemicals on earthworms can be found in Chap. 13, effects of agricultural practices and chemicals on earthworms.

1.2 Chaetotaxy

The setae are bristle-like structures borne in follicles on the exterior of the body wall which can be extended or retracted by means of protractor and retractor muscles that are attached to the base of the follicles and pass through the longitudinal muscle layer into the circular muscle layer below. As the setae are used to grip the substrate,

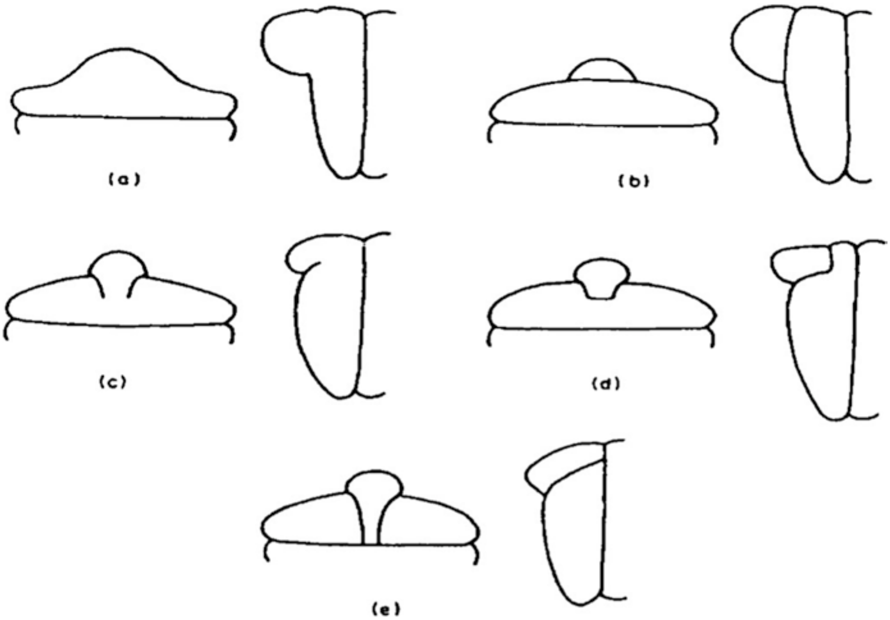

Fig. 1.1 Various forms of prostomium (cephalization). (**a**) Zygolobous; (**b**) prolobous; (**c, d**) epilobous; and (**e**) tanylobous. Some species have unusual segmentation in the region just before the anus. For instance, *Pontoscolex* (Glossoscolecidae) has a swollen posterior end, with narrow segments; it has been suggested this is a tactile sensory region adapted for gripping the sides of the burrow to avoid being pulled from the ground

their principal function is locomotory. Different species of oligochaetes have setae of varying shapes – either rod-, needle- or hair-like. Rarely, the distal end of a seta is forked. The shape of setae varies with their position, the most common form being those of *Lumbricus*, which are sigmoid and about 1 mm long. Some setae are enlarged both at the anterior and posterior ends, as in *L. terrestris*; the setae in the region of the genital pores (particularly the male pores) are sometimes modified in size and shape and situated on raised papillae. The genital setae, which can be up to 7 mm long in some species of Lumbricidae, are usually grooved along their length and may have a hook-like process at the distal end. These setae assist the physiological processes which take place at copulation by providing physical stimuli to the partner, while other setae have been shown to assist in holding copulating earthworms together by gripping, clasping, or penetrating the skin.

The setae are arranged in a single ring around the periphery of each segment, their number, and distribution being termed either lumbricine or perichaetine. The lumbricine arrangement, typical of the Lumbricidae, consists of eight setae per segment in ventral and latero-ventral pairs. If the distance between the setae in each pair is very small, they are termed "closely paired," if wider apart, they are termed "widely paired," or if they are very far apart so that the pairing is not obvious, they

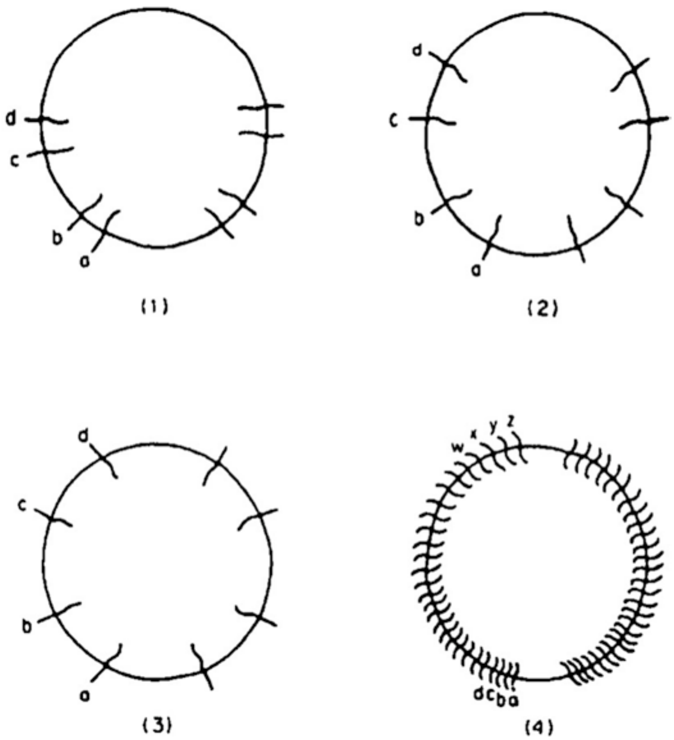

Fig. 1.2 Arrangement of setae in Oligochaeta. 1,2,3, lumbricine arrangement; 4, perichaetine arrangement. 1, Closely paired; 2, widely paired; 3, distant paired

are termed "distant." The distance between each pair of setae and between neighboring pairs is constant for each species. The setae are designated by letters *a*, *b*, *c*, and *d*, beginning with the most ventral setae on each side (Fig. 1.2). The distance between the setae is important as a systemic character and is usually expressed as the ratio of distances between setae. For example, "*aa:ab:bc:cd:dd* = 16:4:14:3:64" is the ratio in the post-clitellar region of *L terrestris*. Alternatively, the distances may be expressed as an equation, $aa = 4ab$, or as $ab<bc>cd$. The distance between the two most dorsal setae on either side is usually compared with the circumference of the body (μ) at that point, thus $dd = 1/2\mu$. For many species of Megascolecidae, particularly *Megascolex*, *Pheretima*, and *Perionyx*, and certain other species, the setal arrangement is termed perichaetine. Here the setae are arranged in a ring right around the segment, although usually with a large or smaller break in the middorsal and midventral regions. (Both types of setal arrangement are shown in Fig. 1.2.) This group of earthworms has more than 8 setae per segment, often 50–100, sometimes more. Setal distributions intermediate between the lumbricine and perichaetine arrangements may be 12, 16, 20, or 24 setae per segment, arranged fairly distinctly in 6, 8, 10, or 12 pairs, or the arrangement may be lumbricine in the anterior and appears perichaetine in the posterior part of the body. The setae are designated usually by the letters *a*, *b*, *c*, and *d* beginning with the most ventral one on each side, and *z*, *y*, *x*, and *w* beginning with the most dorsal one on each side, irrespective of how many there are in between.

1.3 Genital and Other Apertures

Earthworms are hermaphrodite and possess both male and female genital openings to the exterior, consisting of paired pores on the ventral or ventrolateral side of the body. In lumbricid earthworms, the male pores are situated ventrolaterally on the 15th, or occasionally on the 13th segment. Each pore lies in a slit-like depression, which in some species is bordered by raised lips or glandular papillae, often extending on to the neighboring segments. In other families, the male pores may be on quite different segments, and in some, particularly the Megascolecidae, the male pores may be associated with one or two pairs of prostatic pores; these are openings of the ducts of accessory reproductive bodies known as prostates, which are usually absent from lumbricid species. Both the male and prostatic pores may be on raised papillae or ridges or may open directly onto the surface. The male and prostatic pores are sometimes combined as one opening, but when separate, they are usually joined by longitudinal seminal grooves, on either side of the ventral surface of the body.

Usually, earthworms have two or more pairs of spermathecal pores, with a maximum of seven pairs in some species, but in other species, these are absent (*Bimastos tenuis*, *B. eiseni*). Earthworms belonging to two or three families have only a single pair of pores. Spermathecae and their pores are not always paired. For instance, some megascolecid worms, particularly the genus *Pheretima*, have a single series of pores, situated in the midventral line. The same genus has species with many spermathecae per segment. For example, *Pheretima stelleri* has as many as 30. Spermathecal pores are usually intersegmental and are most often situated in the ventral or latero-ventral position, but sometimes they are close to the middorsal line.

The female pores are most commonly a single pair, situated either in an intersegmental groove or on a segment, their position often being diagnostic of a particular family. Thus, in the related family (Enchytraeidae), they are in groove 12/13, and in the Lumbricidae, Megascolecidae, and Glossoscolecidae, they are on segment 14. Sometimes the female pores are united into a single median pore.

The dorsal pores, which are small openings situated in the intersegmental grooves on the middorsal line, occur in most terrestrial oligochaetes but are not present in aquatic and semiaquatic species. These pores communicate with the body cavity and the coelomic fluid. There are usually no dorsal pores in the first few intersegmental grooves. The position of the first dorsal pore is used as a systematic character at the species level, although these pores may be hard to distinguish in some earthworms. Some species have pores, which are readily visible, and some, e.g., *Aporrectodea rosea*, have pores surrounded by a dark pigmented zone.

The other openings in the body wall are the nephridiopores, which are very small and often difficult to see. They are situated just posterior to the intersegmental grooves on the lateral aspect of the body and usually extend in a single series along the body on either side. The nephridiopores are the external openings of the nephridia (the excretory organs of the earthworm) and, like the dorsal pores, are normally kept closed by sphincter muscles.

1.4 Clitellum and Associated Structures

The clitellum which occurs only in adult earthworms is the glandular portion of the epidermis that is associated with cocoon production. It is either a saddle-shaped or annular structure, the former being most usual among lumbricids. It usually appears swollen, although sometimes it can be differentiated externally only by its color, being paler or darker than the rest of the body, or even a different color. In some megascolecids, it appears only as a well-defined constriction. When swollen, the intersegmental grooves are often indistinct or entirely obscured, particularly on the dorsal surface.

The position of the clitellum and the number of segments over which it extends differ considerably among oligochaetes. Lumbricidae have the clitellum on the anterior part of the body, behind the genital pores, beginning between segments 22 and 38, and extending over about 4–10 segments posteriorly (Fig. 1.3). Megascolecidae have the clitellum further forward, beginning at or in front of segment 14, thus including the female pore and posteriorly it may also include the male pore. Some members of the Enchytraeidae have a clitellum which is only a very temporary development during the period of cocoon formation while even in the Lumbricidae it is often only conspicuous during the breeding phases.

Most earthworms possess various markings at sexual maturity in the form of tubercles, ridges, and papillae on the anterior ventral surface, and these differ greatly in number and form in different species of oligochaetes. The tubercula pubertatis are glandular thickenings on the ventral surface, either on or near the clitellum. Lumbricidae have these in the form of a pair of more or less oval longitudinal ridges, which are sometimes partly divided by intersegmental grooves, or they are separate papillae on either side of the ventral surface of the clitellum. The tubercula pubertatis usually extend over fewer segments than those occupied by the clitellum, except in a few species of lumbricids where they extend beyond the clitellum. Those species without spermathecae, e.g., *Bimastos eiseni*, usually have no tubercula pubertatis. It has been suggested that these organs assist in keeping earthworms together during copulation. Earthworms of other families do not always have the tubercula pubertatis situated on the clitellar segments, for example, in the Megascolecidae; they are situated on either side or on both sides of the clitellum, or on the clitellar segments. They may be transverse ridges or small separate pads, usually symmetrically (or sometimes asymmetrically) arranged about the midventral line.

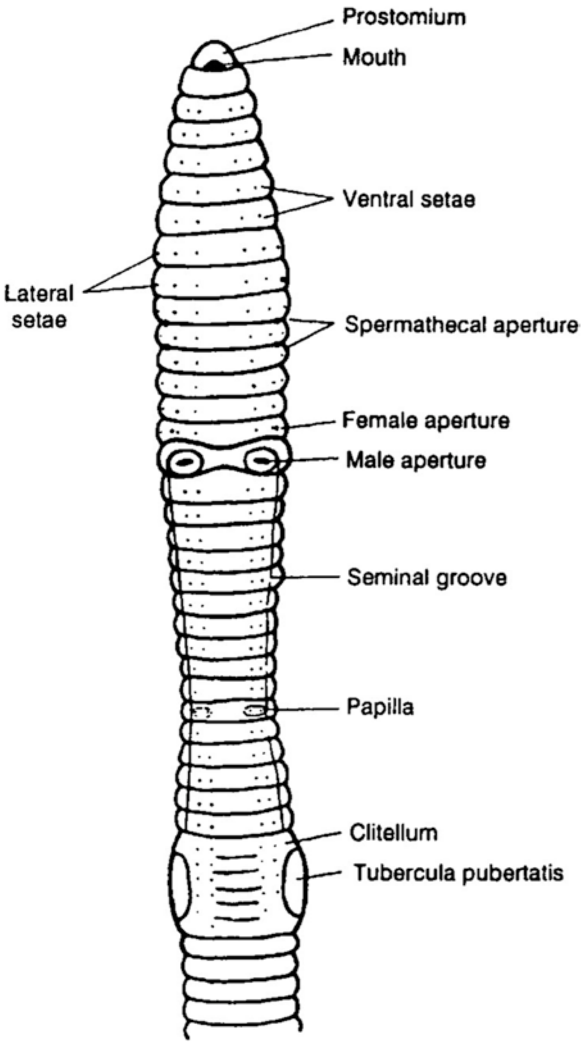

Fig. 1.3 Ventral view of the anterior region of *L. terrestris*

The position of the clitellum is used as a diagnostic character, particularly for lumbricids, because the position and number of segments occupied by the clitellum are, with small variations, constant for each species. Its position is defined by the number of the first and last segments occupied, with the range of variations in position, as, for example, 26, 27–31, and 32. Clitellum has been used as indicators of soil contaminants such as but not limited to hydrophobic organic contaminants (Shi et al., 2018).

1.5 Pigmentation and Coloration

Earthworms have a wide range of colors, and many are iridescent. The color of earthworms depends mostly on the presence or absence of pigment, which is either in the form of granules or in pigmented cells in the subcuticular muscle layer. Pigmented earthworms, such as L. *terrestris*, are usually red, brown, a combination of these colors, or even grayish or greenish. Occasionally, the color is at least partly due to the presence of yellow coelomic fluid or green chloragogenous cells near the body surface. The ventral surface of these earthworms is usually much lighter in color than the dorsal surface, although some deeply pigmented megascolecids are pigmented equally on both dorsal and ventral surfaces. The pigments, which are mainly porphyrins, probably originate as breakdown products of the chloragogenous cells (Stephenson, 1930). Unusually, the pigment is not evenly distributed but appears as dark segmental bands separated by lighter intersegmental zones, as in some strains of *Eisenia fetida*. Lightly pigmented or unpigmented worms often appear reddish or pink, due to the hemoglobin of the blood in the surface capillary vessels showing through the transparent body wall. If the body wall is opaque, unpigmented worms are whitish. In a number of species, the cuticle is strongly iridescent and causes the earthworms to appear bluish or greenish. This is particularly noticeable in species of *Lumbricus* and *Dendrobaena*. The color of pigmented worms, when preserved in formalin, is fairly stable, but the reds and pinks of unpigmented earthworms usually fade rapidly.

1.6 Body Wall

The body wall consists of an outer cuticle, the epidermis, a layer of nervous tissue, circular and longitudinal muscle layers, and finally the peritoneum, which separates the body wall from the coelom. The cuticle, which is a very thin (7 μm in *L. terrestris*), noncellular layer, is colorless and transparent, consisting of two or more layers, each composed of interlacing collagenous fibers with several homogeneous nonfibrous layers beneath. It is perforated by many small pores which are larger and more irregularly distributed about the middle of each segment than in its anterior part and are absent from the posterior part of each segment. The cuticle is thinnest where it overlays the epithelial sense organs, and here it is perforated by many very small pores through which project fine hairs from the sensory cells.

The epidermis consists of a single layer of several different kinds of cells (Fig. 1.4). The supporting cells, which are columnar in shape, are the main structural cells of the epidermis and have processes which extend into the muscle at their bases. These cells secrete material to form the cuticle. Short and round or club-shaped basal cells lie on the inner wall of the epidermis and are also known as "replacing cells," although it is doubtful whether they can replace the epithelial cells. These characteristics offer potentials for the epidermis in bioremediation of

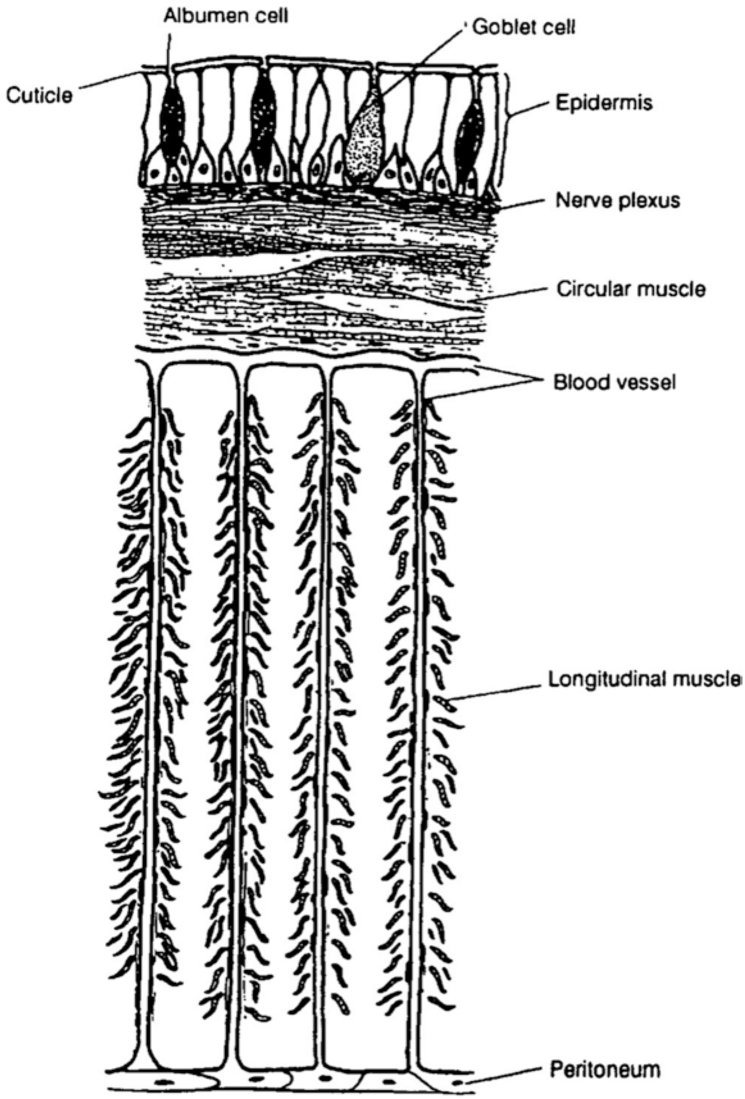

Fig. 1.4 Transverse section of a portion of the body wall

recalcitrant contaminants. For instance, Zhang et al. (2021a) showed that earthworm epidermis transformed by nZVI (nano-zero valent iron, an iron used for groundwater remediation) and undergoing oxidative stress and lipid peroxidation could actually enhance the bioaccumulation of PCB77 through the epidermis layer.

Two forms of glandular cells present are the mucous or goblet cells and albumen cells. Mucous cells secrete mucus over the surface of the cuticle to prevent desiccation and to facilitate movement of earthworms through soil. The function of the albumen cells is not known.

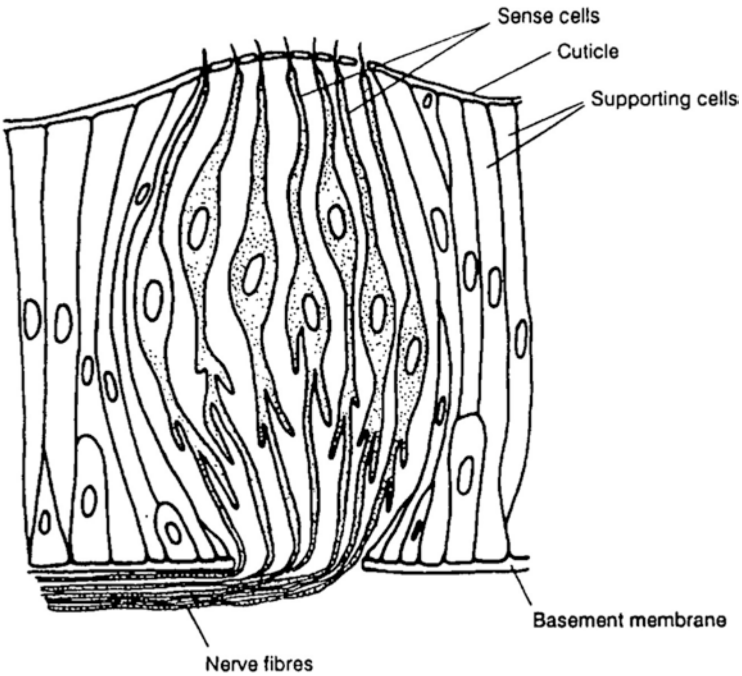

Fig. 1.5 Vertical section of an epidermal sense organ. (After Grove & Newell, 1962)

Large numbers of sensory cells, grouped together to form sense organs which respond to tactile stimuli, are scattered throughout the epidermis (Fig. 1.5). These are more numerous on the ventral than on the dorsal surface. Photoreceptor cells, capable of distinguishing differences in light intensity, occur in the basal part of the epidermis and are most numerous on the prostomium and first segment and on the last segment. There are few or none in the epidermis of the middle segments. The epithelium of the buccal cavity bears groups of sensory cells which can be stimulated by chemical substances associated with taste. The prostomium contains receptors which can detect sucrose, glucose, and quinine, as well as many other chemicals.

The epidermis is bounded at its inner surface by a basal membrane within which lie two muscle layers. The circular muscle layer consists of muscle fibers extending around the circumference of the body, except at the intersegmental positions. The muscle fibers are arranged in an irregular manner, aggregated into groups, each surrounded by a sheath of connective tissue (Fig. 1.4).

The longitudinal muscles, which are in a much thicker layer than the circular muscles, are continuous throughout the length of the body and arranged in groups or blocks around the body. *Lumbricus* has nine such blocks of muscles: two dorsal, one ventral, and three ventrolateral on either side. They have ribbon-like fibers which are arranged into U-shaped bundles in each block; these are surrounded by sheaves of connective tissue, so that the mouth of the "U" is toward the coelom.

Usually the ends of the "U" are closed, forming a box-like structure, but some species, e.g., *Eisenia fetida*, have both ends open, so that the bundles are disposed in radial columns. Between each bundle lies a double layer of connective tissue containing blood vessels. The inner surface of the longitudinal muscle layer is separated from the coelom by a layer of coelomic epithelial cells, the peritoneum.

1.7 Coelom (Body Cavity)

The coelom is a large cavity that extends through the length of the body and is filled with coelomic fluid. It is surrounded on the outer side by the peritoneum of the body wall and on the inner side by the peritoneum covering the alimentary canal. Transverse septa divide it into segmental portions. The peritoneum covering these septa is similar in structure to that covering the inner surface of the muscle layers; in a few species, the peritoneum on the septa is so very much thickened that it almost fills the coelom in this region. The septa usually correspond to the external segmental grooves but often do not occur in the first few segments of the body, and in some species, they are missing in other parts such as the esophageal region of some species of *Pheretima*. Some species have septa that do not correspond with the intersegmental grooves in the anterior end but are displaced backward, sometimes by as much as a segment. Two adjacent septa are sometimes fused at their junction with the body wall. The septa differ in thickness, depending on their position in the body, those in the anterior of the body being markedly thickened and more muscular. The degree of thickening and the position and number of these septa are used as systemic features for identifying many species of earthworm. For example, a species of earthworm recently discovered near the Muling River of Heilongjiang Province, Northeast China (adjacent to Russia), possesses particularly thick and muscular septa with its slightly yellowish, small, heart-shaped ampulla attached to septum $^{7}/_{8}$ (Zhang et al., 2021b). This species of earthworms also has a characteristic single pair of testis sacs which elongate to the middle part of septum 9/10. Septa are constructed from muscle fibers, usually derived from the longitudinal muscle layer, together with some circular muscles on the posterior face with connecting tissue and blood vessels. The septa are usually perforated by pores which allow the coelomic fluid to pass freely between segments, although some septa effectively isolate each body segment and make it virtually self-sufficient with its own supply of blood, central and peripheral nervous system, excretory system, and even gonads.

There are also bands and sheets of mesenteric membranes between the body wall and the gut, forming pouches and dividing off some organs into separate chambers. Some peritoneal cells are modified in the region of the intestine as chloragogen cells, forming chloragogenous tissue. Chloragogenous cells are characterized by the presence of yellow or greenish-yellow globules, the chloragosomes.

The coelomic fluid is a milky white liquid which is sometimes colored yellow by eleocytes (cells containing oil droplets) as in *Dendrobaena subrubicunda*. The coelomic fluid of *E. fetida* smells similar to garlic, hence the name of this species. The consistency of the coelomic fluid differs between different species of earthworms and also depends upon the humidity of the air in which the earthworms live. Thus, it is thicker and more gelatinous in earthworms in dry situations than in those from wetter habitats.

The coelomic fluid contains many different kinds of particles in suspension. The inorganic inclusions are mainly crystals of calcium carbonate, but the corpuscular bodies in the coelomic fluid of lumbricid earthworms include phagocytic amebocytes, which feed on waste materials, vacuolar lymphocytes (small disk-shaped bodies which do not occur in earthworms with large numbers of eleocytes), and mucocytes (lenticular bodies which give the coelomic fluid a mucilaginous component). Other inclusions in the coelomic fluid include breakdown products of the corpuscular bodies, protozoan and nematode parasites, and bacteria. “Brown bodies” are aggregated dark-colored masses or nodules usually found in the coelom at the posterior end of the body. They consist of disintegrated solid debris such as setae and the remains of amebocytes and also cysts of nematodes and *Monocystis*.

Many earthworms eject coelomic fluid through the dorsal pores in response to mechanical or chemical irritation or when subjected to extremes of heat or cold. Some species, such as *Megascolides australis*, can eject fluid to a height of 10 cm, and *Didymogaster sylvaticus* (known as the squirter earthworm) to a height of 30 cm. Coelomic fluid is also expelled through the dorsal pores at times of stress and may have several functions such as preventing desiccation, promoting cutaneous respiration, or providing protection from predators (Vail, 1972).

As with many other earthworm organs, the status of the coelom tissues may be used to assess contamination. Tang et al. (2020) reported that low-level arsenic contamination can damage coelom tissues resulting in overaccumulation of high As concentrations in the earthworm hindgut. This, along with the significant increase in betaine levels and a decrease in dimethylglycine and myo-inositol levels in earthworms, suggests that the osmoregulatory metabolism of earthworms may have been disturbed.

1.8 Alimentary Canal

The alimentary canal or gut of earthworms is basically a tube extending from the mouth to the anus although it is differentiated into a buccal cavity, pharynx, esophagus, crop, gizzard, and intestine (Fig. 1.7). The short buccal cavity flanked by a tube-like prostomium begins at the mouth and occupies only the first one or two segments with one or two diverticula or evaginations. The epithelium lining the buccal cavity is not ciliated, except occasionally in a small dorsal diverticulum, though very young earthworms can have patches of ciliated epithelium on the ventral surface. Overlying the epithelium, except in the ciliated portions, is a thick cuticle.

The pharynx, which is not always differentiated clearly from the buccal cavity, extends backward to about the sixth body segment. The dorsal surface of the pharynx is thick, muscular, and glandular and contains the pharyngeal glands, which secrete mucus and appear as a whitish lobed mass. Some species, e.g., *Bimastos parvus*, have pharyngeal glands which extend back beyond the pharynx and are attached to the septa. Earthworms use the pharynx as a suction pump, so that muscular contractions of its walls draw particles through from the mouth, and some species evert the pharynx in this process.

All terrestrial oligochaetes have an esophagus, which opens from the pharynx as a narrow tube, modified posteriorly as a crop and gizzard. Calciferous glands situated in evaginations or folds in the esophageal wall open into the esophagus. Lumbricidae have these folds developed strongly with their tips fused together, to form esophageal pouches, which separate the glands from the esophageal cavity. Esophageal pouches are usually paired and lateral but may be unpaired and ventral in some megascolecid species. In *Pheretima* spp., they are reduced to low ridges of calciferous tissues. In some species of lumbricids, such as *Lumbricus castaneus*, *Lumbricus rubellus*, and *Dendrobaena* spp., the glands connect with the lumen of the esophagus via a duct.

At the posterior end of the esophagus is the crop, a thin-walled storage chamber situated in front of the gizzard, which is muscular and lined with a thicker cuticle than the crop. Muscular contractions of the gizzard grind up the food into small particles with the aid of mineral particles taken in with the food. The crop and gizzard are situated much further forward in some of the other species of earthworms than in the Lumbricidae; they are immediately behind the pharynx in megascolecid species which commonly have two to ten gizzards, each occupying one segment.

One species of megascolecid, *Pheretima californica*, has no gizzard and a crop situated in the middle of the esophagus. It has no calciferous glands in the strict sense of the term, although there are folds in the wall of the posterior half of the esophagus. The intestine has two conical caecae which originate in segment 26 and extends into three or four segments (El-Duweini, 1965). Megascolecids are extremely variable in terms of gizzard development, some species having as many as ten gizzards.

The rest of the alimentary canal is the intestine, which is a straight tube for most of its length, constricted slightly at each septum. Most of the digestion and absorption of food materials take place in the intestine. The internal surface of the intestine has many small longitudinal folds, and its surface area is increased by a large fold in the medial dorsal line, the typhlosole, which projects from the dorsal wall (Fig. 1.6). This differs in relative size in different species, being largest in the lumbricid earthworms. Such increases in intestinal surface area are common in animals that consume food mostly of plant origin, but the typhlosole may be small in some other species.

The epithelial lining of the intestine is composed mainly of glandular cells and non-glandular ciliated cells. The ciliated cells of *Lumbricus* species are also contractile, acting upon the gland cells which they surround, causing them to open or close. The intestine has two muscular layers, an inner circular and an outer longitudinal layer, the reverse order to that in the body wall.