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GLOBAL EARTHWORM (ANNELIDA: OLIGOCHAETA) FAMILY DIAGNOSIS AND DISTRIBUTION

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ABSTRACT

This paper presents the 25 families of the Megadrili Oligochaeta (terrestrial earthworms) on six of the seven continents. After an introduction to the phylum, each family presentation includes: family name and author, type genus, type species with location of the types where known, diagnosis and remarks. Also included is an illustrated glossary. There is a map of the world which shows the Bioregions and families present in each indicates if they are indigenous taxa only, indigenous and introduced taxa, and introduced taxa only.

Key words: Annelida, Oligochaeta, terrestrial megadriles, world families, type genus, type species, distribution, illustrated glossary.

RÉSUMÉ

Cet article présente les 25 familles de Megadrili Oligochaeta (vers de terre terrestres) présentes sur six des sept continents. Après une introduction au phylum, chaque présentation de famille comprend : le nom de la famille et son auteur, le genre type, l'espèce type avec l'emplacement des types lorsqu'il est connu, le diagnostic et des remarques. Un glossaire illustré est également inclus. Une carte du monde montre les biorégions et les familles présentes dans chacune d'elles, en indiquant s'il s'agit uniquement de taxons indigènes, de taxons indigènes et introduits, ou uniquement de taxons introduits.

Mots clés : Annelida, Oligochaeta, mégadriles terrestres, familles mondiales, genre type, espèce type, distribution, glossaire illustré.

RESUMEN

Este artículo presenta las 25 familias de Megadrili Oligochaeta (lombrices terrestres) en seis de los siete continentes. Tras una introducción al filo, cada presentación de familia incluye: nombre de la familia y autor, género tipo, especie tipo con ubicación de los tipos cuando se conoce, diagnóstico y observaciones. También se incluye un glosario ilustrado. Hay un mapa del mundo que muestra las biorregiones y las familias presentes en cada una de ellas, indicando si se trata de taxones autóctonos, taxones autóctonos e introducidos, o solo taxones introducidos.

Palabras clave: Annelida, Oligochaeta, megadriles terrestres, familias del mundo, género tipo, especie tipo, distribución, glosario ilustrado.

SAMENVATTING

Dit artikel presenteert de 25 families van de Megadrili Oligochaeta (terrestrische regenwormen) op zes van de zeven continenten. Na een inleiding over het phylum bevat elke familiepresentatie: familienaam en auteur, typegeslacht, typesoort met locatie van de types indien bekend, diagnose en opmerkingen. Ook is er een geïllustreerde woordenlijst opgenomen. Er is een wereldkaart waarop de bioregio's en families in elke regio zijn aangegeven, met vermelding of het alleen om inheemse taxa gaat, om inheemse en geïntroduceerde taxa, of alleen om geïntroduceerde taxa.

Sleutelwoorden: Annelida, Oligochaeta, terrestrische megadriles, families wereldwijd, typegeslacht, typesoort, verspreiding, geïllustreerde woordenlijst.

*Published on the traditional territory of the Chonnonton (= Neutral), Anishinaabe, and Haudenosaunee peoples.

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* The 1st page number is the diagnosis, the 2nd page number is the diagram, if one.

INTRODUCTION

Annelida are segmented worms and one of the oldest and largest phyla containing more than 20,000 species (Rouse *et al.*, 2022). These taxa are found on all continents in a variety of habitats, *e.g.*, on terrestrial and in aquatic habitats. They have no appendages, *i.e.*, arms or legs, and no internal or external skeleton.

Historically, the Annelida have been divided into three major classes, Polychaeta, Oligochaeta and Hirudinea, and sometimes a fourth class, Archiannelida (Hermans, 1969). The latter initially was rejected by Fauchald (1977) and more recently by Andrade *et al.* (2015). One of the factors responsible for the issues with the classification of the higher taxa is because very few specialists study and report on only species in one of the major classes or subclasses (Rouse *et al.*, 2022). This Class-based approach has been a detriment to annelid higher level taxonomy.

There have been many important papers during the last two decades which have had a great impact on the higher-level taxon concepts in the Annelida (Weigert *et al.*, 2014, Rouse *et al.*, 2022). These helped to clarify the disparity in the taxonomic characters used in Family identification. The genetic ones are better than the somatic ones; which can be more variable.

Currently, there are six major groups (Classes) in this phylum:

1. Polychaeta (marine bristle worms),
2. Echiura (spoon worms),
3. Sipuncula (peanut worms),
4. Hirudinea (leeches),
5. Microdrili Oligochaeta (aquatic or semi-aquatic worms), and
6. Megadrili Oligochaeta (terrestrial earthworms).

This paper will deal only with the terrestrial earthworms which contain 10,000 ± known species, and make up about half of the phylum.

Data will change, since new species are being described regularly. Based in part on (Mısırlıoğlu *et al.*, 2023), this is my interpretation of megadrile family structure, which may not be accepted by other earthworm taxonomists.

The diagnoses follow the classical format where structures on the external surface are numbered in Roman numerals, while internal structure and organs are numbered in Arabic numerals.

MEGADRILE FAMILIES

Domain: Eukaryota – Woese, Kandler & Wheelis, 1990
Kingdom: Animalia – Haeckel, 1878
Superphylum: Lophotrochozoa – Halanych *et al.*, 1995
Phylum: Annelida – Lamarck, 1802
Subphylum: Euclitellata – Jamieson, 1983
Class: Clitellata – Michaelsen, 1919
Subclass: Oligochaeta – Grube, 1850
Supraorder: Megadrili – Benham, 1890
Order: Crassiclitellata – Jamieson, 1988
Suborder: Lumbricina – de Blainville, 1830

The expanded diagnoses were based on information in one or more of the following texts (full citations are found in the Literature Cited section: Bouché (1972), Celis and Rangel-Ch. (2015), Blakemore (2005, 2006, 2008, 2009), Brinkhurst (1988), Dyne and Jamieson (2004), Easton (1984), Fragoso and Rojas (2009), Hernandez-Garcia *et al.* (2023), James (2000, 2012), James and Davidson (2012), Jamieson (1978, 1988, 1993, 2006), Martin *et al.* (2008), McMahan (1976, 1979, 1998), Nxele *et al.* (2016), Plisko (2012, 2013), Plisko and Nxele (2015), Reynolds (1977a, 1977b, 1977c, 1978, 2022), Reynolds, *et al.* (1974), Sims (1987), Smith and Green (1919), Taylor (1949) and Thorp *et al.* (2019).

Acanthodrilidae Claus, 1880 (Figure 1, p. 146)

Type genus: *Acanthodrilus* Perrier, 1872.

Type species: *Acanthodrilus ungulatus* Perrier, 1872 (Types: **Holotype**, Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. 573; Zoologisches Museum Hamburg, Universität Hamburg, cat. no. 8074; Reynolds and Wetzell, 2025).

Genera 68; species 746; subspecies 48.

Expanded Diagnosis: Secondary annulation present. Clitellum (annular, in xiii-xvii), Tubercula pubertatis, present, anterior to single male pores (usually in xviii), female pores (one or two pairs in xiv). Intestinal origin behind segment 13. Typhlosole, present. Hearts behind segment 11. Spermathecae, diverticulate and anterior to testes. Nephridia, holoic. Seminal vesicles, trabeculate. Prostates, tubular when present. Prostate pores, separate in xvii/xviii.

Remarks (modified from Glasby et al., 2025a, b): Following the concept of James and Davidson (2012), based on molecular phylogenetics which supported a broader concept of Acanthodrilidea (=Acanthodrilinae *sensu* Jamieson 2000, 2006, including Acanthodrilinae, Benhamiinae Michaelsen, 1897, Octochaetinae Michaelsen, 1900 and Exxidae Blakemore, 2000). Therefore, their family concept is much broader than that in WoRMS (2024), which recognizes these subfamilies as families. Acanthodrilidae *s.l.* is similar to Megascolecidae and Ocnerodrilidae. Acanthodrilidae *s.l.* has many species as endemics throughout the former Gondwana (including South America, Africa, Antarctica, Australia, Zealandia, Arabia, and the Indian Subcontinent) and is absent from the Palearctic. The presence of acanthodrilid species in the USA, Mexico and the Caribbean Islands presented by Misirlioğlu *et al.* (2023), with the exception of nearctic *Diplocardia*, may represent introductions. Introduced species also occur in Gondwanan regions. James and Davidson (2012) considered that Benhamiinae should be elevated to family status. Blakemore (1999) reported non-endemic Acanthodrilidae species from Australia, illustrating the family's adaptability for human dispersal. Jamieson *et al.* (2002) and Dyne and Jamieson (2004) provide very useful treatments of the family and subfamilies. Acanthodrilidae is one of only two earthworm families having maritime members. A key to distinguish foreign Acanthodrilidae taxa from native ones of South Africa was provided by Plisko and Nxele (2015).

Reproduction: amphimictic - hermaphroditic.

Almidae Duboscq, 1902 (Figure 2, p. 147)

Type genus: *Alma* Grube, 1855.

Type species: *Alma nilotica* Grube, 1855 (Types: **Holotype**, Zoologisches Museum Hamburg, Universität Hamburg, cat. no. 171, *Paratypes*, Rijksmuseum van Natuurlijke Histoire, Afd. Vermes, Leiden, Nederland, cat. no. 1571; Reynolds & Wetzel, 2025).

Genera 7; species 64; subspecies 4.

Expanded Diagnosis: Body shape more or less cylindrical; muscular dorsal pharynx present; clitellum (saddle, beginning on xxxv) situated posterior to male (in x and/or xi) and female pores (in xiv and/or xiii). Tubercula pubertatis present; branchiae present (wings). Prostomium variable, zygo-, pro-, pro-epi or epilobic. Setae, closely and/or widely paired in lumbricin arrangement. Spermathecae, present with pores post-testicular. Genital setae, small and modified except when on claspers (wings). Typhlosole, present. Prostate-like glands, rarely present.

Remarks (modified from Glasby et al., 2025a, b): Almidae is widely distributed in the tropics and subtropics, excluding Australia. There are 64 species in seven genera (Mısırlıoğlu et al., 2023). The Almidae is one of the few megadrile families that includes aquatic and semi-aquatic species (Martin et al., 2008). A key and accounts of the worldwide *Glyphidrilus* species was presented by Chanabun et al. (2013, 2023).

Reproduction: amphimictic - hermaphroditic.

Arecoidae James, Csuzdi & Brown, 2023 (Figure 3, p. 147)

Type genus: *Areco* Righi, Ayres & Bittencourt, 1978.

Type species: *Areco reco* Righi, Ayres & Bittencourt, 1978 (Types: **Holotype** + 3 **Paratypes** Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil, cat. nos. INPAZ-83A-D; Reynolds & Wetzel, 2025).

Genera 1; species 1; subspecies 0.

Expanded Diagnosis: Species with quadrangular body, and dorsal post-clitellar groove, clitellum (saddle). Tuberculata pubertatis, lacking. Four pairs of closely paired, regularly distributed hook-shaped setae. Dorsal pores present. Genital pores microscopic. Long muscular esophagus, but no gizzard. No calciferous glands, no prostates or copulatory pouches. Intestine begins in 27, typhlosole present. Pretesticular spermathecae, ovaries in 13. Moniliform hearts in segments 8 to 11. No subneural vessel. Nephridia holoic, without bladders. Metandric, with one pair of testicles and seminal funnels in segment 11. Seminal vesicles in 12 to 15.

Remarks (modified from Glasby et al., 2025a, b): Originally these species were included in the Sparganophilidae by Righi et al. (1978). James et al. (2023) found that "Arecoidae shows important genetic divergence and major morphological differences with Rhinodrilidae, lacking gizzard and calciferous glands, so we [James, Csuzdi and Brown] propose here the erection of this new monotypic family to accommodate its only species and genus."

Reproduction: amphimictic - hermaphroditic (?)

Benhamiidae Michaelsen, 1897

Type genus: *Benhamia* Michaelsen, 1888/9 emend. Csuzdi & Zicsi, 1994.

Type species: *Benhamia rosea* Michaelsen, 1892. (Types: Zoologisches Museum Hamburg, Universität Hamburg, missing; Reynolds & Wetzel, 2025, but Csuzdi (2010) says it's there **Syntype**, ZMUH, cat. no. V288.)

Genera 20; species 351; subspecies 6.

Expanded Diagnosis: Male terminalia acanthodriline, sometimes with microlecibe or Balantine reduction, rarely with 3 pairs of prostatic glands. Clitellum (saddle). Prostomium, epilobic. Setae, lumbricin arrangement. Several stalked extramural calciferous glands paired on esophagus behind the genital segments. Gizzard, present. Calciferous glands, three pairs. Excretory system holonephridial, or meronephridial with one pair of caudal megameronephridia (Csuzdi, 2000).

Remarks (modified from Glasby et al., 2025a, b): Native species of the Benhamiidae (351 species and 6 subspecies in 20 genera) are mainly restricted to sub-Saharan Africa, Oceania, Central America and northern South America (Csuzdi, 2010). These species were probably widely dispersed during the centuries of commercial product exchanges between Africa and other continents, where ships could have transported soil in planted pots containing these generally parthenogenetic species (Gates, 1970). The native Benhamiidae in tropical Africa are present in 16 genera and approximately 250 species; while in the Neotropics, there are five genera and about 100 species. In the Caribbean Islands, *Dichogaster* and *Eutrigaster* are mainly endemic species. In many areas of South America there has been limited sampling (Pavlí ek & Csuzdi, 2012; Decaëns et al., 2024).

Reproduction: amphimictic - hermaphroditic (?)

Biwadrilidae Jamieson, 1971 (Figure 4, p. 148)

Type genus: *Biwadrilus* Brinkhurst and Jamieson, 1971.

Type species: *Criodrilus bathybates* Stephensen, 1917 (Types: **Holotype**, Zoological Survey India Calcutta, cat. no. 3; Reynolds & Wetzel, 2025).

Genera 1; species 1; subspecies 0.

Expanded Diagnosis: Dorsal pores on mid-dorsal line absent; clitellum (annular and extensive xiv-xxxii, xxxiv), situated posterior to male pores (in xiii), female pores (in xiv); sperm sacs, absent. Tubercula pubertatis and genital setae, present. Calciferous glands, typhlosole, gizzard, spermathecae, absent. Muscular pharynx and prostate gland (lobular), present. Prostomium zygotelic. Nephridia, holonephridia, lacking terminal bladder, caecum or sphincter, all exonephric. Prostate-like setal glands present in 17. Testes, one pair in each of 10 and 11. Ovaries, a pair in 14. Ovisacs, restricted to 14. Anus, dorsal.

Remarks (modified from Glasby et al., 2025a, b): A monotypic family known only from the Lake Biwa region in Japan (Mısrhođlu et al., 2023). New material of *Biwadrilus bathybates* from Lake Biwa examined by Blakemore (2008) concluded that Biwadrilidae is synonymous with Criodrilidae Vejdovský, 1884, but it appears that it is not widely adopted. These two families display a disjunct distribution in the Palearctic which Criodrilidae only native to the western Palearctic.

Reproduction: amphimictic - hermaphroditic.

Criodrilidae Vejdovský, 1884 (Figure 5, p. 148)

Type genus: *Criodrilus* Hoffmeister, 1845.

Type species: *Criodrilus lacuum* Hoffmeister, 1845 (Types: missing; Reynolds & Wetzel, 2025).

Genera 1; species 2; subspecies 0.

Expanded Diagnosis: Dorsal pores, Tubercula pubertatis, gizzard, caeca, calciferous, supra-intestinal glands, and typhlosole, absent. Clitellum (annular, in xiv, xvi-xlv, xlvi) situated in region posterior to male pores, in xv and female pores in xiv. Setae, lumbricine type, widely paired. Genital setae, present. Nephridia, holoic. Seminal vesicles, trabeculate. Ovaries, in 13 ending in a single egg string. Ovisacs, in 14, small and lobed. Testes, one pair in each of 10 and 11. Spermathecae, absent. Anus, dorsal.

Remarks: Criodrilidae includes two species in a single genus, *Criodrilus*, which are native to the western Palearctic (Mısrhođlu et al., 2023). Criodrilidae is similar to Ocnodrilidae.

Reproduction: amphimictic - hermaphroditic.

Diporodrilidae Bouché, 1970 (Figure 6, p. 149)

Type genus: *Diporodrilus* Bouché, 1970.

Type species: *Diporodrilus pilosus* Bouché, 1970 (Types: **Holotype**, La Collection Ouest-Européenne Centrale d'Oligochètes, Dijon-Cedex, France, cat. no. 14-433-6611; Reynolds & Wetzel, 2025).

Genera 1; species 3; subspecies 2.

Expanded Diagnosis: Prostomium pro or epilobic, closed, setae lumbricine, closely paired. Dorsal pores absent. Clitellum (saddle), coelomic pores and tubercula pubertatis, present. Female pores before the clitellum in ½xivB. Male pores before clitellum in ½xv. Spermatophores, simple at the level of the genital segments. Holonephridia absent in 14. Pregizzard absent and postgizzard well-developed. Seminal sac and prostates, absent.

Remarks: Erected by Bouché (1970) for specimens collected in the Mediterranean islands of Corsica and Sardinia, from where they are endemic. Marchan *et al.* (2022) affirmed this family with molecular analyses, placing it as sister to the Lumbricidae.

Reproduction: amphimictic - hermaphroditic.

Eudrilidae Claus, 1880 (Figure 7, p. 149)

Type genus: *Eudrilus* Perrier, 1871.

Type species: *Eudrilus decipiens* Perrier, 1871 (Types: unknown; Reynolds & Wetzel, 2025).

Genera 45; species 305; subspecies 21.

Expanded Diagnosis: Distinguished from other megadriles by gizzard present; clitellum (saddle, in xiii-xviii), usually situated anterior to male pores (on xvii or xviii); Tubercula pubertatis, present. Setae in lumbricine arrangement. Genital setae, present. Dorsal pores, generally lacking, but may be present in some genera (*Platydrilus*, *Eudriloides*). Testes present, two pairs in total, one pair per segment; present in 10 or 11. Penis present (in xiv). Seminal vesicles, trabeculate. Spermathecae present, post-testicular; spermathecal pores unpaired, often combined with female pores. Female pores one pair (rarely combined with spermathecal pores), in xiv, combined with spermathecal pores. Vaginal sac, present. Nephridia, holoic. Prostate pores in xvii and xviii (paired with male pores).

Remarks (modified from Glasby et al., 2025a, b): Eudrilidae consists of 45 genera and 305 species (Mısırhoğlu *et al.*, 2023). The African Nightcrawler *Eudrilus eugeniae*, sold as fish bait, is widespread in the temperate, tropic and subtropic regions (Blakemore 1999; Reynolds and Wetzel, 2004, 2008, 2012) and the more restricted *Hyperiodrilus africanus*, are considered in many areas as introduced peregrines (Mısırhoğlu *et al.*, 2023). Tayler (1949) erected Hippoperidae which is now considered a junior synonym of Eudrilidae. Sims (1987) provided a key to genera of Eudrilidae, excluding *Hyperiodrilus*. A key to all described species of *Libydrilus* Beddard was provided by Clausen (2003). Plisko and Nxele (2015) provided a key to distinguish foreign Eudrilidae taxa from native ones of South Africa.

Reproduction: amphimictic - hermaphroditic.

Glossoscolecidae Michaelsen, 1900 (Figure 8, p. 150)

Type genus: *Glossoscolex* Leuckart, 1835.

Type species: *Glossoscolex giganteus* Leuckart, 1835 (Types: unknown; Reynolds & Wetzel, 2025).

Genera 6; species 156; subspecies 9.

Expanded Diagnosis: Species in this family have a straight gut (esophageal gizzard) with side branches; clitellum (saddle in xv-xxv), Tubercula pubertatis, present, situated in region of male pore (and posterior to female pore). Nephridia, one pair in each segment (holonephridia). Dorsal pores, lacking. Calciferous glands, present. Hearts, present in 5. Setae, lumbricin arrangement, genital setae, present, penial setae, absent. Testes, one-two pairs in 10 and 10, 11. Sperm sac, absent. Spermathecae, adiverticulate, three pairs in vii-ix. Ovaries, one pair in xiii. Ova sacs, present. Prostates, present or absent; if present, prostate pore united with male pore in xvii. Typhlosole, present.

Remarks (modified from Glasby et al., 2025a, b): Glossoscolecidae is similar to Tritogeniidae. They are native to the Neotropical Region but have been introduced to other continents including oceanic islands. It comprises six genera and 156 species (Mısırlıoğlu et al., 2023). Brinkhurst and Jamieson (1971) provide keys to genera and species at the time. James (2000) produced a key to species of the Samoan Archipelago. Plisko and Nxele (2015) provided a key to introduced and native Glossoscolecidae of South Africa.

Reproduction: amphimictic - hermaphroditic.

Hormogastridae Michaelsen, 1900 (Figure 9, p. 151)

Type genus: *Hormogaster* Rosa, 1887.

Type species: *Hormogaster redii* Rosa, 1887 (Types: **Holotype**, Museo ed Istituto di Zoologia Sistemica dell'Università di Torino, Italia, cat. no. 332; Reynolds & Wetzel, 2025).

Genera 9; species 37; subspecies 3.

Expanded Diagnosis: Clitellum (saddle, beginning in xii-xiv± 17 segments) situated in region of male (xv/xvi) and female pores (in xiv). Tubercula pubertatis forms paired ridges ventral to clitellum; calciferous glands, genital setae, gizzard, prostate glands, typhlosole, present. Setae, lumbricin, genital setae, present. Dorsal pores and prostates with ducts, lacking. Nephridia, holoic, vesiculate. Ovaries in 13. Ovisacs, in 14, small and lobed. Testes, 1-2 pairs in 10 and 11, or 11 only). Spermathecae, adiverticulate homoeotic equivalent in front of 13. Prostates, two+ pairs, pores in xxi-xxiv.

Remarks (modified from Glasby et al., 2025a, b): There are nine genera and 37 species in the Hormogastridae (Marchán et al., 2018). The family is similar to Tritogeniidae. While the Tritogeniidae are found in the Ethiopian Region, Hormogastridae are restricted to the Palearctic Region. James and Davidson (2012) argue that the Ailoscolecidae is a synonym of Hormogastridae. Some have suggested that Hormogastridae may also include the monogeneric Komarekionidae, e.g. Blakemore (2006) who considered it to be a junior synonym of Ailoscolecidae based on Sims (1980). However, molecular data strongly indicates a Komarekionidae - Sparganophilidae relationship. Gates and Reynolds (2017) include *Komarekiona eatoni* in their key.

Reproduction: amphimictic - hermaphroditic.

Kazimierzidae Nxele & Plisko, 2016 (Figure 10, p. 151)

Type genus: *Kazimierzus* Plisko, 2006.

Type species: *Microchaetus hamerae* Plisko, 1998 (Types: Natal Museum, Pietermaritzburg 3200 South Africa, **Holotype**, Olig.02650, **Paratypes**, Olig.02006-8, Olig.02651, Olig.02612-4; Reynolds & Wetzel, 2025).

Genera 1; species 25; subspecies 0.

Expanded Diagnosis: Pigment may or may not be present. Clitellum (saddle), Tubercula pubertatis, present, but variable in shape and position. Secondary annulation, present. Setae, minute in paired lumbricin arrangement. Secondary annulation preclitellar, present. Calciferous glands, present in one or two segments (9, 10 or 11). Spermathecal pores, posterior to Seminal vesicles, one or two pairs, in 11 or 12, or in 11 and 12. Ovaries, in 13. Female pores in xiv. Nephridia, holoic.

Remarks (modified from Glasby et al., 2025a, b): This family includes 25 species all in the genus *Kazimierzus* which is restricted to the south western Atlantic region of South Africa in the Western and Northern Cape provinces. Myers et al. (2000) consider this a biodiversity hotspot which should lead to the discovery of new earthworm species according to Nxele et al. (2016).

Reproduction: amphimictic - hermaphroditic.

Komarekionidae Gates, 1974

Type genus: *Komarekiona* Gates, 1974.

Type species: *Komarekiona eatoni* Gates, 1974 (Types: **Holotype** + 19 **Paratypes**, Canadian Museum of Nature, Ottawa, cat. nos. 1978–256–8, 266–76; Reynolds & Wetzel, 2025).

Genera 1; species 1; subspecies 0.

Expanded Diagnosis: Clitellum (saddle in xix-xxv, xxvi, red), Tuberculata pubertatis, present and white. Prostomium tanylobic. Dorsal pores, genital, copulatory, penial setae, prostates, genital tumescences, secondary annulation, and pigmentation lacking. Setae, closely paired. Hearts, in 6-11. Nephridia, holoic, one pair per segment. Spermathecal pores, three pairs near *C* in vii-ix. Ovaries, in 13, with a short egg string. Testes, holoandric, paired in 10-11. Prostates, two+ pairs, pores in xxi-xxiv. Supra-intestinal glands and typhlosole, lacking.

Remarks: Found primarily in the mid-Atlantic states and west to southern Illinois, USA (Gates, 1974; Reynolds, 2020). Interestingly, the specimens east of the Smoky Mountains are amphimictic while those west of the Smokies are parthenogenetic (Reynolds, 1977b, 2020).

Reproduction: amphimictic - hermaphroditic, east of the Appalachian Mountains and parthenogenetic west of the mountains.

Kynotidae Jamieson, 1971 (Figure 11, p. 152)

Type genus: *Kynotus* Michaelsen, 1891.

Type species: *Geophagus darwini* Keller, 1887 (= *Kynotus madagascariensis* Michaelsen, 1891) (Types: unknown; Reynolds & Wetzel, 2025).

Genera 1; species 22; subspecies 0.

Expanded Diagnosis: Branchiae absent; clitellum (annular in xviii-xlvi) present, situated posterior to male (in xvi) and female pores (in xiv); Tubercula pubertatis, absent. Genital chaetae and genital setal glands, present. Setae, lumbricin closely paired. Calciferous glands, lamellae, seminal vesicles and typhlosole, lacking. Spermathecae three pairs, post testicular (in 14, 15, 16), pores in xiii-xvii. Testes two pairs (in 10 and 11). Ovaries in 13. Male pores one pair (in copulatory pouches, associated with paired retractile claspers), in xvi. Tubular prostates present, pores in xiii-xiv.

Remarks: This family includes a single genus (*Kynotus*) and 22 species which are endemic to Madagascar (Mısırlıoğlu *et al.*, 2023). Razafindrakoto *et al.* (2017) provided a key to the species of *Kyntous*.

Reproduction: amphimictic - hermaphroditic.

Lumbricidae Rafinesque-Schmaltz, 1815 (Figure 12, p. 153)

Type genus: *Lumbricus* Linnaeus, 1758.

Type species: *Lumbricus terrestris* Linnaeus, 1758 (Types: British Museum Natural History, cat. no. 1973:1:1–**Neotype**, see Sims (1973); Reynolds & Wetzel, 2025).

Genera 47; species 615; subspecies 74.

Expanded Diagnosis: Digestive system: with an intramural calciferous gland comprising longitudinal chambers that open at their anterior ends into the esophageal lumen, a terminal esophageal valve reaching into xv, an intestine beginning with a "crop" followed by a gizzard, a sacculated as well as an unsacculated portion and ending in an atyphlosolate region, but without intestinal caeca and supra-intestinal glands. Vascular system: with complete dorsal, ventral, and subneural (and lateroneural?) trunks, the latter adherent to nerve cord, extraesophageal trunks median to the hearts passing to dorsal trunk in region of x–xii, without supra-esophageal and lateroparietal trunks. Hearts: lateral, the last pair anterior to segment xii. Nephridia: holoic, vesiculate, ducts passing into parietes in region of *B*. Setae, sigmoid and single pointed, eight per segment, in regular longitudinal ranks, in genital tumescences elongated but slender and longitudinally grooved ectally. Dorsal pores, present. Prostomium epilobic, prolobic, or tanylobic. Reproductive system: apertures, all minute,

female pores anterior to the male pores, equatorial and anterior to the multilayered clitellum which is always behind xvii. Spermathecae, adiverticulate, pores at intersegmental levels. Ovaries, in xiii, bandlike, each terminating distally in a single eggstring. Ovisacs, in xiv, small, lobed. Prostates, none.

Remarks (modified from Glasby et al., 2025a, b): This family contains about 615 species and 47 genera (Mısırlıoğlu *et al.*, 2023). Species in this family are found on all continents, except Antarctica) wherever Europeans colonized. Plisko and Nxele (2015) provided a key to distinguish introduced and native species of South Africa. Gates and Reynolds (2017) provided a key to North American members of the family. Blakemore (1999, 2009) reported approximately 33 species in which 24 were non-endemic and widespread in Australia.

Reproduction: amphimictic - hermaphroditic, some genera parthenogenetic, e.g. *Bimastos*.

Lutodrilidae McMahan, 1976 (Figures 13, 13a, p. 154)

Type genus: *Lutodrilus* McMahan, 1976.

Type species: *Lutodrilus multivesiculatus* McMahan, 1976 (Types: **Holotype** + **Paratype**, United States National Museum, Washington, cat. nos. 53283–4; Reynolds & Wetzel, 2025).

Genera 1; species 1; subspecies 0.

Expanded Diagnosis: Dorsal pores lacking. Secondary annulation, present. Clitellum (annular, in xx-lxxi) in region of male pores (xxxii/xxxiii). Tubercula pubertatis, Genital tumescences and typhlosole, present. Crop, gizzard, prostates, sperm sacs and calciferous glands, lacking. Spermathecae, present, in 16-25, spermathecal pores, absent, spermatophore present. Testes, 10 pairs (in 12-21). Seminal vesicles, 12 pairs. Ovaries, one pair in 23. Female pores, in xxiv. Hearts, 11 pairs, in 11-15. Typhlosole, present.

Remarks. Lutodrilidae is a monotypic family represented by *Lutodrilus multivesiculatus* McMahan, which is restricted to eastern Louisiana, USA (McMahan, 1976; Mısırlıoğlu *et al.*, 2023).

Reproduction: amphimictic - hermaphroditic.

Megascolecidae Rosa, 1891 (Figure 14, p. 155)

Type genus: *Megascolex* Templeton, 1844.

Type species: *Megascolex caeruleus* Templeton, 1844 (Types: missing; Reynolds & Wetzel, 2025).

Genera 85; species 2208; 127 subspecies.

Expanded Diagnosis: Digestive system, with intestinal origin behind ovarian segment. Vascular system, with a supra-esophageal trunk or trunks, extra-esophageals median to the hearts, which are in part latero-esophageal and with the terminal pair behind the last testis segment. Setae, sigmoid, with simply pointed tip. Dorsal pores, present. Hearts, present posterior to 11. Male pores (in xviii), behind female pores (in xiv). Spermathecae, in front of gonadal segment, with seminal chambers. Clitellum, annular, multilayered, in xiii-xx. Tubercula pubertatis, absent in parthenogenetic species. Ovaries, usually in xiii, fan-shaped and with numerous egg strings. Testes, one or two pairs, in 10, 11. Seminal vesicles, trabeculate. Nephridia, holoic or meroic. Prostates, tubular, one to three pairs, with pores in xvii-xix, or xviii. Ventral pore may be united with male pore in xviii. Typhlosole, present.

Remarks (modified from Glasby et al., 2025a, b): This is the largest family of 'earthworms' with over 2200 species and 85 genera (Mısırlıoğlu *et al.*, 2023). One genus, *Pontodrilus*, also occurs in the littoral zone. Unfortunately, there appears to be few morphological characters that clearly define the genera and species in the family. Blakemore (1999) believes 20 species have been introduced into Australia. Plisko and Nxele (2015) provided a key to the native and introduced species in South Africa. Gates and Reynolds (2017) provide a key to North American members of the family. Gates and Reynolds (2017) provided a key to North American species of the family, which was been updated by Chang *et al.* (2016); and James (2004) provided a key to species in the Solomon Archipelago.

Reproduction: amphimictic - hermaphroditic.

Microchaetidae Beddard, 1895 emend. Plisko, 2012 (Figure 15, p. 156)

Type genus: *Microchaetus* Rapp, 1849.

Type species: *Lumbricus microchaetus* Rapp, 1849 (Types: unknown; Reynolds & Wetzel, 2025).

Genera 3; species 81; subspecies 6.

Expanded Diagnosis: Distinguished from other megadriles by secondary annulation absent; calciferous glands, gizzard, sperm sacs, spermathecae, typhlosole, present. Prostomium, prolobic. Clitellum (saddle in x-xxxiii+) situated in region of both male and female pores. Tubercula pubertatis, present. Setae, lumbricin arrangement, closely paired; branchiae absent; gonadal segments bearing genital papillae. Hearts, in 9-11. Testes, one or two pairs, in 10 or 10 and 11, pores in xv-xix. Ovaries, in 13, pores in xiv. Nephridia, holoic, bladders U- or J-shaped. Prostate glands, absent.

Remarks (modified from Glasby et al., 2025a, b): This family consists of at least three genera and 81 species found only in southern Africa and Madagascar (Mısırlıoğlu et al., 2023). Despite the connotation, the family contains some of the largest earthworms including *Microchaetus rappi*, the African giant earthworm. Nxele et al. (2016) separated Kazimierzidae from Microchaetidae based on characters associated with the circulatory and excretory systems. Plisko and Nxele (2015) provided a key to the foreign and native taxa of South Africa.

Reproduction: amphimictic - hermaphroditic.

Moniligastridae Claus, 1880 (Figure 16, p. 156)

Type genus: *Moniligaster* Perrier, 1872.

Type species: *Moniligaster deshayesi* Perrier, 1872 (Types: unknown; Reynolds & Wetzel, 2025).

Genera 5; species 185; subspecies 19.

Expanded Diagnosis: First segment with setae arranged in pairs (lumbricine arrangement). Clitellum (annular, in ix-xiv) structure multilayered but thin. Tubercula pubertatis, present. Genital setae, absent. Dorsal pores on mid-dorsal line present. Testes, one or two pairs, in 9-12. Male pores in segment following testicular segment (in 8 or 8 and 9, plesioporous). Spermathecae with basal diverticula. Ovaries, one pair in 11 or 13. Nephridia, metanephridia. Prostate glands, lobular, one or more pairs, pores in ix-xiii.

Remarks (modified from Glasby et al., 2025a, b): This family is distributed widely especially in the Oriental region. It includes 185 species in five genera and three species are particularly widespread, e.g., *Drawida barwelli*, *Drawida japonica* and *Drawida nepalensis* (Mısırlıoğlu et al. 2023). Blakemore (1999) reported *D. barwelli* as introduced into Australia. James (2000) provided a key to species of the Samoan Archipelago. Gates and Reynolds (2017) provided a key to North American species of the family.

Reproduction: amphimictic - hermaphroditic.

Ocnerodrilidae Beddard, 1891 (Figure 17, p. 157)

Type genus: *Ocnerodrilus* Eisen, 1878.

Type species: *Ocnerodrilus occidentalis* Eisen, 1878 (Types: **Holotype** + 5 **Paratypes**, British Museum Natural History, London, cat. nos. 1904:10:5:231-6, Paratype, Zoologisches Museum, Museum für Naturkunde der Humboldt, Universität Invalidenstrasse, Berlin, Deutschland, cat. no. 2363 – missing; Reynolds & Wetzel, 2025).

Genera 37; species 172; subspecies 4.

Expanded Diagnosis: Distinguished from other megadriles by prostate gland present; dorsal pores on mid-dorsal line present. Clitellum (annular, in xiii-xviii, or xiv-xix), situated in region of male pore (in xvii or xviii). Tubercula pubertatis, present, forming paired ridges on the ventrolateral margins of clitellum; branchiae absent. Calciferous glands, if present is in 9 or 10, or 9 and 10. Hearts, extend into 11. Setae, lumbricin arrangement, dorsal pair closely paired, ventral pair widely paired. Esophagus, short without intestinal caeca. Spermathecae, seminal vesicles (tabeculate), present. Nephridia, holoic, avesciculate. Ovaries in 13, fan-shaped and with several egg-strings. Female pores, one or two pairs in xiv. Prostate gland, one pair, tubular. Prostate pores, in xvii-xix, where ventral pore may be united with male

pore. The type species shows genetic polymorphism (see Gates, 1973).

Remarks (modified from Glasby et al., 2025a, b): Ocnerodrilidae is similar to Megascolecidae, Criodrilidae and Eudrilidae. This family is cosmopolitan with several peregrine species, e.g. *Ocnerodrilus occidentalis* (Mısırlıoğlu et al. 2023). Blakemore (1999) reported four species introduced to Australia. Plisko and Nxele (2015) provided a key for the native and introduced species in South Africa. Fragoso and Rojas (2009) provided a key to the genera of Ocnerodrilidae. Gates and Reynolds (2017) provided a key to North American species of the family.

Reproduction: amphimictic - hermaphroditic.

Rhinodrilidae Benham, 1890 (Figure 18, p. 157)

Type genus: *Rhinodrilus* Perrier, 1872.

Type species: *Rhinodrilus paradoxus* Perrier, 1872 (Types: unknown; Reynolds & Wetzel, 2025).

Genera 40; species 376; subspecies 7.

Expanded Diagnosis: Setae first appearing on second segment after peristomium. Dorsal pores, sperm sacs, absent; calciferous glands (three pairs, in some or all 7-14), prostate gland, typhlosole, present. Male pores in segment following testicular segment (one or two pairs in xi and xii, plesioporous), behind female pores. Clitellum (saddle, in xiv-xxii). Tubercula pubertatis, present. Setae, lumbricin arrangement. Genital setae, in xviii-xxiii. Esophageal gizzard, present in 6. Hearts in 10 and 11. Testes, two pairs, in 10 and 11. Ovaries, in 13, pores one pair in xiv. Spermathecae, adiverticulate in front of gonadal segments. Spermathecal pores (three pairs in vi/vii-viii/ix). Nephridia, holoic stomate.

Remarks: This family includes 38 genera and approximately 376 species, which are found in the Nearctic and Neotropical regions. *Pontoscolex corethrurus* (Müller, 1857), is probably the most widely distributed earthworm in the world (Mısırlıoğlu et al., 2023). North American distribution was reported by Reynolds and Wetzel (2004, 2008, 2012). According to Blakemore (1999), it has been widely introduced into Australia.

Reproduction: amphimictic - hermaphroditic.

Sparganophilidae Michaelsen, 1918 (Figure 19, p. 158)

Type genus: *Sparganophilus* Benham, 1892.

Type species: *Sparganophilus tamesis* Benham, 1892 (Types: **Holotype** + **Paratype**, British Museum Natural History, London, cat. nos. 1892:12:16:1-2; Reynolds & Wetzel, 2025).

Genera 1; species 21; subspecies 2.

Expanded Diagnosis: Digestive system: without gizzard, calciferous glands, lamellae, caeca, typhlosole, or supra-intestinal glands, with an intestinal origin in front of the testis segments. Vascular system: with complete dorsal and ventral trunks, two pairs of anterior lateroparietal trunks, one of which passes to the dorsal vessel and the other to the ventral vessel in xiv, but without subneural and supra-esophageal trunks. Hearts: lateral, moniliform, in vii-xi. Blood glands: protuberances from capillaries in septal glands. Nephridia: holoic, aborted at maturity in first 12 or more segments, avesciculate, peritoneal cells investing postseptal portions enlarged, ducts without muscular thickening passing into parieties in AB. Nephropores: inconspicuous, in AB. Setae: eight per segment. Dorsal pores and pigment, lacking. Prostomium, zygotobous. Anus, dorsal. Reproductive apertures: all minute and superficial, female pores in xiv, spermathecal pores in front of testis segments (in vi-ix or v-vi). Clitellum multilayered, including male pore segment. Seminal vesicles, trabeculate. Ovaries, in xiii, each terminating in a single eggstring. Ovisacs, in xiv, small and lobed. Spermathecae, adiverticulate. Prostate glands, absent or present; when present, pores in 9-11.

Remarks (modified from Glasby et al., 2025a, b): Sparganophilidae has only one genus (*Sparganophilus*) and 21 species primarily in the Northern Hemisphere. Most species occur in the Nearctic, but the family also occurs in the Palearctic and Neotropical realms (Reeves et al., 2024; Reynolds, 1980, 2008); at least one species (*S. tamesis*) is widespread in the

Northern Hemisphere (Mısırlıoğlu *et al.*, 2023). This is one of the few megadrile families that include species that are aquatic or semi-aquatic (Reynolds, 1980, 2008; Reeves *et al.*, 2024). Molecular data by Jamieson *et al.* (2002) and James and Davidson (2012) strongly supported a sister-group relationship between Sparganophilidae and Komarekionidae. But Sims (1980) using morphology only suggested a closer relationship between *Ailoscolex* and *Komarekiona* thus synonymising Komarekionidae with Ailoscolecidae (now Hormagastridae). Gates and Reynolds (2017) and Reynolds (1980) provided a key to North American members of this family. Carrera-Martínez *et al.* (2025?) recently described seven new species plus three as yet unnamed from the Southeastern Appalachian Piedmont of the United States. Gladsby *et al.* (2025?) believe the family is similar to Tritogeniidae.

Reproduction: amphimictic - hermaphroditic.

Syngenodrilidae Smith & Green, 1919 (Figure 20, p. 158)

Type genus: *Syngenodrilus* Smith & Green, 1919.

Type species: *Syngenodrilus lamuensis* Smith & Green, 1919 (Types: **Holotype**, United States National Museum, Washington, cat. no. 36433; Reynolds & Wetzel, 2025).

Genera 1; species 1; subspecies 0.

Expanded Diagnosis: Body transparency opaque, gut usually not visible, gizzard present. Clitellum (annular, ix xi-xxvii), Tubercula pubertatis form paired ridges on the ventrolateral margins of the clitellum. Secondary annulation, genital setae, present or absent. Dorsal pores, absent. Setae, lumbricin arrangement. Gizzard, in 8 and 9. Testes, two pairs in 10 and 11; male pores (on xiii) two or more segments following testicular segment (opisthoporous). Ovaries, one pair in 13, female pores in xiv. Nephridia paired with pyriform terminal dilation. Spermathecal pores two, located near male and female pores; prostate gland present, three pairs in 11, 12 and 13 without diverticula. Spermathecae, two pairs in 8 and 9. Spermathecal pores, intersegmental in 7/8 and 8/9. Nephridia, metanephridia. Prostates, three pairs in 11, 12 and 13, pores in xi to xiii.

Remarks (modified from Glasby et al., 2025a, b): This family contains a single genus and one species from Lamu, Kenya in east Africa. This family shares several reproductive features in common with earthworms, but have a single-celled clitellum like microdriles (Jamieson 2006, Timm 2012).

Reproduction: amphimictic - hermaphroditic.

Tiguassidae Brinkhurst, 1988 (Figure 21, p. 159)

Type genus: *Tiguassu* Righi, Ayres & Bittencourt, 1978.

Type species: *Tiguassu reginae* Righi, Ayres & Bittencourt, 1978 (Types: **Holotype**, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil, cat. no. 80; Reynolds & Wetzel, 2025).

Genera 1; species 1; subspecies 0.

Expanded Diagnosis: Body opaque, gut not visible; prostomium anteriorly with an anterior tentacle-like extension ('proboscis'); setae arranged in closely spaced lateral and ventrolateral pairs (lumbricine arrangement). Clitellum (saddle in xii-xvii) situated in region of male pores (equatorial in xi); spermathecal pores, two, located near male pores (in xi) and female pores (in pair equatorial in xiii). Gizzard in 6-8. Hearts, in 10. Spermathecae, simple without diverticula anterior to gonadal; segments, in 9 and 10. Testes in 11; ovaries in 12. Seminal ducts in 11 and 12, without atria or associated glands. Three muscular gizzards fused in 6, 7 and 8. Nephridia, metanephridia. Prostate gland, absent.

Remarks: Tiguassidae is a monotypic family, known for *Tiguassu reginae* Righi, Ayres & Bittencourt, 1978 of the Amazon region, Brazil. Little is known about its biology, including the form of its clitellum. Jamieson (2006) suggested a close relationship with the Family Haplotaxidae which is not included here.

Reproduction: amphimictic - hermaphroditic.

Tritogeniidae Plisko, 2013 (Figure 22, p. 159)

Type genus: *Tritogenia* Kinberg, 1867.

Type species: *Tritogenia sulcata* Kinberg, 1867 (Types: **Holotype**, Department of Zoology, Swedish Museum of Natural History, Stockholm, cat. no. 157; Reynolds & Wetzel, 2025).

Genera 2; species 39; subspecies 0.

Expanded Diagnosis: Length variable, from 25 to 2600 mm. Body cylindrical, occasionally flattened at clitellar area. Secondary annulation, present or absent. Clitellum, saddle in xiii-xxviii. Tubercula pubertatis, present. Segment number is variable, secondary annulation of preclitellar segments occurs as the external, transverse furrows, or grooves, demarcating segments externally into shorter portions. Gizzard, in 6-7, if second in 9. Prostomium, prolobous. Setae, lumbricin arrangement. Testes, two pairs, one each in 10 and 11. Male pores, in xviii or xix. Spermathecal pores, five or more in ix/x-xv/xvi or xvi/xvii. Ovaries, in 13. Female pore, in xiv. Prostate gland, absent. Multiple, minute, nephridia in each segment (meronephridia).

Remarks (modified from Glasby et al., 2025a, b): Tritogeniidae, which was erected by Plisko (2013), includes two genera, *Michalakus* with a single species and *Tritogenia* with 38 species; all species are endemic to southern Africa (Mısırlıoğlu et al., 2023). Plisko (1997) includes a key to species and species groups of *Tritogenia* from southern Africa, and Plisko & Nxele (2015) provide a key to distinguish foreign Tritogeniidae taxa from native ones of South Africa. Tritogeniidae is similar to both Hormogastridae and Sparganophilidae (Glasby et al. (2025)).

Reproduction: amphimictic - hermaphroditic.

Tumakidae Righi, 1995 (Figure 23, p. 160)

Type genus: *Tumak* Righi, 1995.

Type species: *Tumak hammeni* Righi, 1995 (Types: **Holotype**, Instituto de Ciencias, Naturales Museo de Historia Natural, Universidad Nacional Bogota, Columbia, cat. no. An064, **Paratypes**, Rijksmuseum van Natuurlijke Historie, Afd. Vermes, Leiden, Nederland, cat. nos. 20178, 20100; Reynolds & Wetzel, 2025).

Genera 2; species 4; subspecies 0.

Expanded Diagnosis: Secondary annulation present; gut more-or-less straight, lacking side branches. Clitellum (saddle in xiv-xxv) situated in region of male pores. Tubercula pubertatis forms paired ridges on the ventrolateral margins of the clitellum. Gonadal segments bearing genital papillae. Dorsal pores, typhlosole, present. Hearts, five pairs in 5-9. Sperm sac absent. Testes, two pairs, one pair in each of 10 and 11. Male pore single median in xvii-xix. Ovaries, in 13. Female pores, one pair in xiv. Nephridia, metanephridia. Prostate gland, absent.

Remarks: There are currently only three species in the genus *Tumak* which are found in the soils of South America (Mısırlıoğlu et al., 2023).

Reproduction: amphimictic - hermaphroditic.

ILLUSTRATED GLOSSARY

The definitions are taken from Gates (1972), Reynolds (1977c, 2022) and Reynolds et al. (1974):

acanthodriline - Having prostatic pores in segments 17 and 19, male pores in 18, and all pores often in seminal furrows.

amphimictic - reproduction involving fertilization of an ovum by a sperm.

Balantine reduction - With male and prostatic pores in segment xix.

basal diverticula - A small pouch at the base of an organ.

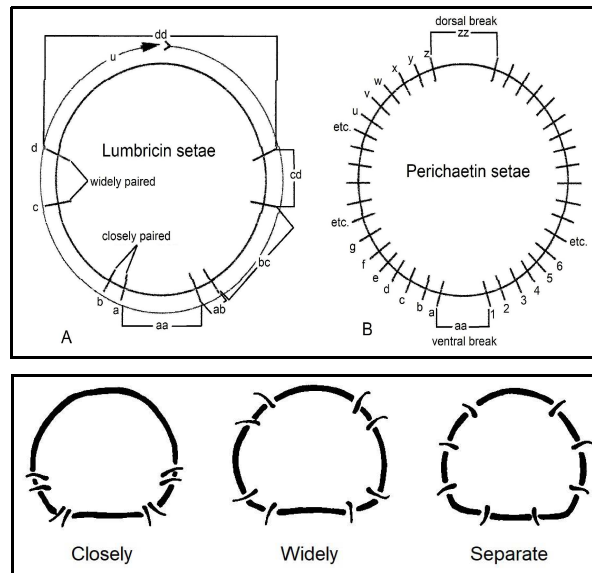
branchiae - Gills or similar organs for respiration.

caecum - a blind diverticulum or pouch from the alimentary canal.

calciferous gland - whitish gland that secretes calcium carbonate and opens into the gut via the esophageal pouches. In Lumbricidae, it is generally found in segments 10-14.

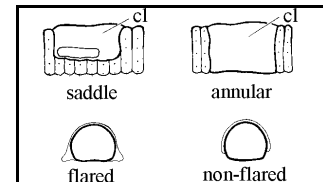
chaetae (setae) - a solid rod or bristle secreted by cells at the ental end of a tubular epidermal ingrowth, the setal follicle. Several types: 1) general, sigmoid with pointed outer tip, 2) genital, not sigmoid, associated with genital tumescences, and 3) penial, not sigmoid, associated with the male pores.

chaetal (setal) pairings - Setae may be closely paired, widely paired, or separate (A, left). Perichaetine arrangement (B, right). The pheretimoid earthworms have numerous setae (as many as 150) per segment. Perichaetine setae are arranged in a ring, circumventing all segments of the specimen (with the exception of the first and last segments). The numbers of setae vary slightly from one segment to another and from one specimen to another. Within specimen variations are usually largest in the pre-clitellar region. The closest seta to the mV is *a* and they increase to the mL; the seta closest to the mD is *z* and they decrease to the mL. This type of setal arrangement is quite different from that in the earthworm families Lumbricidae and Spaganophilidae, which have only eight setae per segment in four pairs (lumbricin, A, left) and from native North American species which also have a lumbricine setal arrangement. Examples: *Aporrectodea rosea* (lumbricin) $AB=CD$, $AA>BC$, $DD\approx\frac{1}{2}C$; *Amyntas agrestis* (perichaetin) setal rings closed dorsally; ventral setae enlarged anteriorly, but diminishing regularly from the middle line, $a > b$, $b > c$, etc., intersetal intervals also diminish, $aa > ab$, $ab > bc$, $bc > cd$ thenceforward equal, in mid body $aa > ab$, $ab > bc$, rest are equal.



caspers - are anatomical structures found in various animal groups, typically used by males to grasp or hold onto females during copulation. In annelids, especially within the class Hirudinea (leeches) and Kynotidae, caspers may appear as modified suckers or appendages that help align the reproductive organs during mating.

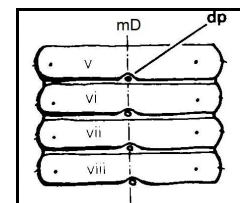
clitellum (cl) - a regional tumescence of the epidermis, the gland cells of which secrete the material to form the cocoon; types are annular and saddle.



crop - a widened portion of the digestive system in front of the gizzard and lacks muscularity.

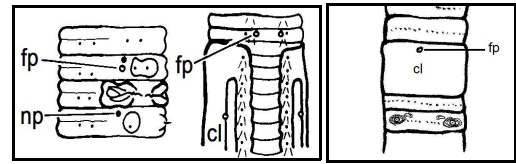
diverticulate - having a diverticulum, an outgrowth of some sort from the main axis.

dorsal pores (dp) - small intersegmental openings in the mid dorsal line leading to the coelomic cavity.



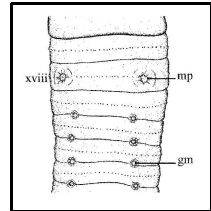
esophagus (oesophagus) - The portion of the gut between pharynx (anterior) and crop (posterior).

female pore - The external openings for the oviducts on segment xiv and ventrad of the mid-lateral line. They are usually more difficult to see than the male pores. [**fp** = female pore, **np** = nephropore]

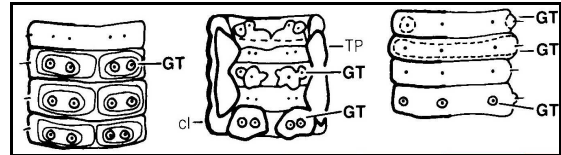


genital papillae - see genital tumescences.

genital markings - Glandular swellings, pits or grooves of the epidermis. [**gm** = genital markings, **mp** = male pore]



genital tumescences (GT) - Areas of modified epidermis (glandular swellings) without distinct boundaries and through which follicles of genital setae open. (**TP** = Tubercula pubertatis)



gizzard - The muscularized portion of the digestive system, usually posterior to the crop and anterior to the intestine.

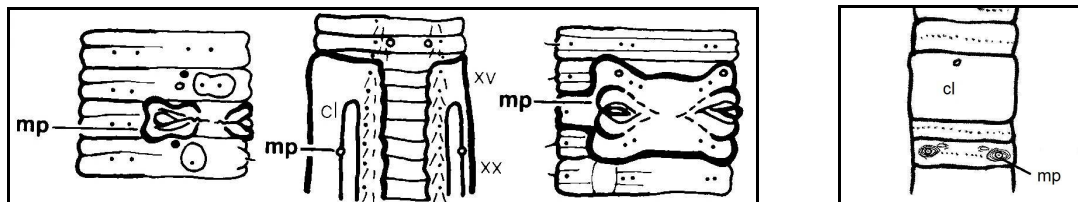
holonephridial (holoic) - A pair of nephridia in each segment except in first and last.

intestinal caeca - A pouch (tube-like structure) in the intestine.

lamellae - Thin membranes of plates of tissue.

lumbricin(e) - Having 8 setae per segment.

male pore (mp) - The external paired openings for the male ducts through which sperm are liberated during copulation.

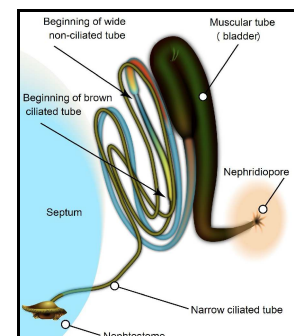


male tumescences - see Genital Tumescences

meronephridial (meroic) - Nephridial tubules formed by longitudinal or transverse fragmentation of the original single pair of embryonic rudiments of each segment.

metagnous (metandry) - having ovaries only in xiii, or a homoeotic equivalent (a genetic process that leads to a major shift in the developmental fate of an organ or body part).

Metanephridium is an excretory organ found in invertebrates like earthworms. It has ciliated funnel structures which open into the body cavity that is attached to a duct. This structure finally opens to the earthworm's exterior. The excretory product obtained by

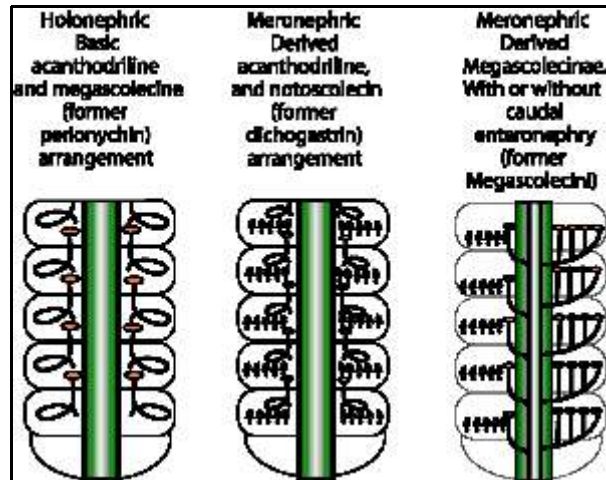


filtration of blood is later modified into the urine. This modification happens due to the selective reabsorption in the cells lining the metanephridium. They are found in pairs in segments where they occur.

microlecibe - A small tube.

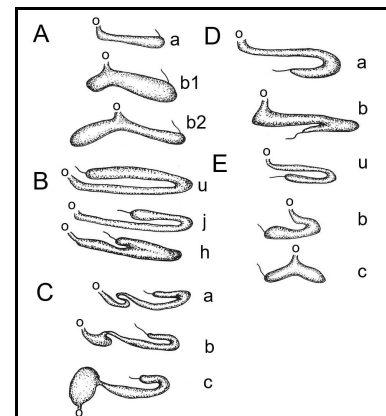
nephridium - An organ for nitrogenous excretion. nephridium – (pl. nephridia); excretory organs: large, paired in one segment are referred to as holoic; small, multiple in segment are meroic. Their shapes are one of the most important characters in earthworm taxonomy.

Diagrammatic representation of types of nephridia in the Megascolecidae. The holonephric arrangement of one pair of stomate nephridia per segment occurs in most acanthodrilids; the meronephric arrangement, here with a median stomate meronephridium and lateral astomate meronephridia (micromeronephridia) is seen in *Neodiplostrema*. [after Jamieson, 2000]



nephridial bladders - storage of waste before discharging from the body via the nephropore.

Different types of nephridial bladders in earthworms: **A.** Sausage-shaped and its variations, **a** = sausage-shaped, **b1** = biscuit-shaped (octaedra-type), **b2** = bilobate; **B.** Cephalad bent, **u** = U-shaped, **j** = J-shaped, **h** = hook-shaped; **C.** Nephridial bladders with ectal ampulla, **a** = nephridial bladders from there anteclytellar segments, **b** = nephridial bladders from posterior segments of *A. (s.l.) leoni*, **c** = sigmoid nephridial bladders from the postclytellar segments of *Allolobophora (s.l.) nematogena*, **D.** Caudad bent nephridial bladders, **a** = J-shaped, **b** = ocarina-shaped, **E.** Caudad bent n.b., **u** = U-shaped, **b** = inverse J-shaped, **c** = bilobate; **o** = opening to the nephridiopore. (from Csuzdi & Zicsi, 2003, p. 32).



nephropore (nephridiopore) - the external opening of a nephridium.

opisthoporous - Where male pores are a complete segment or more posterior to the intersegmental furrow of the septum bearing the sperm funnels, or exceptionally with one of two pairs less than the length of a segment.

ovary - the organ for ova (egg) production.

oviducal funnel - They are ciliated and found below the ovary. Each funnel has a fimbriated and ciliated margin.

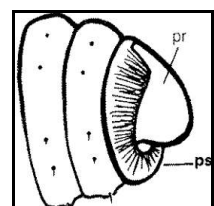
oviducal pore - see female pore.

pharynx - The portion of the gut between the buccal cavity (anterior) and the oesophagus (posterior).

perichaetin - The location of setae, when more than 8 per segment, in a more or less complete circle around the equator of a segment.

peristomium - The first body segment, asetal, and containing the mouth.

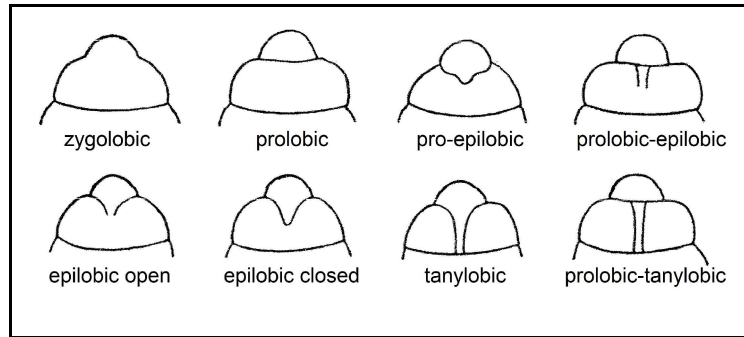
plesioporous - excretory system where the genital ducts lead from each segment to pores in the next segment



proboscis - An elongated appendage from the head of certain worms (see Tiguassidae).

prostomium - The anterior lobe projecting in front of the peristomium and above the mouth.

There are 4 basic types, or forms, and four subforms as seen in the dorsal view below: 1) **zygobolic**: prostomium not demarcated in any manner. 2) **prolobic**: prostomium demarcated from the peristomium without a tongue. 3) **pro-epilobic**: an epilobic prostomium with an open tongue, the beginning of the tongue is divided by a transverse groove. 4) **prolobic-epilobic**: prostomium demarcated from the peristomium as in the prolobic type but with an open tongue. 5) **epilobic open**: tongue of the prostomium partly divides the peristomium, tongue not delimited posteriorly by a transverse groove. 6) **epilobic closed**: tongue of the prostomium partly divides the peristomium, tongue delimited posteriorly by a transverse groove. 7) **tanylobic**: with a tongue that completely divides the peristomium. 8) **prolobic-tanylobic**: with a tongue that completely divides the peristomium, the beginning of the tongue is divided by a transverse groove.

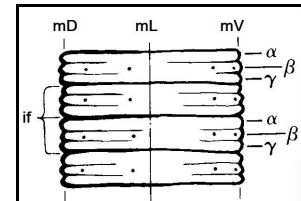


prostates - Without stalks are characterized as atrial glands, and of unknown function. They are more or less associated with the male pores. The paired glands, producing fluid supporting the transport of sperm during copulation; associated with vasa deferentia that extend to the exterior through male pores; each consists of a prostatic gland, muscular prostatic duct and prostatic pores

pygidium - The terminal portion of the body, sometimes referred to as the anal segment.

quincunx - a pattern involving location of setae of 3 consecutive segments in a group of 5 with one centrally located, e.g., *Pontoscolex corethrurus* (Rhinodrilidae). [**if** = intersegmental furrow, **sa** = secondary annulation]

secondary annulation (sa) - The furrows which occur between the intersegmental furrows. These demarcations are only external and are labelled α , β , or γ . [**mD** = mid Dorsal, **mL** = mid Lateral, **mV** = mid Ventral, **if** = intersegmental furrow]

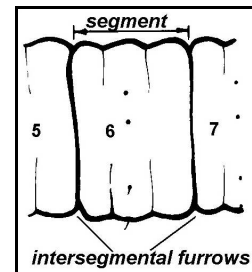


segment - A portion of the body, along the anteroposterior axis, between two consecutive intersegmental furrows and the associated septa. Segments were numbered classically with Roman numerals, but more recently with Arabic numerals, with the peristomium as number 1.

seminal vesicles - The storage sacs for an earthworm's own sperm until copulation.

spermatophore - A capsule of albuminous matter containing a number of sperm.

spermiducal funnel - They are ciliated and found below the testes. Each funnel has fimbriated and ciliated margin.



spermaducial pore - see male pore.

spermathecae - The pouches developed in the septa which receive sperm from another individual during copulation; the sperm are stored here until the period of cocoon laying.

stomate - having a mouth, referring to a nephridium, with a funnel. A nephridium with a funnel sometimes is said to be "open".

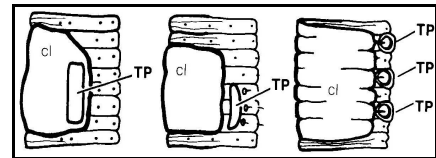
supra-intestinal glands - part of the excretory system exporting waste out of the body, found above the intestine and below the dorsal blood vessel.

testis (pl. testes) - The organs for sperm production; it may occur only in one segment: 10 (proandric condition) or 11 (metandric); or in two segments, 10 and 11 (holandric)

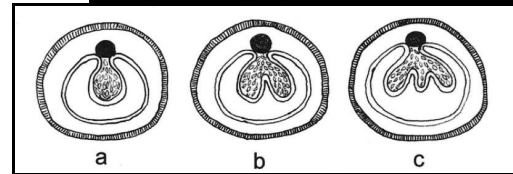
testis sac (sperm sac, spermathecae) - Usually a closed off coelomic space containing one or both testes and male funnels of a segment.

trabeculate - characterizing megadrile seminal vesicles that develop as connective tissue proliferations from a septum so as to have numerous irregular spaces that remain inconsiderable until spermatogonia begin to enter.

tubercula pubertatis (TP) - A glandular swelling appearing near the ventrolateral margins of the clitellum. It is not always present, and it may be continuous or discontinuous, and of varied size and shape. [cl = clitellum]



typhlosole - Any longitudinal fold in the gut wall projecting into the gut lumen, usually at mid dorsal or mid ventral; shape and commencement are species features. Main types: **a** = simple lamelliform, **b** = bifid, and **c** = trifid (from Csuzdi & Zicsi, 2003, p. 30).



vas deferens - ducts carrying sperm from testes to the exterior.

vas efferens - duct leading from the testes to the vas deferens.

vesiculate - with reference to a nephridium – provided with a bladder, with reference to reproductive system – having seminal vesicles, with reference to tissue or organ structure – having small spaces.

DISCUSSION

Like many plants and animals there are unique or endemic continental species (Reynolds, 1994). This is also true for earthworms. There are two ecological reasons why an earthworm species may or may not be in a particular region: 1) ecological, it cannot exist there, or 2) zoogeographical, it has not arrived there (Udvardy, 1969). The first is governed by the earthworm species itself, dependent upon the physical environment (see Reynolds, 1994). The second is dependent on a vector, *e.g.*, animals, machine or human, as the earthworm cannot travel very far on its own (see Reynolds, 1977d, *Philohela minor* now *Scolopax minor*).

The global distribution in the zoogeographical regions is presented in **Figure 24**.

The map (Figure 24) shows the distribution from a zoogeographical viewpoint. Following is the family distribution by continents:

- | | |
|--|--|
| <ol style="list-style-type: none"> 1. Acanthodrilidae (indigenous in Africa, North, Central and South America, introduced elsewhere), 2. Almididae (Africa, South America), 3. Arecoidae (South America), 4. Benhamiidae (Africa, Australia, South America), 5. Biwadrilidae (Asia (Japan)), 6. Criodrilidae (western Asia), 7. Diporodrilidae (Europe), 8. Eudrilidae (indigenous in Africa, introduced elsewhere), 9. Glossoscolecidae (indigenous in Central and South America, introduced elsewhere), | <ol style="list-style-type: none"> 10. Hormogastridae (Europe), 11. Kazimierzidae (Africa), 12. Komarekionidae (North America, USA), 13. Kynotidae (Africa), 14. Lumbricidae (indigenous in Europe, North America, introduced elsewhere), 15. Lutodrilidae (North America, USA), 16. Megascolecidae (indigenous in Asia, North America, introduced world wide), 17. Microchaetidae (Africa), |
|--|--|

18. Moniligastridae (indigenous in Asia, introduced elsewhere),
 19. Ocerodrilidae (indigenous in South America, introduced else-where),
 20. Rhinodrilidae (North and South America),
 21. Sparganophilidae (North America, Europe, Philippines),
 22. Syngenodrilidae (Africa),
 23. Tiguassidae (South America),
 24. Tritogeniidae (Africa),
 25. Tumakidae (South America).

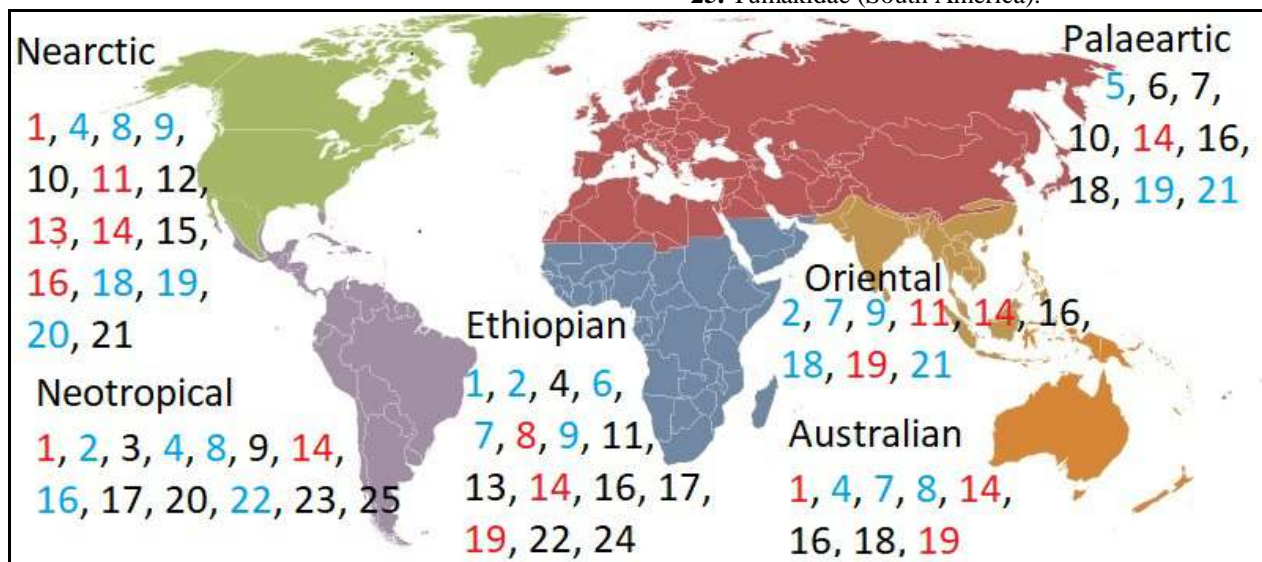


Figure 24. The origin and dispersal of terrestrial earthworm families (modified and updated from Reynolds, 1994 and utilized by Hendrix *et al.*, 2008) [# indigenous taxa only, # indigenous and introduced taxa, # introduced taxa only]:
 1. Acanthodrilidae, 2. Almididae, 3. Arecoidae, 4. Benhamiidae, 5. Biwadrilidae, 6. Criodrilidae, 7. Diporodrilidae, 8. Eudrilidae, 9. Glossoscolecidae, 10. Hormogastridae, 11. Kazimierzidae, 12. Komarekionidae, 13. Kynotidae, 14. Lumbricidae, 15. Lutodrilidae, 16. Megascolecidae, 17. Microchaetidae, 18. Moniligastridae, 19. Ocerodrilidae, 20. Rhinodrilidae, 21. Sparganophilidae, 22. Syngenodrilidae, 23. Tiguassidae, 24. Tritogeniidae, 25. Tumakidae.

In spite of the recent studies in ecological and phylogenetic annelid taxonomy, identification is still difficult for the non-specialist. For megadrile oligochaetes, there are many exotic/peregrine species that have been deliberately or accidentally deposited around the world (Gates, 1970), which can be identified at the family level, if these families are known to be introduced and not part of the endemic fauna. Thus, good family level determination would be most useful for scientists and students at all levels undertaking ecological and environmental studies.

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FIGURES

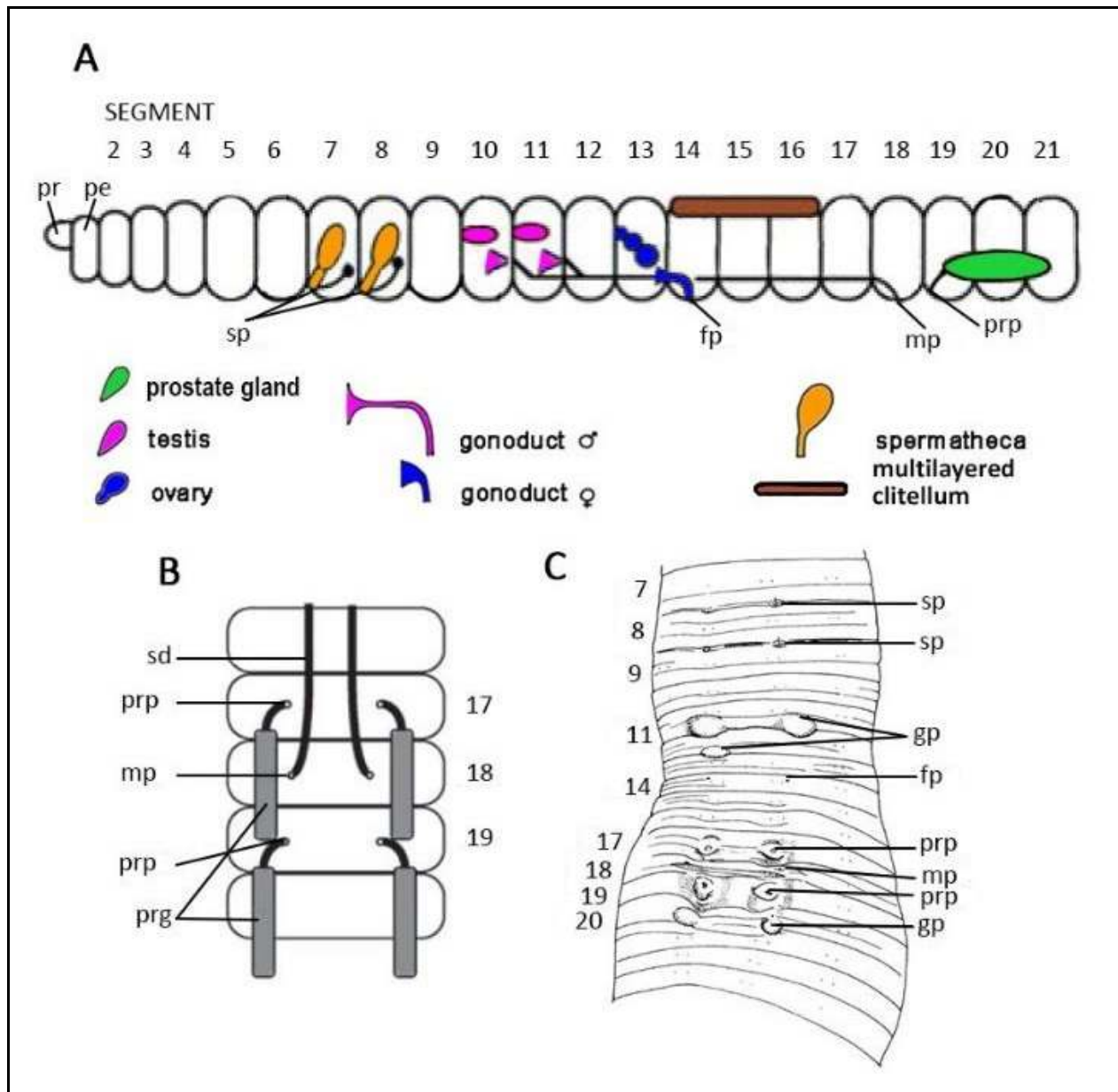


Figure 1. Acanthodrilidae. **A.** schematic drawing of reproductive organs. **B.** arrangement of pores. **C.** genital field of *Diploptrema australis* (Michaelsen, 1889): **fp** = female pore, **gp** = genital papillia, **mp** = male pore, **pe** = peristomium, **prp** = prostatic pore, **pr** = prostomium, **prg** = prostate gland, **sd** = sperm duct, **sp** = spermathecal pore (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006 and Dyne & Jamieson, 2004, used with permission).

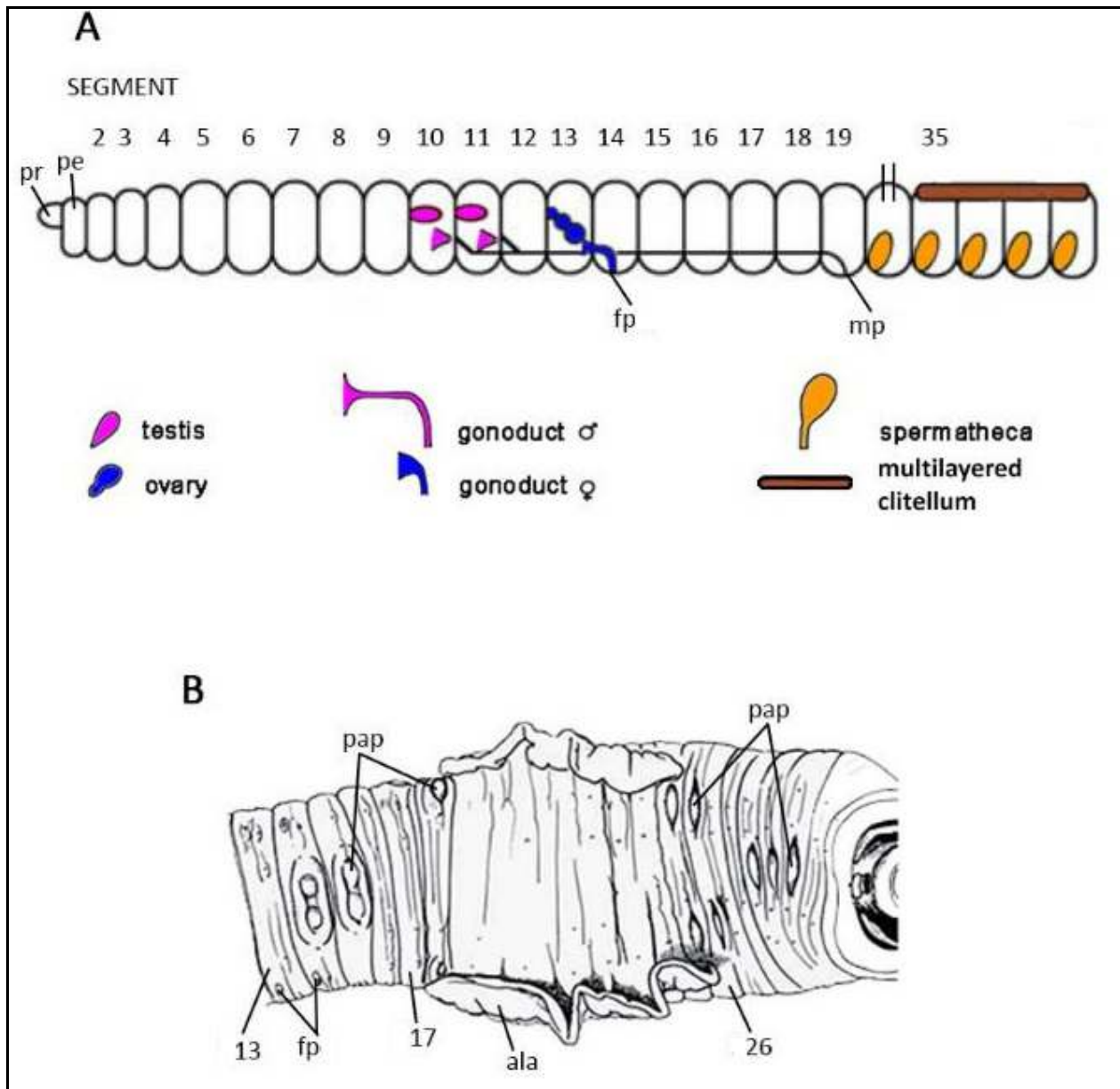


Figure 2. Almidae. **A.** schematic drawing of reproductive organs. **B.** Ventral view of genital region of *Glyphidrilus kukenthalii* Michaelsen, 1896: **ala** = alae (wing), **fp** = female pore, **pap** = p[apilla, **pe** = peristomium, **pr** = prostomium, (from Gladsy *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

Figure 3. Arecoidea. Ventral view of genital region of *Areco reco* Righi *et al.*, 1978.: **gt** = genital tumescence, **tp** = tubercula pubertatis (modified from Righi *et al.*, 1978).

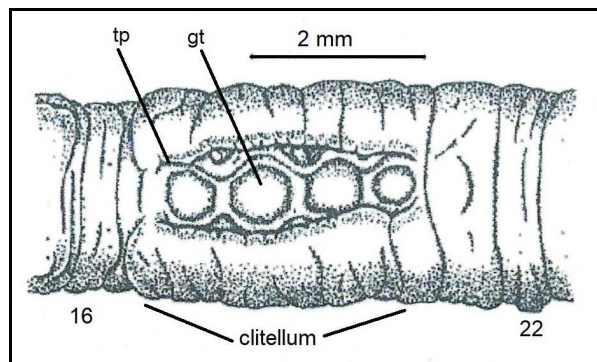


Figure 4. Biwadrilidae. . **A.** schematic drawing of reproductive organs. **B.** Ventral view (anterior) of *Biwadrilus bathybates* (Stephenson, 1917): **clt** = clitellum, **pe** = peristomium, **pr** = prostomium (from Gladys *et al.*, 2025, additionally Jamieson and Ferraguti, 2006 & Blakemore, 2008, used with permission).

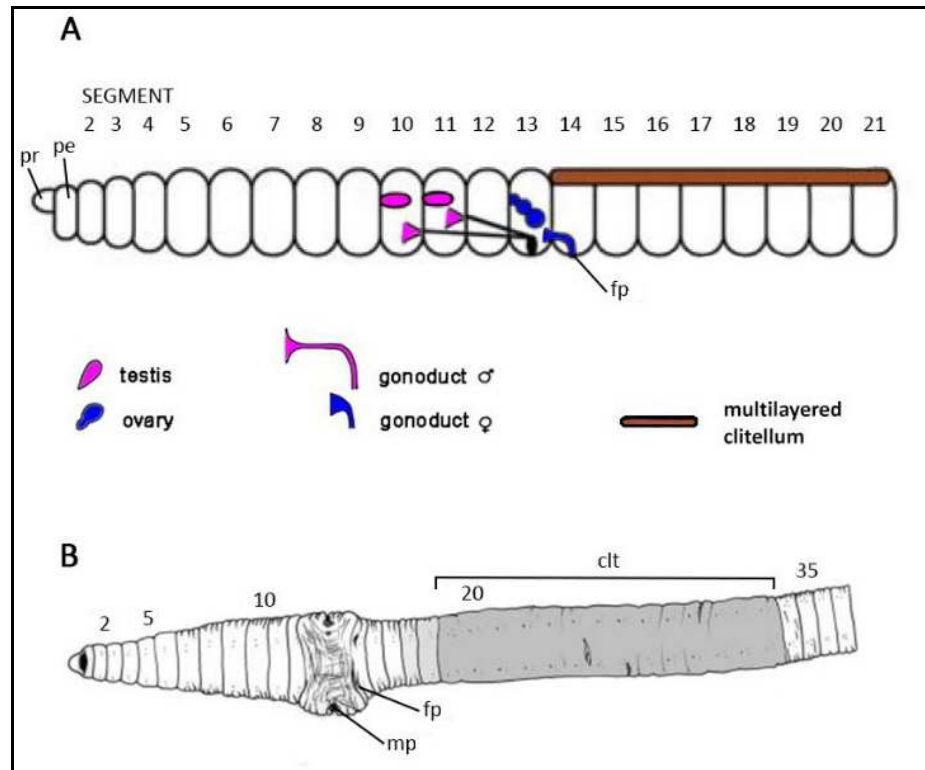


Figure 5. Criodrilidae. **A.** schematic drawing of reproductive organs. **B.** ventral view (anterior) of *Criodrilus lacuum* Hoffmeister, 1845: **C.** spermathecal chaeta. **D.** chaetal bundle. **fp** = female pore, **sch** = spermathecal chaeta, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **scc** = simple crochet chaeta (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006 and Thorp & Covich, 2019, used with permission).

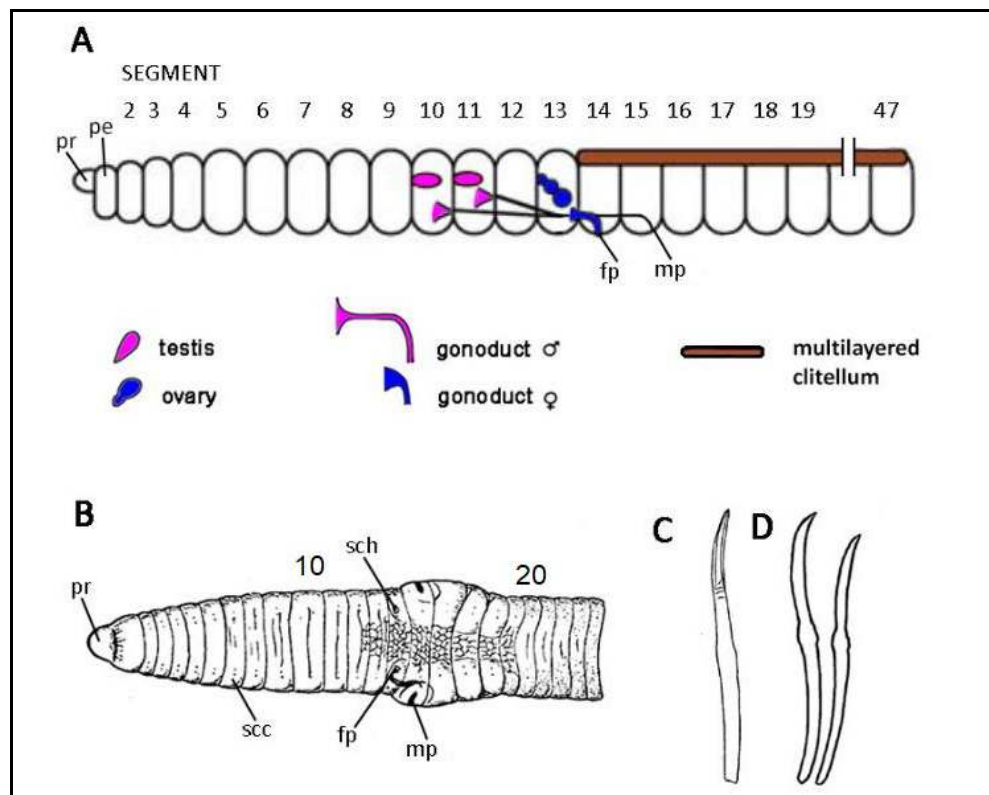


Figure 6. Diporodrilidae. Lateral view of *Diporodrilus pilosus* Bouché, 1972: **cd** = coelomic pore, **clt** = clitellum, **fp** = female pore, **gt** = genital tumescence, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **sp** = spermathecal pore, **tp** = tubercula pubertatis (modified from Bouché, 1972).

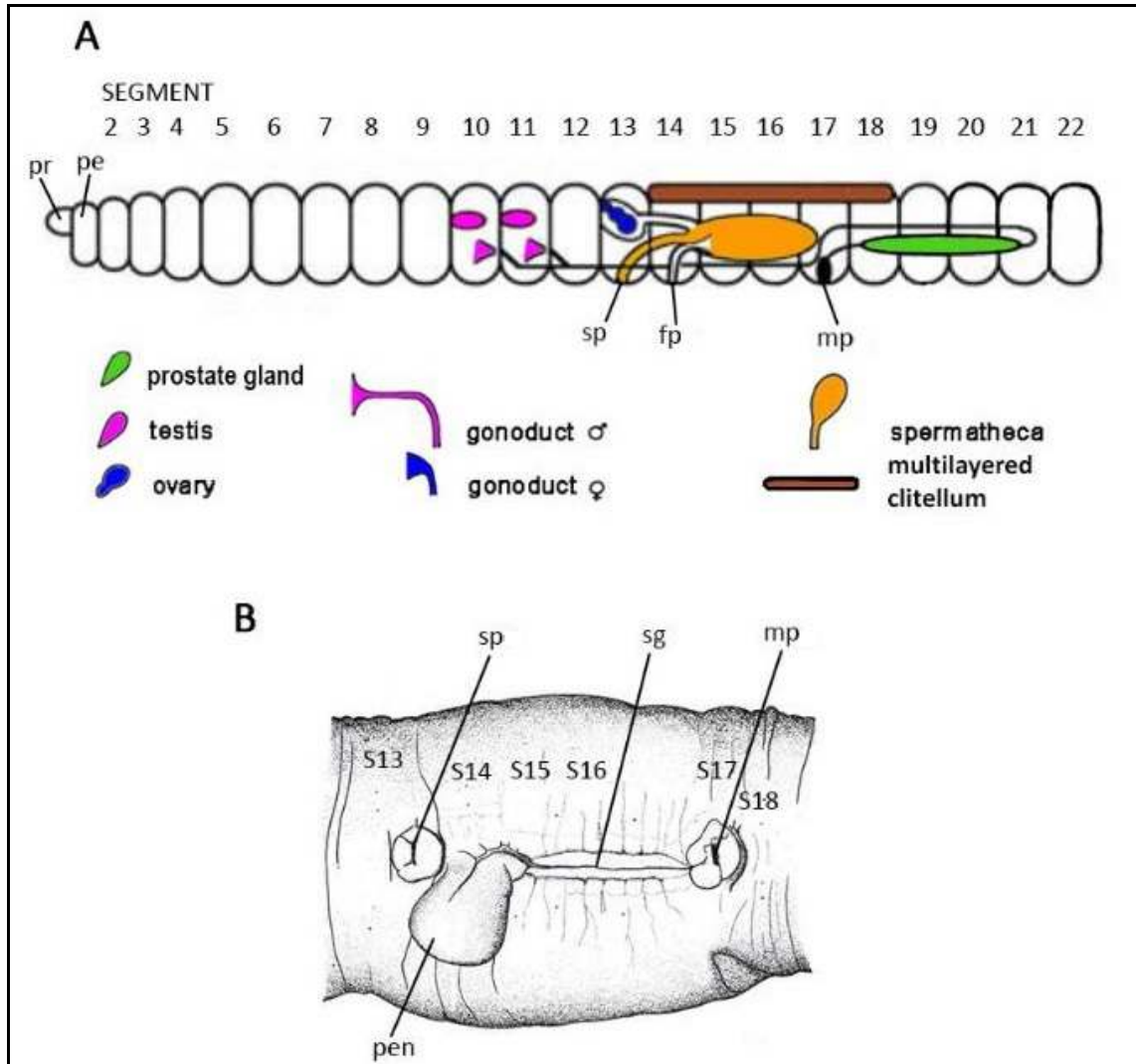
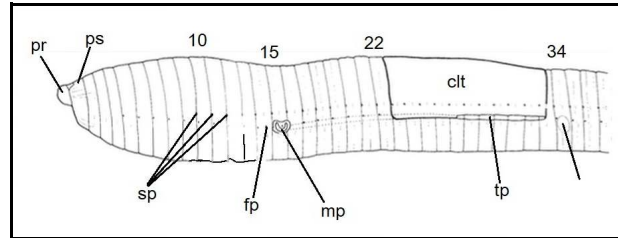


Figure 7. Eudrilidae. **A.** schematic drawing of reproductive organs. **B.** ventral view of *Stuhlmannia variabilis* Michaelsen, 1890 showing seminal groove. **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pen** = penis, **pr** = prostomium, **s** = segment number, **sg** = seminal groove, **sp** = spermathecal pore (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

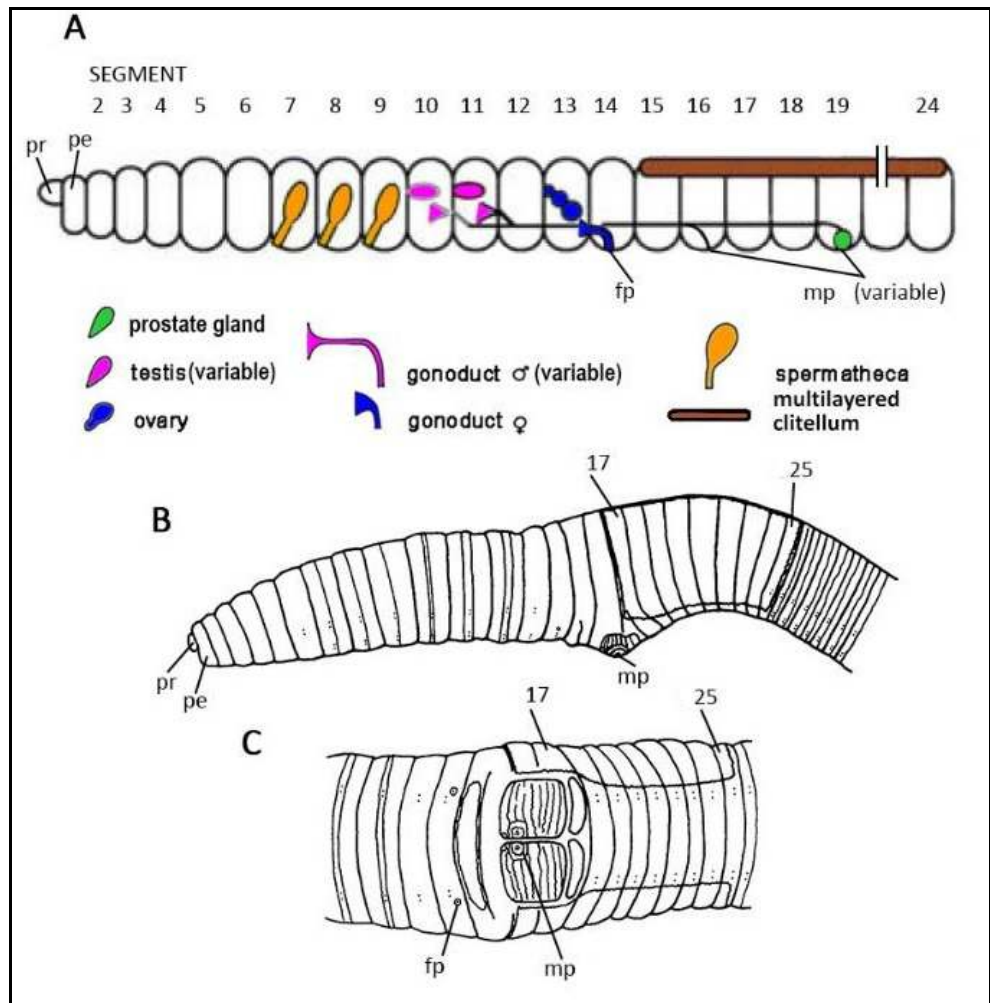


Figure 8. Glossoscolecidae. **A.** schematic drawing of reproductive organs. **B.** Lateral view of *Glossoscolex lutocolus* Bartz and James, 2012. **C.** Ventral view of *G. lutocolus*. fp = female pore, mp = male pore, pe = peristomium, pr = prostomium (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, and Bartz *et al.*, 2012, used with permission).

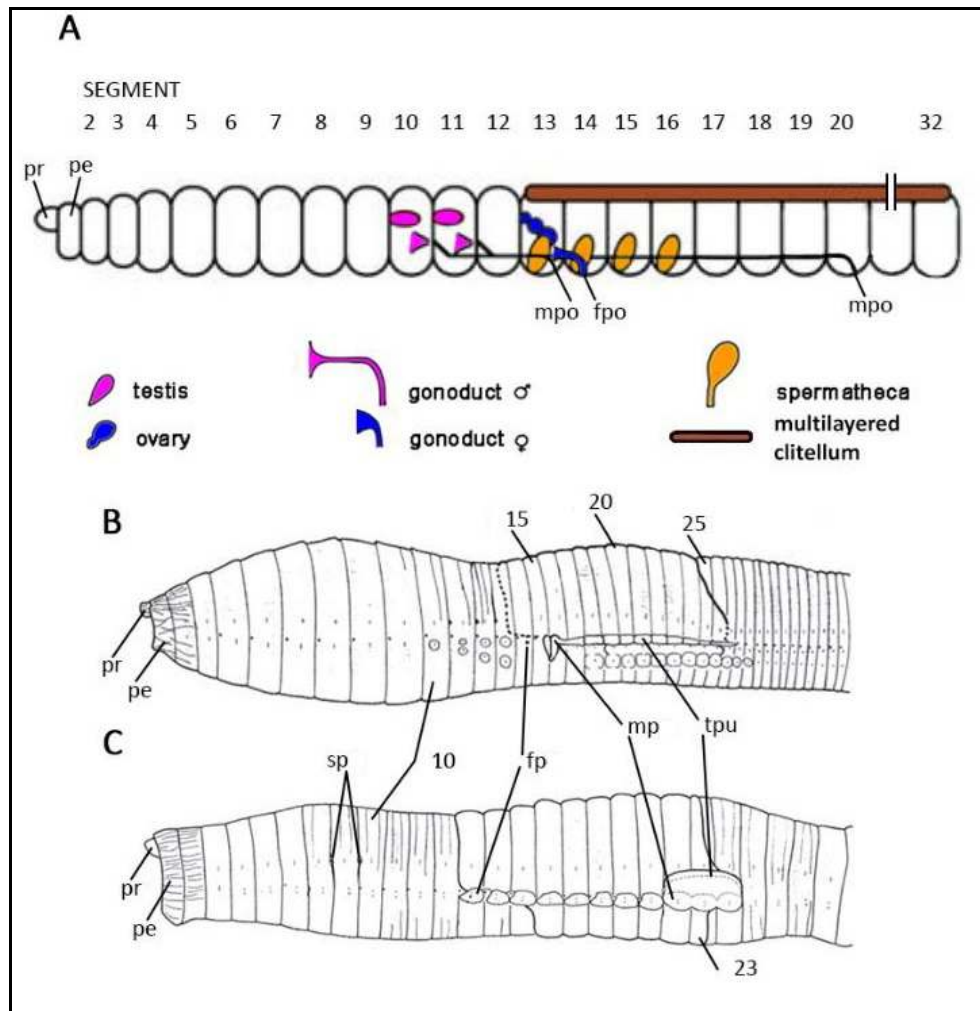


Figure 9. Hormogastridae. **A.** schematic drawing of reproductive organs. **B.** anterior view of genital field in *Hormogaster redii insularis* Bouché, 1970. **C.** anterior view of genital field in *Ailoscolex lactospumousus* Bouché, 1969. **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **sp** = spermathecal pore. **tpu** = tubercula pubertatus (from Gladsy *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

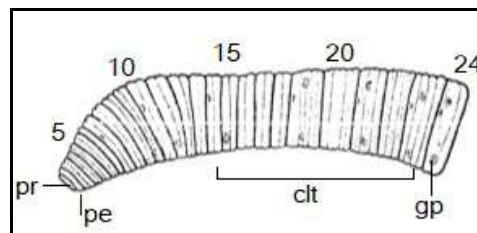


Figure 10. Kazimieridae. *Kazimierzus pearsonianus* (Pickford, 1975): anterior end of Holotype, showing details of annulation and position of nephridial pores, 1/3 *bc* below setal line *C* (modified from Pickford, 1975).

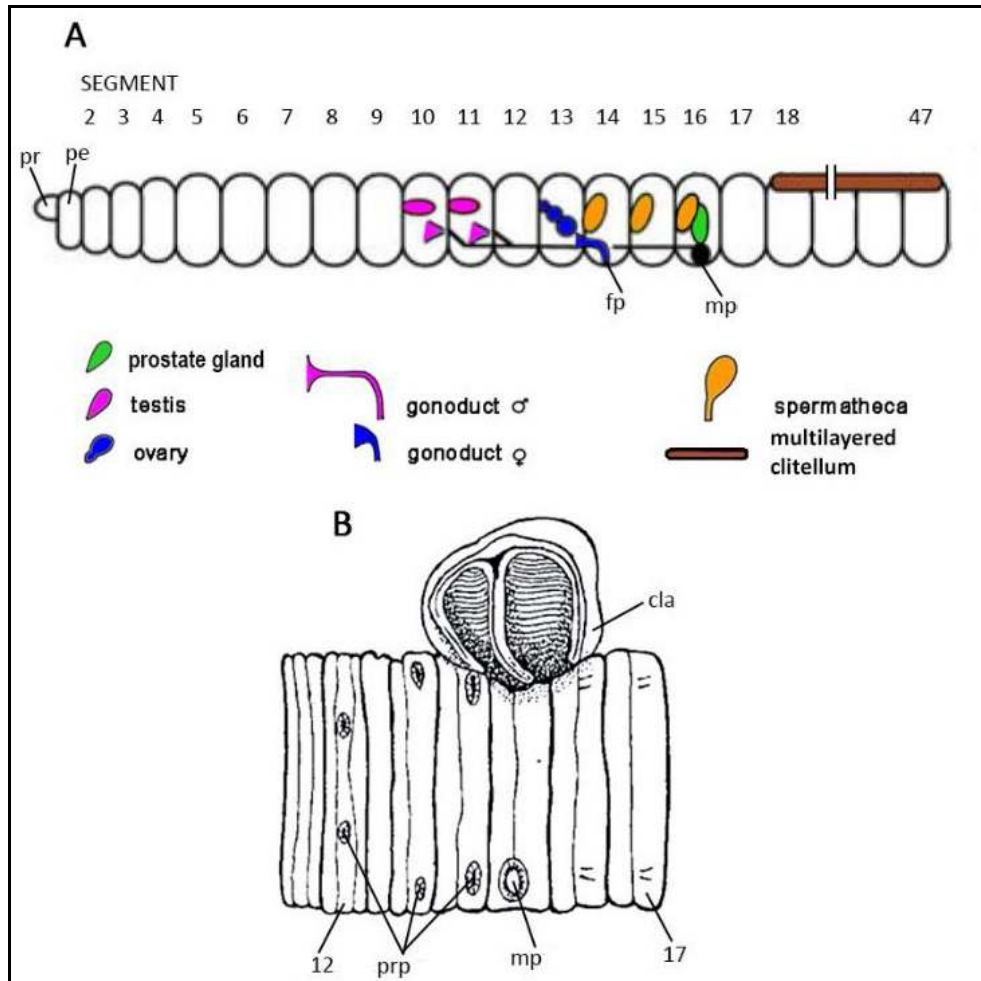


Figure 11. Kynotidae. **A.** schematic drawing of reproductive organs. **B.** Ventral view of segments 13–16 of *Kynotus cingulatus* Benham, 1896, showing 3 pairs of prostatic pores and a 4th that discharges at the male pore (clasper pore) **cla** = clasper, **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **prp** = prostatic pores (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

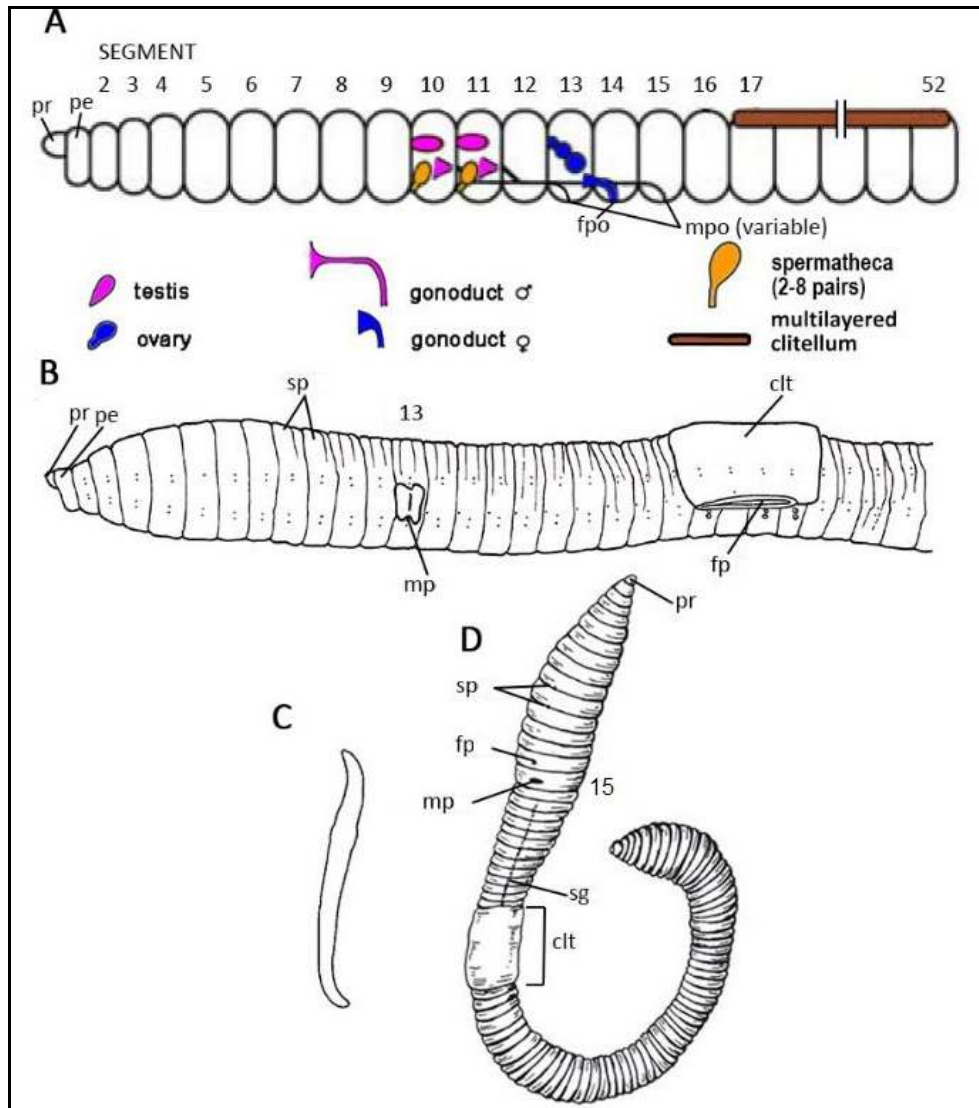


Figure 12. Lumbricidae. **A.** schematic drawing of reproductive organs. **B.** lateral view of *Eiseniella tetraedra* (Savigny, 1826). **C.** chaeta Greek (seta Latin) **D.** External features of *Lumbricus terrestris* Linnaeus, 1758 showing genital pores, seminal groove and clitellum. **clt** = clitellum, **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **sg** = seminal groove, **sp** = spermathecal pore (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, Martin & Boughrous, 2012, and Timm, 2009, used with permission).

Figure 13.

Lutodrilidae. **A.** schematic drawing of reproductive organs. **B.** anterior ventral view of *Lutodrilus multivesiculatus* McMahan, 1979 showing genital region and alae (wing). **ala** = alae, **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prosomium, **spm.** = spermatophore (from Gladsy *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

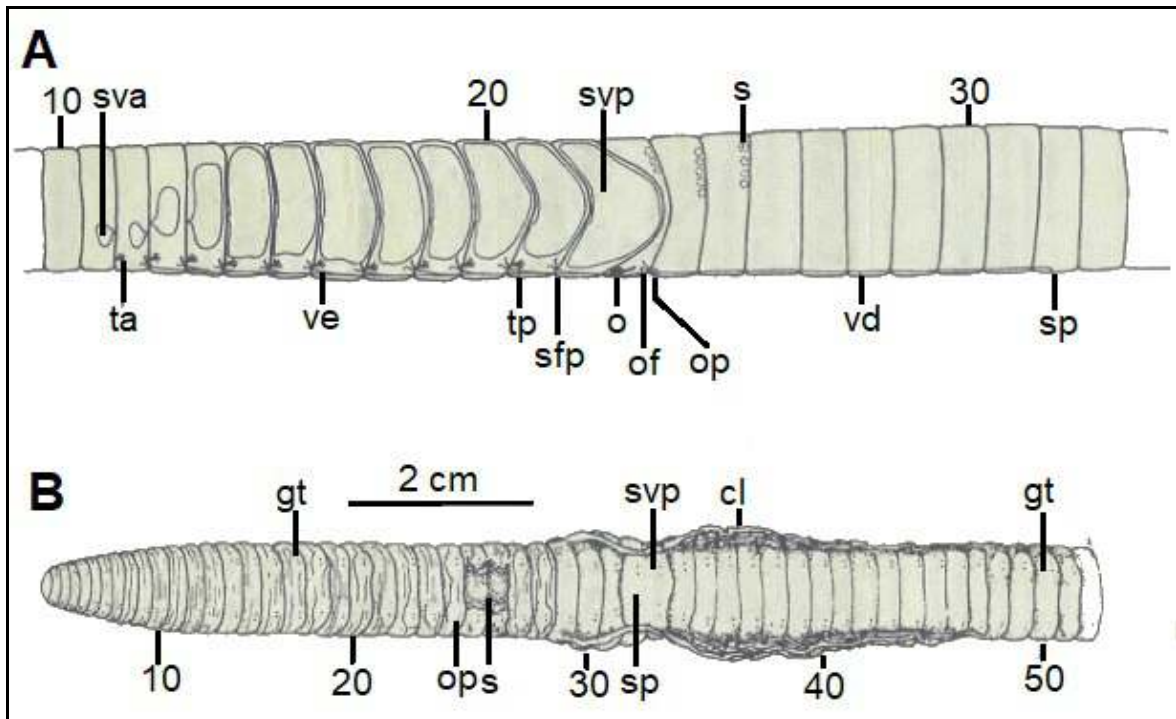
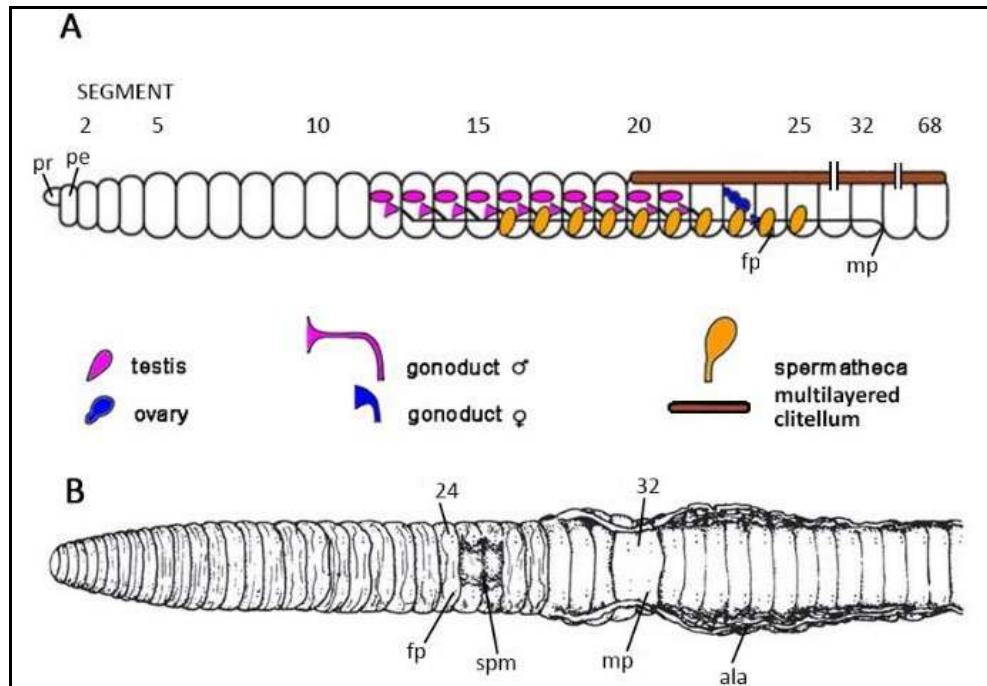


Fig. 13a. *Lutodrilus multivesiculatus* McMahan, 1979. **A.** Diagrammatic longitudinal section of genital region, not drawn to scale, **o**, ovary; **of**, oviducal funnel; **op**, oviducal pore; **s**, spermatheca (spermathecae illustrated in only 3 intersegmentals); **sfp**, posteriormost spermiducal funnel; **sp**, spermiducal pore; **sva**, anteriormost seminal vesicle; **svp**, posteriormost seminal vesicle; **ta**, anteriormost testis; **tp**, posteriormost testis; **vd**, vas deferens; **ve**, vas efferens. **B.** Anterior end of clitellate specimen of *Lutodrilus multivesiculatus* McMahan, 1979, ventral view, **cl**, clitellum; **gt**, genital tumescence; **mt**, male tumescence; **ops**, location of oviducal pore; **s**, spermatophore; **spm**, location of spermiducal pore (from McMahan, 1979).

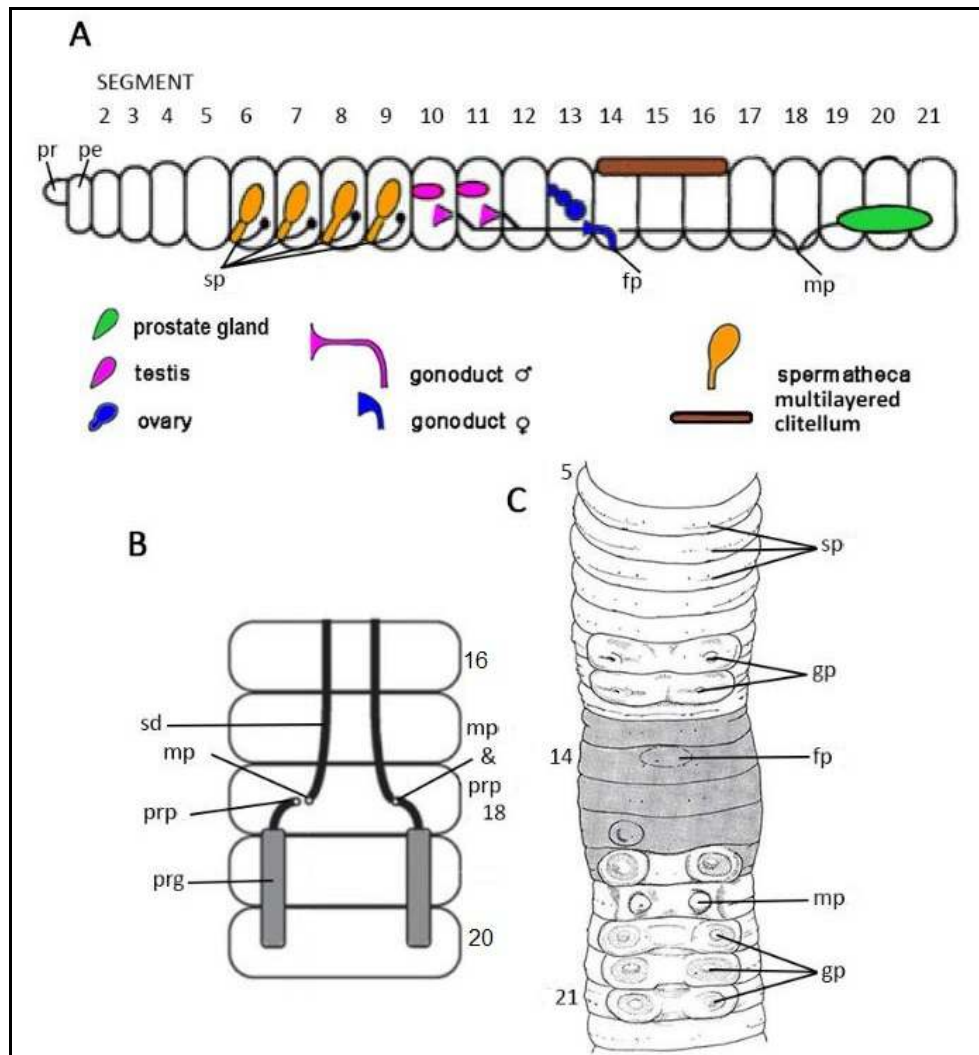


Figure 14. Megascolecidae. **A.** schematic drawing of reproductive organs. **B.** Pore arrangement. **C.** Genital markings in *Spenceriella penolaensis* Jamieson, 1974. **fp** = female pore, **gp** = genital papilla, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **prp** = prostatic pore, **prg** = prostate gland, **sd** = sperm duct, **sp** = spermathecal pore (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

Figure 15. Microchaetidae. **A.** schematic drawing of reproductive organs. **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

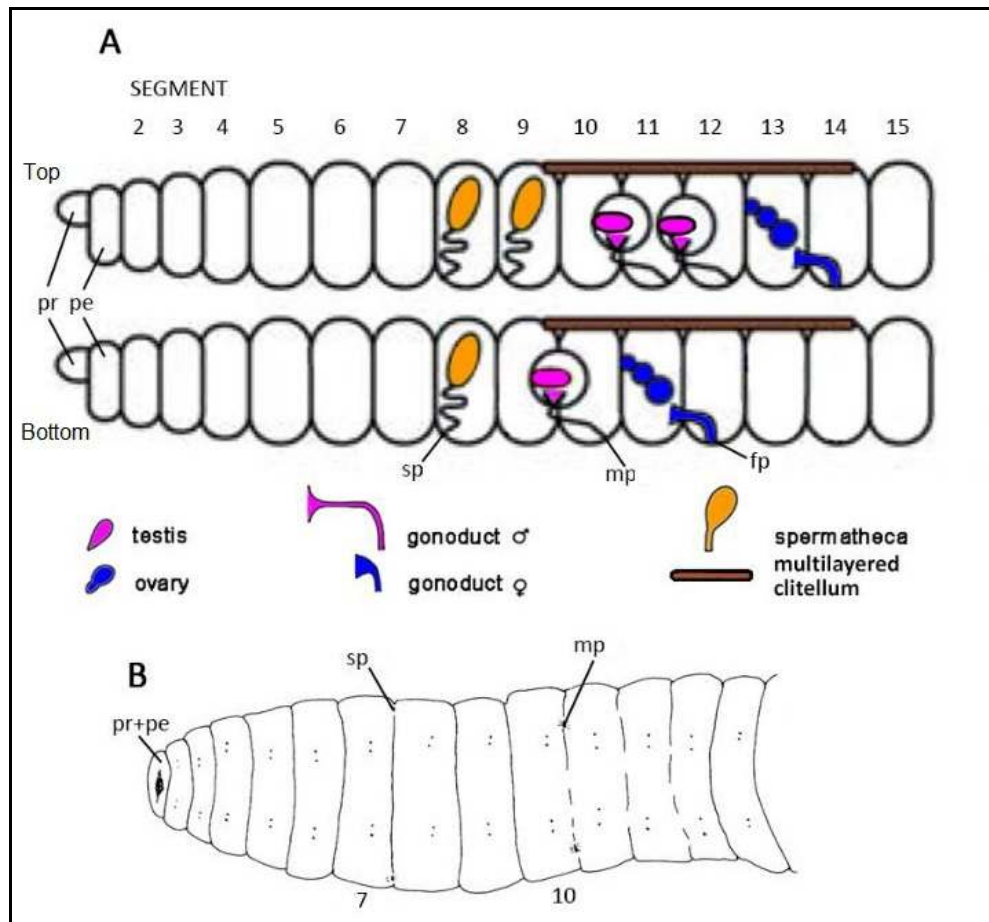
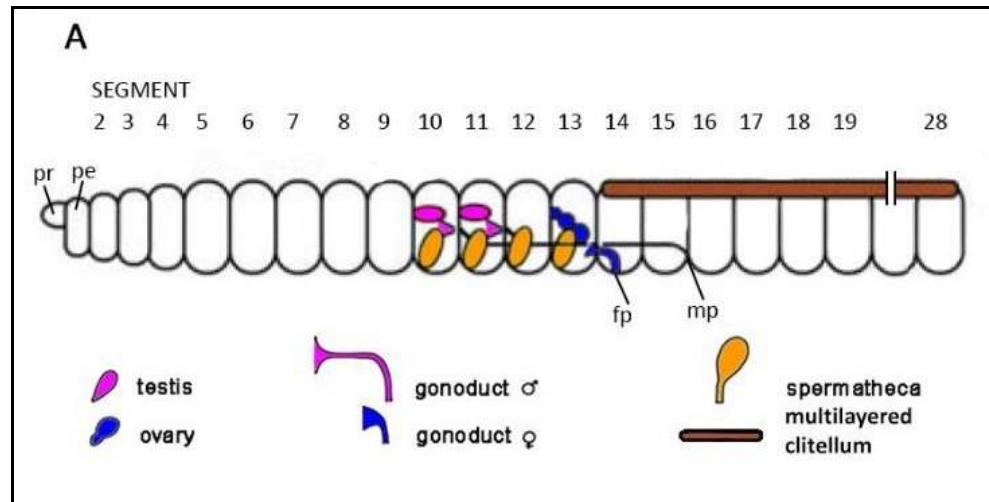
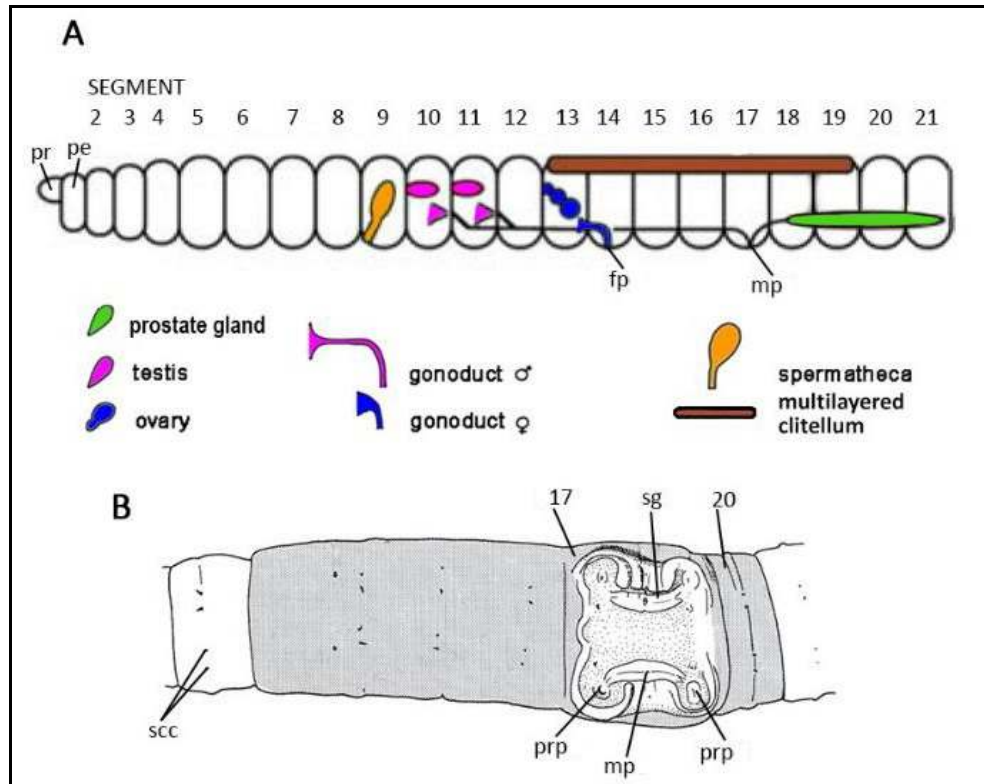


Figure 16. Moniligastridae. **A.** schematic drawing of reproductive organs; Top *Desmogaster*, Bottom *Drawida* and *Moniligaster*. **B.** Ventral view of *Drawida polydiverticulata* Narayanan and Julka, 2017. **fp** = female pore, **gp** = genital papilla, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **sp** = spermathecal pore (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, Martínez-Ansemil (1993), Narayanan *et al.* 2017, used with permission).

Figure 17.

Ocneroдрilidae. **A.** schematic drawing of reproductive organs. **B.** ventral view of *Eukerria borellii* (Cognetti, 1900) showing seminal grooves connecting prostate and male pores. **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **scc** = simple crochet chaeta (seta), **sg** = seminal groove, **sp** = spermathecal pore (from Gladsy *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

**Figure 18.** Rhinodrillidae.

A. anterior and lateral view of *Pontoscolex corethrurus* (Müller, 1856). **B.** posterior region showing quincunx setael arrangement (outlined in red). **C.** ventral view of clitellar region in *Pontoscolex bora*. **D.** common chaeta (seta). **E.** genital chaeta (seta). **ch** = chaeta, **clt** = clitellum, **tp** = tubercula pubertatis (from Gladsy *et al.*, 2025, additionally Feijoo & Celis, 2012 used with permission).

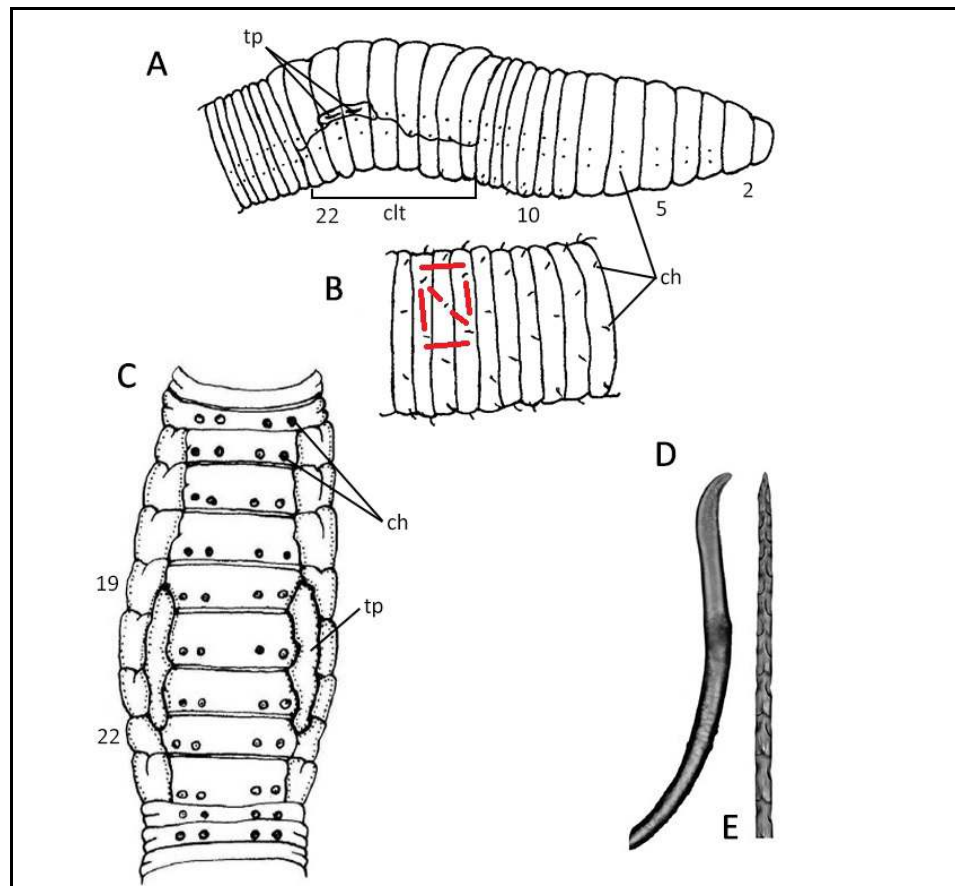


Figure 19. Sparganophilidae. **A.** schematic drawing of reproductive organs. **B.** anterior ventral view of genital region of *Sparganophilus tamesis* Benham, 1892. **clt** = clitellum, **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **tp** = tubercula pubertatis (from Gladsy *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

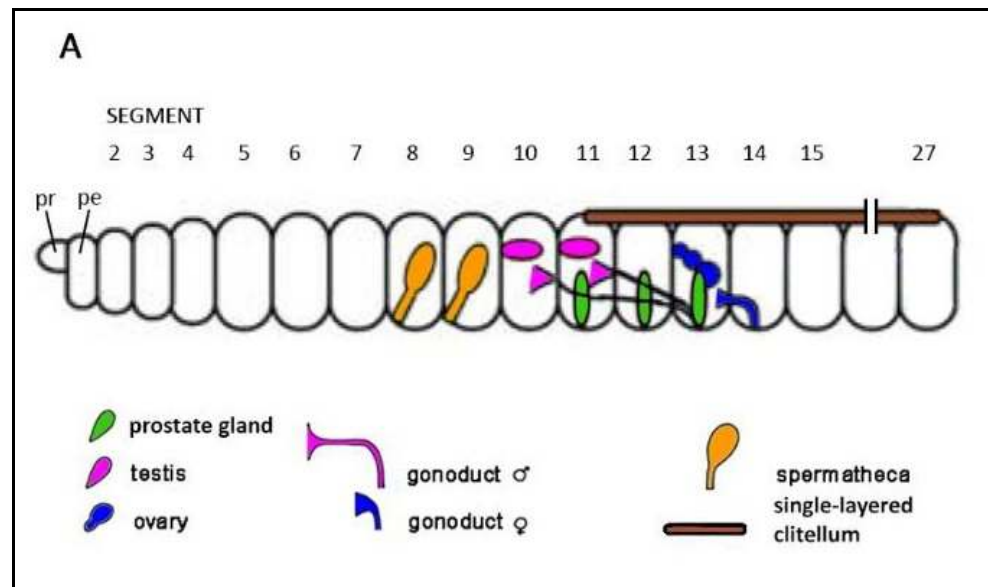
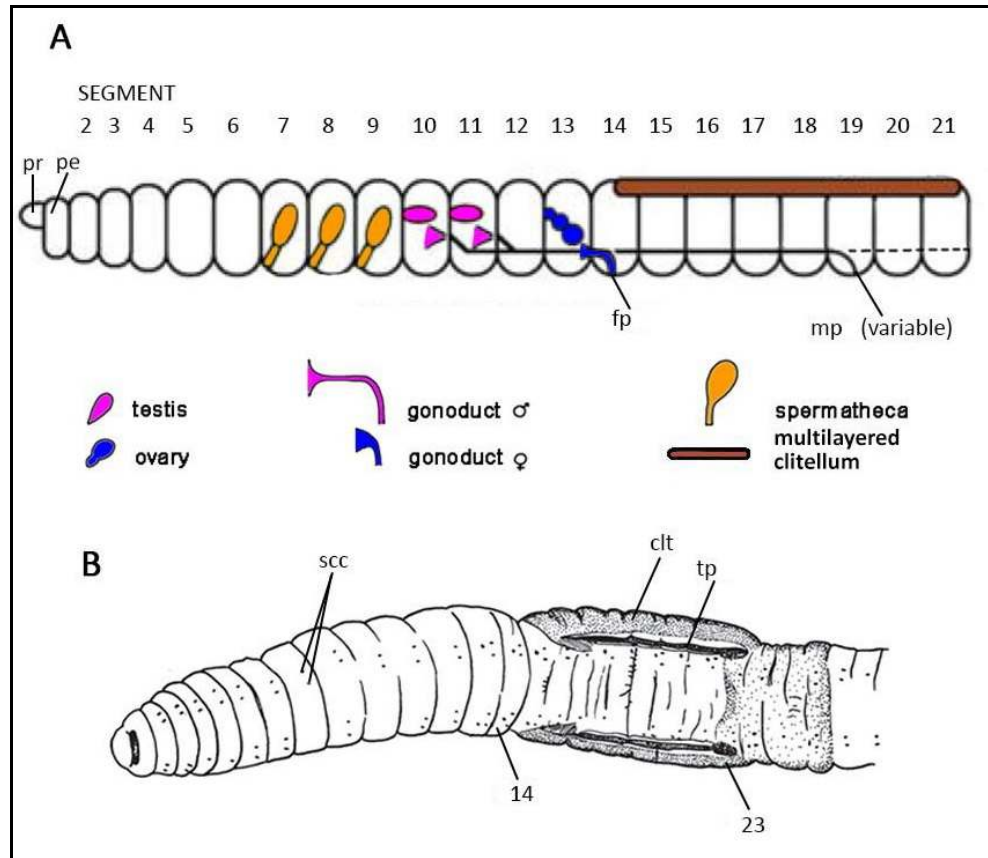


Figure 20. Syngenodrilidae. **A.** schematic drawing of reproductive organs. **fp** = female pore, **mp** = male pore, **pe** = peristomium, **pr** = prostomium (from Gladsy *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

Figure 21. Tiguassidae. **A.** schematic drawing of reproductive organs. **B.** Anterior region of *Tiguassu reginae* Righi, Ayres and Bittencourt, 1978 showing proboscis-like prostomium (**pr**), **pe** = peristomium, **fp** = female pore, **mp** = male pore (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, used with permission).

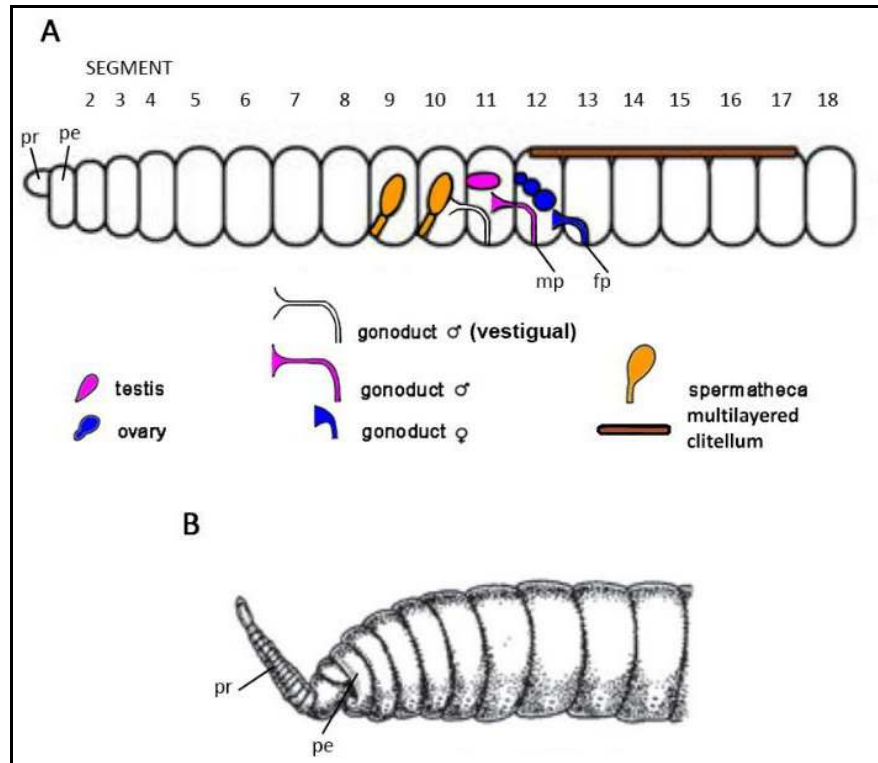
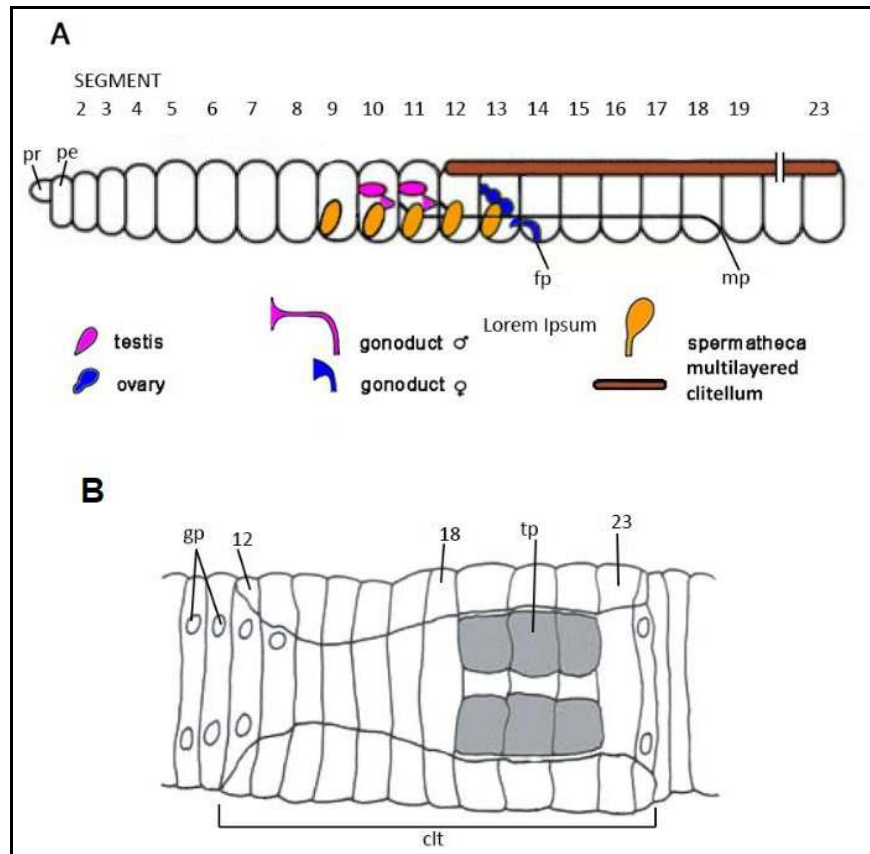


Figure 22. Tritogeniidae. **A.** schematic drawing of reproductive organs. **B.** Genital markings in *Michalkus initus* Plisko, 1996. **clt** = clitellum, **fp** = female pore, **gp** = genital papilla, **mp** = male pore, **pe** = peristomium, **pr** = prostomium, **tp** = tubercula pubertatis (from Gladys *et al.*, 2025, additionally Jamieson & Ferraguti, 2006, and Plisko, 2013, used with permission).



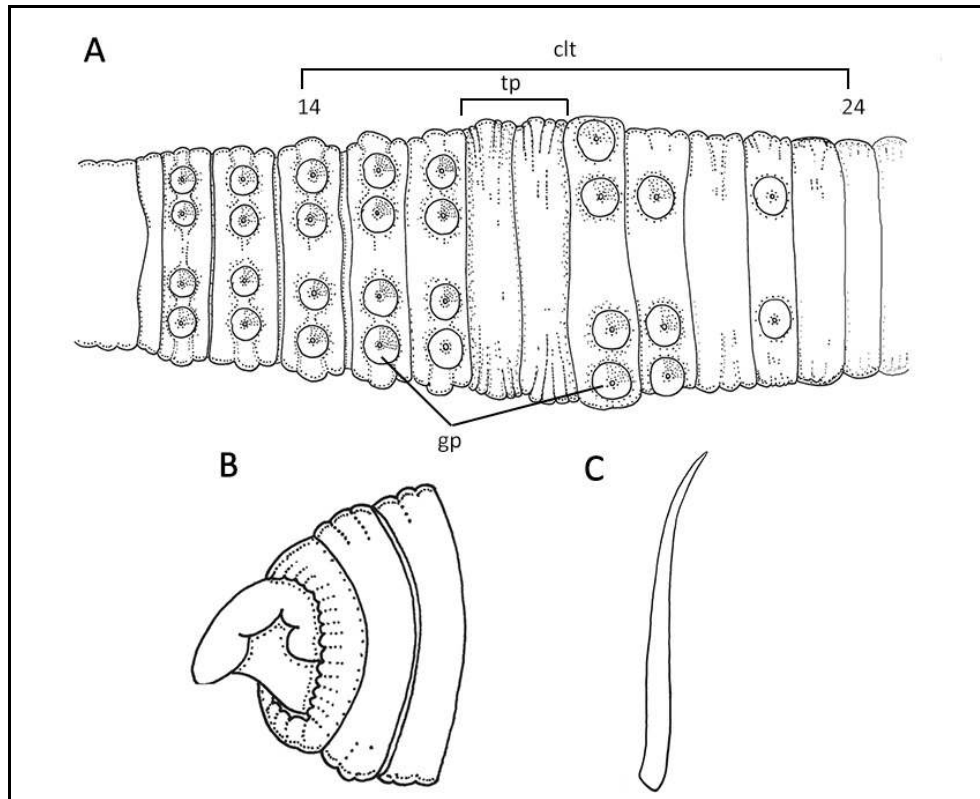


Figure 23. Tumakidae. **A.** midbody ventral view of *Tumak amari* Celis and Rengel, 2015, showing clitellum and genital field. **B.** pygidium. **C.** crotchet chaeta (seta). **clt** = clitellum, **gp** = genital papilla, **tp** = tubercula pubertatis (from Gladsy *et al.*, 2025, additionally Celis & Rengel, 2015, used with permission).

Web Site for the Journal *Megadrilologica*:

<https://www.inhs.illinois.edu/people/mjwetzels/megadrilologica/>

Web Site for *Nomenclatura Oligochaetologica – Editio Secunda*

A catalogue of names, descriptions, and type specimens of the Oligochaeta:

<https://www.inhs.illinois.edu/people/mjwetzels/nomenoligo/>