

The Earthworms (Lumbricidae, Megascolecidae and Sparganophilidae) in Canada

John Warren Reynolds



Canadian Food
Inspection Agency

Agence canadienne
d'inspection des aliments

Canada

The Earthworms (Lumbricidae, Megascolecidae and Sparganophilidae) in Canada

John Warren Reynolds



Canadian Food
Inspection Agency

Agence canadienne
d'inspection des aliments

Canada

© 2022 His Majesty the King in Right of Canada (Canadian Food Inspection Agency), all rights reserved. Use without permission is prohibited.

CFIA P1045E-22

Catalogue No.: A104-252/2022E

ISBN: 978-0-660-44874-9

Cette publication est aussi disponible en français.

Front cover: *Eisenia fetida* in soil.

Back cover: earthworm site for *Arctiostrotus fontinalis* in the Yukon.

Contact information:

Martin Damus, M.Sc.
Senior Risk Assessor (entomology)
Plant Health Risk Assessment Unit
Canadian Food Inspection Agency/Government of Canada
Telephone: 343-550-6418
Fax: 613-773-5391
martin.damus@inspection.gc.ca

Address:
1400 Merivale Road
Ottawa, ON K1A 0Y9

Contents

Preface i

Introduction 1

General biology 1

- General activity 2
- Parasites and predators 2
- Environmental requirements and the effects of pesticides 3

Methods of study 5

- Sampling techniques 5
- Fixation and preservation of specimens 7
- Transport of live specimens 7
- Storage of specimens 7
- Permancy of collections 8
- Rearing and culturing earthworms 8
- Figure coding 9

General morphology 9

- External structures 9
- Internal structure 10

Scientific and common names 12

Glossary 13

Identification of the earthworms of Canada 25

Key to sexually mature earthworms found in Canada 26

Systematic section 28

- Family LUMBRICIDAE Claus, 1880 29
 - Genus *Allolobophora* Eisen, 1873 31
 - Allolobophora chlorotica* (Savigny, 1826) 31
 - Genus *Aporrectodea* Örley, 1885 34
 - Aporrectodea bowcrowensis* Reynolds and Clapperton, 1996 35
 - Aporrectodea icterica* (Savigny, 1826) 37
 - Aporrectodea limicola* Michaelsen, 1890 39
 - Aporrectodea longa* (Ude, 1885) 41
 - Aporrectodea rosea* (Savigny, 1826) 44
 - Aporrectodea trapezoides* (Dugès, 1828) 47
 - Aporrectodea tuberculata* (Eisen, 1874) 50
 - Aporrectodea turgida* (Eisen, 1874) 53
 - Genus *Bimastos* Moore, 1893 56
 - Bimastos beddardi* Michaelsen, 1894 57
 - Bimastos lawrenceae* Fender, 1994 59

- Bimastos parvus* (Eisen, 1874) 62
- Genus *Dendrobaena* Eisen, 1873 64
 - Dendrobaena attemsi* Michaelsen, 1902 64
 - Dendrobaena lusitana* Graff, 1957 67
 - Dendrobaena octaedra* (Savigny, 1826) 69
- Genus *Dendrodrilus* Omodeo, 1956 72
 - Dendrodrilus rubidus* (Savigny, 1826) 73
- Genus *Eisenia* Malm, 1877 76
 - Eisenia fetida* (Savigny, 1826) 77
 - Eisenia hortensis* Michaelsen, 1890 80
- Genus *Eiseniella* Michaelsen, 1900 82
 - Eiseniella tetraedra* (Savigny, 1826) 83
- Genus *Lumbricus* Linnaeus, 1758 86
 - Lumbricus castaneus* (Savigny, 1826) 87
 - Lumbricus festivus* (Savigny, 1826) 89
 - Lumbricus rubellus* Hoffmeister, 1843 91
 - Lumbricus terrestris* Linnaeus, 1758 94
- Genus *Octolasion* Örley, 1885 98
 - Octolasion cyaneum* (Savigny, 1826) 99
 - Octolasion tyrtaeum* (Savigny, 1826) 102
- Genus *Satchellius* Gates, 1975 105
 - Satchellius mammalis* (Savigny, 1826) 106

Family MEGASCOLECIDAE Rosa, 1891 109

- Genus *Amyntas* Kinberg, 1867 110
 - Amyntas agrestis* (Goto and Hatai, 1899) 110
 - Amyntas hilgendorfi* (Michaelsen, 1892) 114
- Genus *Arctiostrotus* McKey-Fender, 1982 117
 - Arctiostrotus fontinalis* McKey-Fender, 1994 118
 - Arctiostrotus perrieri* (Benham, 1892) 121
 - Arctiostrotus vancouverensis* McKey-Fender, 1994 124
- Genus *Toutellus* Fender and McKey-Fender, 1990 127
 - Toutellus oregonensis* (Smith, 1937) 128

Family SPARGANOPHILIDAE Michaelsen, 1921 131

- Genus *Sparganophilus* Benham, 1892 132
 - Sparganophilus tamesis* Benham, 1892 133

Arctic earthworm migration and climate change 136

Literature cited 139

Acknowledgements 172

About the author 172

Subject index 173

Taxonomic index 173

List of figures 174

Colour plates of earthworm species 176

Preface

This book was written at the request of the Plant Health Risk Assessment Unit of the Canadian Food Inspection Agency in Ottawa, Ontario. It will update and expand *The Earthworms (Lumbricidae and Sparganophilidae) of Ontario* (Royal Ontario Museum) to include all of Canada, which means going from 19 to 33 species, both native and introduced taxa.

The book is also modelled in part on the similar CFIA-published book: *Identifying land snails and slugs in Canada* by the Canadian Food Inspection Agency, Ottawa using normally employed oligochaete style, nomenclature and conventions for similar texts.

It has often been said, "you can't teach an old dog new tricks," (Ammer, 2003). Those who may have read some of my previous books and papers over the past 50+ years will notice changes in some nomenclatural reference herein.

In my early career, I used to think that all earthworm activities were positive, but in recent decades the spread of invasive species at the expense of native earthworms has become evident. Some of this is due to climate change permitting native and more tropical species to extend their range northward and in some cases into Canada. Since earthworms have no skeleton or bones, fossil records are virtually nil. The last glacial period removed any trace of significant record of what may have been in the pre-glaciation period.

I have often thought of myself as the antithesis of Johnny Appleseed, whose popular image is of a man crossing the continent spreading apple seeds randomly everywhere he went (Means, 2011). For over 50 years I have travelled the ten provinces and the Yukon, plus 45 of the 49 continental United States, and various foreign countries, collecting specimens at every opportunity.

This book describes and illustrates 33 species of terrestrial earthworms that are known to be introduced and/or are native species: 23 species are introduced European taxa, 2 species are Oriental introduced taxa, and 8 are native to Canada. Greenhouse aliens are not included in the species accounts, but are mentioned at the beginning of the Systematics Section (p. 31). There have been several species over the years which have been intercepted by regulatory agencies and sent to me for identification, but not released into the country, e.g. *Amyntas corticis* (= *A. diffringens*), *Dendrobaena veneta*, *Dichogaster bolau*i, *Microscolex dubius* and *Perioynx excavatus*.

A key is included for native and introduced species of terrestrial earthworms. A diagnosis of the species is accompanied by illustrations of the species. An illustrated glossary is included for all terms mentioned in this book.

Much has been published in recent years concerning DNA sequencing in the identification of earthworms as well as other animals and plants. Even though this will be increasingly important in the future, there will still be a need to have taxonomists who are able to identify and describe new and established species. Hopefully, this book will be the inspiration and guide for those who will carry on this science.

Introduction

Earthworms (Annelida, Clitellata, Oligochaeta) are familiar to almost everyone. As one of the most popular forms of live bait for fishing (Harman, 1955; Miesen, 2005), earthworms comprise most of the early northern records in North America. Gardeners hold them in high esteem as nature's ploughmen (Darwin, 1881). Folklore and scientific accounts describe their medicinal uses (Reynolds and Reynolds, 1972, 1979), and soil inhabiting vertebrates (moles, voles, *etc.*) store them as a source of food (Evans, 1948; Skoczeń, 1970; Salmon *et al.*, 2006). They are also the primary food of several species of birds (Reynolds *et al.*, 1977), many reptiles (McAlpine *et al.*, 2019) and amphibians (Reynolds, 1980), as well as some species in other major groups of organisms, such as insects or flat worms (Dindal, 1970). The role of some species in organic matter decomposition and mineral cycling may be important (Lemtiri *et al.*, 2014); and a great deal has been written concerning earthworm farming (Ernst, 1995; Munroe, 2008; Steckley, 2020). Currently their impact on the litter layer and associated declines in biodiversity have attracted attention. Biology students the world over study their anatomy (mainly *Lumbricus terrestris*) in great detail (Reynolds and Reynolds, 2004a). Although they are a well known group in many respects, their biology, ecology and distribution is still poorly understood (Reynolds, 1977a). Many of the world's thousands of megadriles (= terrestrial oligochaetes) species are known only from a limited series of one or a few specimens (Reynolds and Wetzel, 2021).

Almost 45 years ago, I published the Earthworms of Ontario (Reynolds, 1977a) and this book expands and updates that publication. Following that format, this book also has been designed to introduce the non-specialist to the taxonomy, nomenclature, morphology, distribution, and general biology and ecology of earthworms in Canada and neighbouring areas. The identity, distribution, and habitats of these animals have been surveyed for a variety of habitats in the provinces and territories of Canada. An illustrated glossary is included, together with a new key to the identification of the earthworms of Canada and the northern tier of the states of the United States. French and English common names are included for each species.

The first records of earthworms from each province and territory of Canada and the continental United States can be found in Reynolds (2018). Up to date checklists of earthworms in each province, territory and American state were summarized in Reynolds (2019).

The technical terms and conventions necessary for earthworm discussion and identification will be found in the glossary (pp. 13–25).

General biology

There can be little doubt that earthworms are the best known of all soil animals. It is common knowledge that they have a beneficial effect on the structure and properties of the soil and that they influence the decomposition processes in organic materials. However, it cannot be denied that much work purporting to demonstrate these aspects has been far from rigorous. In fact, far less is known than is generally believed, and most work is applicable only to Europe. The problem is compounded by the fact that many of the hundreds of described species are known only from a morphological study of a few individuals. Fortunately, nearly all of the species present in Canada and the neighbouring areas are the widely distributed European species that have received the greatest attention. The exceptions are the seven native species of the 33 species reported from Canada. Major limitations to the interpretation of the literature have been old nomenclatural and taxonomic designations (Reynolds and Wetzel, 2021).

Sources of information on various biological attributes for species found in Canada and the surrounding region are Evans and Guild (1948), Bouché (1972), Gates (1972a), Reynolds (1973b), Reynolds *et al.* (1974), Edwards (2004), and Rogers and Thorp (2019). Recent reviews of earthworm activity will be found in Kevan (1962), Wallwork (1970), and Hendrix (1995).

General activity

The main activities of earthworms that affect the soil involve the ingestion of soil and the mixing of the main soil ingredients of clay, lime, and humus; the production of castings of a fine crumb structure which are ejected on the soil surface by some species; the construction of burrows that enhance aeration, drainage, and root penetration; and the production of a tilth that makes suitable habitats for the smaller soil fauna and micro-organisms. It should be remembered, however, that not all Lumbricidae work in the same manner. Some, for example, burrow deeply whereas others do not.

The influence of earthworms on the translocation of soil material may be quite considerable. There have been abundance estimates as high as three million worms per acre and their role in soil fertility is very important. Studying forms that eject casts to the surface, Darwin (1881) estimated that between 7½ and 18 tons of soil per acre (0.40 ha) per year (about 3 cm per 10 years) can be moved, and the burial of many Roman ruins in Europe has been attributed to the activity of earthworms (Atkinson, 1957).

Earthworms are omnivorous and can utilize many materials in the soil as food, including plant remains, and occasionally animal remains. Lumbricids can withstand considerable starvation and, in *L. terrestris* at least, a water loss of up to 70 of the body weight. Some species can withstand total immersion in water for many weeks, though normally they avoid waterlogged soils.

The reproductive cycle of many Lumbricidae is quite straightforward. Although hermaphroditic, they possess a mechanism to prevent self-fertilization. During copulation the two worms lie side by side with their anterior ends overlapping. A mucous sheath envelops the worms and holds them tightly together. Sperm are released from the testes and flow down the seminal groove in the side of each worm to the spermathecae of its partner. Both worms do this at the same time. Some time after copulation has taken place, and after the worms have separated, the egg cocoons are formed. A mucous tube or belt is secreted around the clitellum. The worm then wriggles out of this belt and as the belt passes the female apertures the eggs are deposited in it. Spermatozoa to fertilize the eggs are deposited as it passes the spermathecal openings. On release, the ends of the belt close over to form a cocoon in which the young worms develop.

Cross-fertilization does not occur in all earthworms, however, despite assertions to the contrary in many textbooks. In some species there is parthenogenesis, with concomitant reduction of the male apparatus. Pseudogamy, in which sperm play no part in the development of the egg other than as a stimulant, also may occur. Thus, even if copulation has been observed, the exchange of sperm alone is not evidence for amphimixis. The whole question of reproduction in earthworms has been reviewed by Reynolds (1974a).

Parasites and predators

Some earthworms (*Allolobophora chlorotica* and *Aporrectodea rosea*) are parasitized by *Pollenia rudis* (Fabr.), a calliphorid fly known as the cluster fly, which may lay its eggs directly in the earthworm or merely on the surface of the soil (Thomson and Davies, 1973a, 1973b) and more recently (Reynolds *et al.*, 2020b). Cluster flies are the most common and annoying of the flies that overwinter in buildings. Other insects such as ants and beetles are predaceous on earthworms (McLeod, 1954). Furthermore, some earthworms may act as intermediate hosts of parasitic worms that affect domestic animals (Kevan, 1962). Reports of mites (Acari) parasitizing earthworm cocoons and adults (*Allolobophora chlorotica* and *Eiseniella tetraedra*) were made by Stone and Ogles (1953) and Oliver (1962).

Earthworms are also an important component of the diet of many birds and mammals. In Europe moles may store them as a source of food (Evans, 1948; Skoczen, 1970; Gates, 1972a), usually after biting off four or five of the anterior segments to prevent the worms from escaping (Evans, 1948b). In North America they are eaten by many organisms, including some of economic or recreational importance. According to Liscinsky (1965), for example, the diet of the woodcock (*Scolopax minor* Gmelin), a favourite game bird in eastern North America, is primarily earthworms. From my current surveys, and from gut analyses of woodcock, it appears that in the area bounded by Ontario to Nova Scotia and Minnesota to Maryland, 90% of the earthworms in the diet of these birds are *Aporrectodea tuberculata*, *Dendrobaena octaedra*, *Dendrodrilus rubidus*, and *Lumbricus rubellus*. Snakes, too, may prey

extensively on earthworms. This is true especially of two of our most common species, the red-bellied snake (*Storeria occipitomaculata* Say) and the eastern garter snake (*Thamnophis sirtalis* L.), and perhaps of four or five other species as well (Logier, 1958). This author has examined the gut contents from *Thamnophis butleri* Cope collected in southwestern, Ontario. The earthworms identified in these snakes' stomachs were *Allolobophora chlorotica*, *Aporrectodea tuberculata*, and *Lumbricus terrestris*. According to the author and the late Dr. Stanley W. Gorham (pers. comm.), this was the first valid report of earthworm species identified from snake stomachs in North America. A recent case from New Brunswick where *Thamnophis sirtalis pallidulus* (Maritime Garter Snake) regurgitated ten adult *Aporrectodea turgida* (McAlpine *et al.*, 2019). In January 2021, I received one *Eisenia hortensis* clitellate adult from the stomach of a recently born red-sided garter snake (*Thamnophilus sirtalis*). Salamanders (*Desmognathus fuscus*, *Eurycea bislineata*, *Pseudotriton ruber* and others) have been reported as predators on earthworms (*Sparganophilus* spp.) (Reynolds, 1980; Brunges *et al.*, 2020). An account was presented by Dindal (1970) of a terrestrial turbellarian, *Bipalium adventitium* Hyman, attacking *Dendrodrilus rubidus* and *Lumbricus terrestris*. According to Dindal, this flatworm is a major pest in outdoor earthworm beds.

There was a recent discovery of a gregarine parasite (*Zygozystis* spp.) from earthworm species recorded from North America (Ramadan *et al.*, 2019). These parasites have long been recorded from earthworms (Hesse, 1909; Cognetti, 1923; Segun, 1978; and numerous others). A recent review of parasites, parasitoids and predators of earthworms can be found in Reynolds (2021).

Environmental requirements and the effects of pesticides

Daylight and ultraviolet light are injurious to earthworms unless the intensity is very low. Temperature relations, reviewed by Reynolds (1973a), and Gates (1970), quote interesting accounts of lumbricids studied from the Arctic circle; *Eisenia fetida*, for example, has been found in snow, even though generally associated with warm habitats such as manure piles, and it remains vigorous below 5° C. In Maine *L. terrestris* has been seen copulating while bathed with melt water, and other individuals crawled from under the ice and remained active (Gates, 1970).

The pH tolerance (see glossary) of earthworms varies from species to species (Reynolds, 1973b). Usually they occur in soil with a pH range of about 4.5 to 8.7 and the earthworm density diminishes as the soil acidity increases. Generally speaking, the greatest earthworm densities are found in neutral soils.

The type of soil also may influence the distribution and abundance of the various species. Gates (1961), for example, divides the earthworms of Maine into three groups depending upon whether or not they are geophagous, in that they pass much soil through the intestine; limiphagous (mud-eating) or limicolous (mud-inhabiting); or, finally, litter-feeding, and hence found primarily in organic matter. From his studies in Sweden, Julin (1949) divided the Lumbricidae into four ecological groups. These were hemerophiles, species favoured by human culture; hemerophobes, species averse to culture; hemerodiaphores, species indifferent to the influence of culture; and hemerobionts, species entirely dependent on culture. Julin's classification has never been applied to the North American Lumbricidae, with the exception of a preliminary attempt for the earthworms of Tennessee by Reynolds *et al.* (1974). Regrettably, there are as yet insufficient data to permit an attempt for the Canadian earthworms; this is a topic worthy of further study.

There is another system used to categorize earthworms using their ecology and morphology first described by Gisin (1943) and Delamark-Deboutteville (1951) for Collembola and first introduced for earthworms by Bouché (1970) and later expanded by myself in several papers (Reynolds, 1977d); Reynolds and Misirlioğlu, 2018; Reynolds and Reeves, 2019; Bottinelli *et al.*, 2020, and Reynolds *et al.* 2020).

The terrestrial earthworms based on their location in soil layers are categorized as epigeic, endogeic and anecic earthworms. *Epigeic* (épigée) are smaller to medium sized worms which mainly feed on plant litter and dwell on the soil surface or in litter layers, usually red or pink with a normal tail (Fig. 1, 3). *Endogeic* (endogée) are medium sized worms, soil feeders, which live in horizontal burrows, generally unpigmented with a normal tail (Fig. 1, 2). *Anecic* (anéciq) worms are large size and live in vertical burrows, mainly feeding on plant litter and soil, generally brown in colour with a lanceolate to elliptic tail (Fig. 1, 1). There are two other types that have been used for years – corticole and limicolous. The *corticole* (corticole) species are those which live under the bark of downed trees in the

frass (the sawdust-like material under the bark) between the bark and the treewood (Fig. 1, 4). *Limicolous* (limicoles) species are those which live in very wet habitats, often in saturated soils on stream or river banks, and flood plains, generally unpigmented with no tail (Fig. 1, 5). Many of these species are found in the litter as well. Their habitat usage depends on geographical location and the other earthworm species present. Another term used, *epi-endogeic* (epi-endogée) are species living at the interface between the organic matter layer and the layer located just below. There are other subtypes which can be employed, but these are the main ones. A recent study on the morphological and functional characterization of the burrow systems of six earthworms in different ecotypes was reported by Capowicz *et al.* (2015). Knowing these classifications may be useful to farmers, naturalists and gardeners, as well as students and colleagues. Recently, Singh *et al.* (2020) developed an ecological system based on habitat and food preferences (Table 1):

Table 1. Ecological category, habitat and food preference of earthworms

Ecological category	Subcategory	Habitat	Food preference
Epigeic	Epigeic	Litter	Leaf litter, microbes
	Epi-anecic	Surface soil	Leaf litter and soil
	Epi-endogeic	Interface between organic matter layer and layer located just below	Leaf litter and soil
Anecic	Anecic	Burrows	Leaf litter and soil
Endogeic	Polyhumic	Upper 0–20 cm of soil	Soil with high organic matter
	Mesohumic	Upper 0–20 cm of soil	Soil from 0–10 cm
	Endo-anecic	0–50 cm of soil	Soil from 20–40 cm
	Oligohumic	15–20 cm of soil	Soil from 0–10 cm

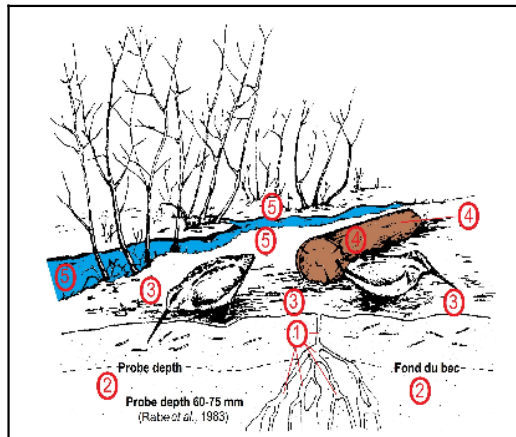


Fig. 1. The location of the earthworm ecological types: 1 = anecic, 2 = endogeic, 3 = epigeic, 4 = corticole; and 5 = limicolous (modified from Reynolds, 1977d).

The application of pesticides to control soil pests, or the earthworm parasites mentioned above, may also kill the earthworms. This devastating effect on earthworm populations has frequently occurred after the application of orchard sprays. Fruit growers have long held earthworms in high esteem for their help in controlling the disease apple scab which is produced by the fungus *Venturia inaequalis* (Cooke) Winter. This disease overwinters on the fallen leaves in the orchard. One method of cultural control is to burn the fallen leaves and twigs in the fall of the year. An equally effective and less costly method is to introduce earthworms (preferably *Lumbricus terrestris*), which will pull the fallen leaves into the soil for food and eventual decomposition. According to the findings of Reynolds and Jordan (1975), for example, earthworms have a distinct preference for apple leaves over those of maple. Once the leaves are beneath the soil surface, the conidiospores of the fungus are ineffectual inoculating agents of the disease. The preventive measure most commonly used for control of apple scab is frequent spraying of copper sulphate solutions which are toxic to earthworms (Raw and Lofty, 1959).

Many studies have been conducted to determine the effects of pesticides on earthworms. There is little effect on earthworms with normal doses of Aldrin (Edwards and Dennis, 1960; Edwards *et al.*, 1967; Hopkins and Kirk, 1957; Legg, 1968), or benzene hexachloride (BHC) (Dobson and Lofty, 1956; Lipa, 1958); chlordane is extremely

toxic to them (Edwards, 1965; Schread, 1952). DDT, of course, has been studied by many workers. In general, the application of this pesticide at normal rates does not harm earthworms (Edwards *et al.*, 1967; Hopkins and Kirk, 1957; Thompson, 1971). An exception to this is Ivermectin, a vermicide used on cattle, who later pass it on to earthworms as droppings in a pasture, or in manure spreading (Reynolds, 1996a; Tixier *et al.*, 2016). A recent thorough review of pesticides and their effect on earthworms was presented by Pelosi *et al.* (2014).

In a current study (Pelosi *et al.*, 2021) using *Allolobophora chlorotica* as a test organism they determined out of 31 different pesticides that Imidacloprid (insecticide) and Diflufenican (herbicide) were detected in highest concentrations in the earthworm. Their research also illustrated that earthworms play a key beneficial role in soil structure, functioning and productivity (Liu *et al.*, 2019) and are important prey for numerous predators (King *et al.*, 2010; Reynolds, 2021). Earthworm abundance has been shown to increase when pesticide use decreases (Pelosi *et al.*, 2013) and to be lower in conventional than organic fields (Pelosi *et al.*, 2015), although it is difficult to isolate the effects of pesticides, due to biotic and abiotic factors operating at the same time.

Although earthworms are not susceptible to many pesticides at normal dosages, they do concentrate these toxic chemicals in their tissues. Since many of these chemicals have long-lasting residual periods in the soil, there is ample opportunity for earthworms to absorb them from the soil. The importance of this phenomenon is that these pesticides can become concentrated in the food chain. Earthworms are eaten by many species of birds and certain species of amphibians, reptiles and mammals, which can continue to concentrate these pesticides in their bodies (Hunt and Satcho, 1969). Additional reports of pesticides and their effects on earthworms can be found in Edwards and Lofty (1972).

Herbicides, another group of chemicals, also can affect earthworm populations (Edwards, 1970; Fox, 1964). These chemicals may kill earthworms directly, or indirectly by killing the vegetation on which they feed.

One last group of potential poisons that could become concentrated in the food chain are metal residues. Gish and Christensen (1973) found that concentrations of certain metals (cadmium, nickel, lead, and zinc) in earthworms were many times that of the surrounding soils. This study was the first report of metal residues in earthworms. Because of the earthworms' position in the food chain and the current studies in other fields on metal toxicity, this is an area requiring further investigation.

Tiwari *et al.* (2016) who illustrated the impact of pesticides on different species of earthworms, indicated that the pesticide induced alterations in the functions of some key enzymes regulating the neurotransmission system, energy metabolism, oxidative system and amino acid metabolism of the earthworm. It was observed that these enzymes could serve as potential indicators of pesticide toxicity.

Methods of study

Much of the following section was gained and worked out in over 50 years of studying earthworms, alone and with my colleague Mark Wetzel, some of which appeared in Reynolds and Wetzel (2004) and Reynolds (1977a).

Sampling techniques

Numerous methods for sampling earthworm populations have been presented in the literature. These methods can be divided into four categories: *digging and hand sorting*, *chemical extraction*, *electrical extraction*, and *vibration*. The effectiveness of these methods is dependent upon the habitat present at a study site, and the earthworm species occurring there; no one method is equally suitable for all species in all habitats.

Digging and hand sorting is the most reliable sampling method. Though laborious, this method has been widely used for sampling earthworms and for assessing the effectiveness of other methods. Digging to locate earthworms should be conducted with two factors in mind: moisture and organic matter; collecting success will be high if digging efforts are concentrated at sites where both are present. A variety of tools can be used for digging (*e.g.*,

shovel, trowel, garden fork, or soil cores). The soil can then be pressed and passed through the fingers, or sieves may be employed. The advantages of this method are two-fold: within a sample area active individuals, aestivating individuals, and cocoons may be collected, and, in addition, a well defined sampling area may be chosen so that quantitative data may be obtained. There are some disadvantages associated with digging methods: digging is labourious and time consuming, specimens less than 2 cm in length may escape collection, and, if digging is restricted to the top layers of soil, very large individuals may escape into the deeper layers. Furthermore, specimens may be damaged, and considerable habitat destruction may occur.

Chemical extraction is a method widely used to collect earthworms. Initial studies on chemical extraction were done by Evans and Guild (1947) using potassium permanganate solution (K_2PO_4) to expel earthworms from the soil. Additional experiments with chemical extraction, notably formalin, were conducted by Raw (1959) and Waters (1955). The standardized sampling procedure that I have employed over the years for quantitative extraction of specimens is based on one or more 0.25 m² quadrats of soil surface at a site. A solution of 25 ml of full strength formalin (37% Formaldehyde Solution, U.S.P.) in 4.5 litres of water is sprinkled over each quadrat so that all of it infiltrates the soil without runoff. The earthworms that surface in the ten minutes following the application of the expellant are collected. If the collection is to be obtained for other than scientific purposes (e.g., for bait), the time, strength, and number of applications can be varied, but it should be noted that solution stronger than 15 ml formalin per litre of water may kill the grass in lawns, and if specimens are to be kept alive for more than a few minutes they must be washed in fresh water immediately upon surfacing because formalin can act as a vermicide. In recent years, formalin, a known carcinogen, has fallen into disfavour with many groups.

Dr. Catherine Fox of Agriculture Canada experimented with a mustard solution, a procedure that has been quite effective based on some of my more recent quantitative sampling, and was a method used by Cindy Hale in her ongoing studies of introduced and native earthworms populations in forested areas of Minnesota (Reynolds *et al.*, 2002; Byron, 2003). Additional information on this methodology was evaluated by Chana and Munroa (2001) and Bartlett *et al.* (2006). With a chemical extraction method the sampling time and labour are reduced, a well-defined sampling area may be chosen, and there is minimum disturbance of the habitat. The disadvantages of the method are that only active individuals are collected, not cocoons and aestivating or hibernating individuals; only shallow-dwelling species (endogenic) or species with burrow systems (anecic) are collected; effective penetration of the vermicide is dependent upon soil conditions, and there can be variability in response to vermicides by different species. This technique is generally effective for the collection of lumbricids, but less so for species in other families. A recent evaluation of the mustard extraction technique was presented by Starking and Roloff (2019).

Electrical extraction, a method described by several authors (Walton, 1933; Johnstone-Wallace, 1937; Doeksen, 1950; Satchell, 1961), has long been used by fishermen to obtain bait. The method requires a generator and one to three electrodes. The current conducted through the soil acts as an expellant. The advantage of this method is minimal disturbance to the habitat. The disadvantages are the excessive time required per sample, the difficulty of defining the exact limits of the volume of soil treated, and the variability of the physical and chemical properties of the soil (for example, when soil is moist, deep dwelling species will surface, but if the surface soil is dry the earthworms may go deeper into the soil). The use of too much current kills the earthworms near the electrodes, and the response to electricity varies in different species. This technique was reviewed recently by Bartletta *et al.* (2010), Lardo *et al.* (2012) and Mazur-Pączka *et al.* (2020).

Vibration methods, or *mechanical extraction*, also known as "grunting" or "fiddling", are generally limited to the southeastern United States. Various modifications of this technique are employed by fish bait collectors and yield earthworms in amazing quantities (Reynolds, 1972b; 1977a). Mechanical stimulation by vibrations seems to have very little effect on the Lumbricidae, but it is extremely successful for some Acanthodrilidae and Megascolecidae. These latter two families are not generally found in Canada or Europe, which may account for omission of this technique in European discussions of earthworm sampling. The advantages of mechanical extraction are the minimal habitat destruction and the reduced time required for each sample. The disadvantages are the difficulty of defining the exact volume of soil treated, the effects of the variability of the physical and chemical properties of the soil, and the variable response of the different species.

Several other sampling techniques have been noted in the literature: wet sieving, floatation, heat extraction (various funnels), and pitfall traps. These techniques have been employed in only a few studies, however, because they often yield earthworm specimens that are in poor physical condition, interfering with or preventing positive identification. Reynolds (1977a) and Fender (1985) provided additional information and literature references for these techniques. Recent reviews of extraction techniques were presented by Singh *et al.* (2015) and González *et al.* (2020).

Fixation and preservation of specimens

The proper fixation and preservation of specimens for identification, shipping, and storage has long been a problem. Few good accounts of fixing and preserving techniques are readily available to those who wish to send material to specialists for examination. One of the best media for earthworm preservation is 10–15% formalin because it hardens the specimens to facilitate handling. Weak alcohol solutions leave the specimens soft and limp while strong solutions produce an undesirable brittleness. In both cases, alcohol also causes a condition known as "alcohol browning"; thus, the reporting of colour of preserved alcohol specimens has little diagnostic value. Generally, formalin does not distort the colour greatly. As noted elsewhere, I recommend that collectors record the colour of live specimens *prior* to fixation or preservation.

The use of buffered formalin eliminates the formation of undesirable acid-formalin-hematin-pigment in tissue sections, and will retard the dissolution of calcium-based entities associated with the specimens. Formalin can be buffered with Borax [sodium borate, sodium tetra decahydrate: $\text{Na}_2\text{B}_4\text{O}_7 \cdot 10\text{H}_2\text{O}$] as it is widely available as a common laundry detergent booster. Calcium carbonate [CaCO_3], or magnesium carbonate [MgCO_3] are also commonly used for buffering formalin. A general formula of one part borax, calcium carbonate, or magnesium carbonate to 15 parts full strength formalin is suggested; shake this mixture vigorously, then let settle before using. Hexamine [$(\text{CH}_2)_6\text{N}_4$] (8 mg hexamine/litre of 2% formalin solution) also has been used effectively for the buffering of formalin, but may be more difficult to obtain.

A simple end-effective technique for preparing specimens for study is to kill the worms by immersing them in 70% ethyl alcohol. When movement stops they should be placed on absorbent paper in a straight position, and allowed to dry for a few minutes. For proper tissue fixation and long-term preservation, specimens should then be transferred to a container of 10–15% buffered formalin where they will harden in the position thus placed. They must be straight because curled or twisted specimens are more difficult to handle when internal examination and dissection are required. The specimens should be left in this container overnight and may then be stored in bottles or vials filled with fresh 10–15% formalin solution without much danger of curling. For best results, the formalin solution should be changed within a week, or more often if it discolours quickly. As a general rule, the formalin solution should be changed at weekly intervals until it remains clear.

Transport of live specimens

The transportation of live material can be detrimental to the health of specimens, particularly since removal from their natural environs subjects oligochaetes to changes in temperature and moisture. Respiration is through moist skin; prolonged periods of high temperature or low relative humidity could easily prove lethal to earthworms. Because ultraviolet light is extremely lethal to earthworms, they must be transported in containers that restrict exposure to light. Unlike many high metabolic animals, however, nutrient availability to earthworms in transport is not particularly restrictive, as they can live off body reserves for a long time (Brown, 1944).

Storage of specimens

The storage of a study collection soon becomes a problem for any serious taxonomist. Specimens are subject to damage or destruction by pests; they can be ruined by light, evaporation of preservation fluids, or recession of slide-mounting media; they may accumulate until their volume and numbers exceed available space – particularly common when individuals and institutions receive unsolicited gifts of collections from retiring individuals or from their estates.

Permanency of collections

Often, a valuable collection that has grown to such status through the extensive and usually years long efforts of a dedicated collector or taxonomist is forgotten or "temporarily" set aside after he/she retires or dies. In some cases, valuable collections, even those retained in the natural history collections of renowned museums, deteriorate because of decreasing interest from managerial and curatorial staff, and increasing demands on limited funds for specimen/collection maintenance. These all-too-common situations often result in significant if not complete loss to science of the collection and its associated data.

Every person who collects specimens or assembles a collection for taxonomic purposes should make provision for care of the material in perpetuity. Advance contact by the collector with major museums – with facilities and long-term funding for permanent maintenance of natural history and taxonomic collections – will facilitate transfer of material at the appropriate time, and in agreement between both parties. Most large museums will gladly accept the gift of a collection (frequently in exchange for a tax receipt), occasionally with a proviso that the donor retain control and possession during his/her lifetime.

Rearing and culturing earthworms

It may be of interest to some readers to discuss briefly the rearing or culturing of earthworms. This is not difficult for some of the species found in Canada. There are many books available describing techniques (e.g., Ball and Curry, 1956; Myers, 1969; Morgan, 1970; Shields, 1971), although their citation here must not be taken as an endorsement. The location for earthworm containers depends upon the climate of the region. Outdoor containers or pit-runs (benches) in northern areas will require insulation during the winter period when the soil is normally frozen. Smaller wooden pit-runs, or one of the various types of metal tubs, can be housed in a basement or shed to avoid winter freezing problems. Since the indoor facilities permit year-round activity, these can be a source of replenishment for outside gardens, compost piles, flower beds or earthworm beds, etc. The size of the container can vary. A convenient size is a box 50 cm long × 35 cm wide and 15–20 cm deep. Larger containers, when filled with medium and earthworms, will be extremely hard to move. These boxes should have holes 0.5 cm in diameter drilled in the bottom. Plastic window screening should be placed on the inside bottom of the box, with a burlap lining on top of the screen and sides of the box, before the soil is added. This permits the excess water to drain and prevents the soil medium from sticking to the box, and also prevents the earthworms from escaping through the holes (Reynolds and Eggen, 1993a).

Various combinations of soil and organic matter can serve as a medium in which to raise earthworms. A frequently-used mixture is $\frac{1}{3}$ soil and $\frac{2}{3}$ organic matter. Sources of suitable organic matter are: decayed sawdust, hay, leaves, manure, peat moss, sod, or straw. Additional materials which can be added to the medium to serve as food sources are: chicken starter, cornmeal, and kitchen scraps and fats. Earthworms are omnivorous and can utilize many materials as food sources. Some important facts to remember are: 1) the medium should contain sufficient organic matter so that it will not pack into a dense, soggy mass, 2) the containers must not be over watered, and 3) the presence of low-watt bright white or blue light will prevent the earthworms from crawling on the surface of the medium and eventually out of the box (Reynolds and Eggen, 1993b).

The species most frequently used as fish bait, and therefore the ones most likely to be cultured, are: *Aporrectodea trapezoides*, *Ap. tuberculata*, *Ap. turgida*, and *Eisenia fetida*. Two other species, *Lumbricus rubellus* and *Octolasion tyrtaeum*, have also been sold or reared as fish bait, though not so commonly as the others mentioned. The night-crawler *Lumbricus terrestris* is widely used by fishermen, but cannot be commercially cultured economically because of its long life cycle, low reproductive rate, and large spatial requirements (Steckley, 2020).

Figure coding

The figures for each species were drawn with a camera lucida from preserved specimens in the author's collection and selected museum collections. The source of the specimens for each drawing is given in parentheses after each figure caption. The abbreviations used in all figures are:

a	anus	n	nephridium
bc	buccal cavity	nb	nephridial bladder
cag	calciferous gland	np	nephropore
cg	cerebral ganglion	ns	nephrostome
chl	chloragogen cells	nt	nephridial tube
cl	clitellum	o	ovary
clm	coelom	od	oviduct
cm	circular muscle	os	ovisac
cpc	circum pharyngeal connectives	ph	pharynx
cr	crop	phm	pharyngeal muscle
cut	cuticle	pp	periproct
dp	dorsal pore	pr	prostomium
dv	dorsal vessel	ps	peristomium
epi	epidermis	ptm	peritoneum
es	oesophagus	s	seta
fp	female pore	sep	septum
g	gizzard	sg	seminal groove
gl	gut lumen	sm	setal muscle
GM	genital markings	snv	subneural vessel
GS	genital setae	sp	spermathecae
GT	genital tumescence	spp	spermathecalpore
h	heart	sv	seminal vesicle
if	intersegmental furrow	t	testes
lm	longitudinal muscle	TP	tubercula pubertatis
lnv	lateral neural vessel	typ	typhlosole
m	mouth	vd	vas deferens
mf	male funnel	ve	vas efferens
mp	male pore	vnc	ventral nerve cord
mL	mid-lateral line	vv	ventral vessel

General morphology

The Oligochaeta are defined as annelids with internal and external metamerism throughout the body, without parapodia but possessing setae on all segments except the peristomium and periproct, with a true coelom and closed vascular system, generally hermaphroditic with gonads few in number in specific locations, with special ducts for discharge of genital products, with a clitellum that secretes cocoons in which ova and spermatozoa are deposited, and which are fertilized and develop without a free larval stage.

The following brief discussion refers primarily to the Lumbricidae, which make up nearly all of the Canadian megadrile fauna. The terms used in this section that are not explained in detail in the text will be found in the illustrated glossary. For additional information and details of megadrile morphology consult Stephenson (1930) or Reynolds (1977a) for English accounts, and Avel (1959) or Bouché (1972) for French.

External structures

Terrestrial oligochaetes vary greatly in size. Some *Bimastos* spp. are less than 20 mm long, the largest tropical species are over 1200 mm (*Glossoscolex*, *Megascolides*), and some Australian forms may reach 3000 mm in length. The largest species in Canada is *Lumbricus terrestris* (p. 95), which varies from 90 to 300 mm when mature. The body shape is generally cylindrical though usually flattened dorsoventrally in the posterior region in the case of burrowing species.

The entire body is divided along the longitudinal axis into segments separated by intersegmental furrows and septa. This is primary segmentation. There are also secondary annuli, or furrows, which appear to subdivide some of

the individual segments, usually in the anterior region. These demarcations are only external. Ljungström and Reinecke (1969) have suggested using α and β for these subdivisions and I use γ for a third subdivision; the primary segments are numbered by Roman numerals. There is a loss of uniformity in segmentation at the anterior end of the earthworm; this condition is referred to as cephalization (*cf.* Gates, 1972a). The first body segment, containing the mouth, is known as the peristomium and may have a tongue-like lobe projecting anteriorly. The prostomium is located above the mouth, and is not a true segment. Its appearance is often important in species identification. The last, or caudal, body segment is referred to as the periproct.

Sometimes a swelling may be seen around the body, the clitellum. The layman frequently mistakes this for the scar of a regenerated animal. In fact it is an epidermal modification of sexually mature specimens where gland cells secrete material to form the cocoon.

Characteristic of all earthworms are the short bristles or setae, retractile structures that add to the worm's grip during tunnelling and locomotion. The setae are produced by cells in the body wall. In the Lumbricidae and Sparganophilidae there are four pairs of setae per segment, except for the peristomium and periproct, which are asexual. The type and position of these setae have been used as taxonomic characters (see glossary – setae, setal formula, setal pairings).

The colour of the megadriles is primarily a result of pigment in the body wall. But it may be a secondary result of lack of pigment and the red colour of some forms is due to haemoglobin in the blood. Some colour is due to the presence of yellow coelomic corpuscles near the surface, but the presence of chloragogen cells near the surface is rarely, if ever, an influence on colour. Preliminary results of current North American studies indicate that the physical and chemical properties of the soil are a possible influence on earthworm colour.

The body wall, upon which the excretory, genital, and reproductive apertures all open, comprises six layers. From the outside these are: cuticle, epidermis, nerve plexus, circular muscle, longitudinal muscle, and peritoneal layer. The well-developed muscle layers are important in locomotion. The body wall is the foundation for many glandular swellings such as the clitellum, tubercula pubertatis, and genital tumescences, all of which have long been employed as taxonomic characters.

Internal structure

The annelids have often been characterized as possessing a "tube-within-a-tube" body style (Figs. 2 and 3). The outer tube is formed by the body wall and the inner tube by the alimentary canal. Between these two tubes is the secondary body cavity, or coelom, which is divided at each segment by a septum at the intersegmental furrow. Non-segmental alignment may occur anteriorly in some species as a result of cephalization. The coelomic cavity is filled with a fluid that varies in composition interspecifically, and also intraspecifically for those species that are euryecious in that they tolerate a wide range of habitat conditions. Pores in the septa permit the coelomic fluid to pass freely between segments.

The alimentary canal or digestive tract is essentially a tube extending from mouth to anus. The anteriormost part of the tract consists of a muscular buccal cavity, followed by a pharynx which has a sucking action during feeding, the oesophagus, the crop, a crushing organ known as the gizzard, and finally the intestine. The intestine may possess a dorsomedian fold, the typhlosole, that serves to increase the absorptive surface. Many associated structures are connected to the alimentary system, *viz.*, blood glands, chloragogen cells, calciferous glands, and salivary glands. An extensive account of the alimentary canal is found in Gansen (1963).

The circulatory system is closed but there is an extensive sinus between the intestinal epithelium and the chloragogen cells. Extending almost the total length of the body are three main vessels (Fig. 3): the dorsal vessel, closely associated with the alimentary canal for most of its length, and two ventral vessels (ventral and sub-neural vessels). The ventral vessel is located between the nerve cord and the alimentary canal, while the sub-neural vessel is

located between the nerve cord and the body wall. These main vessels are connected in each segment by paired connectives. In several anterior segments these connectives, termed "hearts", are enlarged and contractile, and possess valves. There are other trunks and branches which anastomose throughout the body. The circulatory or vascular system has not yet achieved its proper position in oligochaete systematics. Its importance has been discussed by Gates (1972a) and Reynolds (1973b).

There is no formalized respiratory system in earthworms; exchange of oxygen and carbon dioxide takes place through the moist cuticle. Respiration normally occurs in air but earthworms can exist in water for long periods of time (*e.g.*, six months) if the water is highly oxygenated (Brown, 1944, Roots, 1956).

The excretory system is composed of a series of coiled tubes called nephridia (sing. nephridium). These are the main organs for nitrogenous excretion in earthworms. In the Lumbricidae, they are paired organs in each segment except the first three and the last. A nephridium occupies part of two successive segments where the nephrostome, or funnel, is in the anterior segment and the coiled tube and nephridial bladder are in the posterior segment. The nephridial bladder passes through the body wall opening to the outside forming the nephropore. The position of the nephropore, as well as the structure and type of nephridium, are used as taxonomic characters. The most complete discussion of nephridia and their classification was presented by Bahl (1947).

The nervous system is concentrated, with a bilobed mass of nervous tissue (cerebral ganglia) on the dorsal surface of the pharynx which is connected to subpharyngeal ganglia by a pair of circumpharyngeal connectives. The nerve cord, a fusion of the circumpharyngeal connectives, extends caudad from the subpharyngeal ganglia ventrally between the alimentary canal and the body wall (Fig. 2). In each segment, posterior to iv, a ganglion is formed and three pairs of nerves (peripheral nervous system), one pair anterior to the ganglion and two pairs posterior to the ganglion, extend to the motor and sensory areas. The nervous system is another portion of somatic anatomy that has not yet achieved its proper position in oligochaete systematics.

The reproductive system has long been used as the main source of taxonomic characters. In amphimictic species the male gonads are paired testes found in segments x and xi close to the anterior septa, a condition termed holandric. Anterior to each testis, in segments ix and x, and also posteriorly in segments xi and xii, lobed seminal vesicles occur in which the sperm develop.

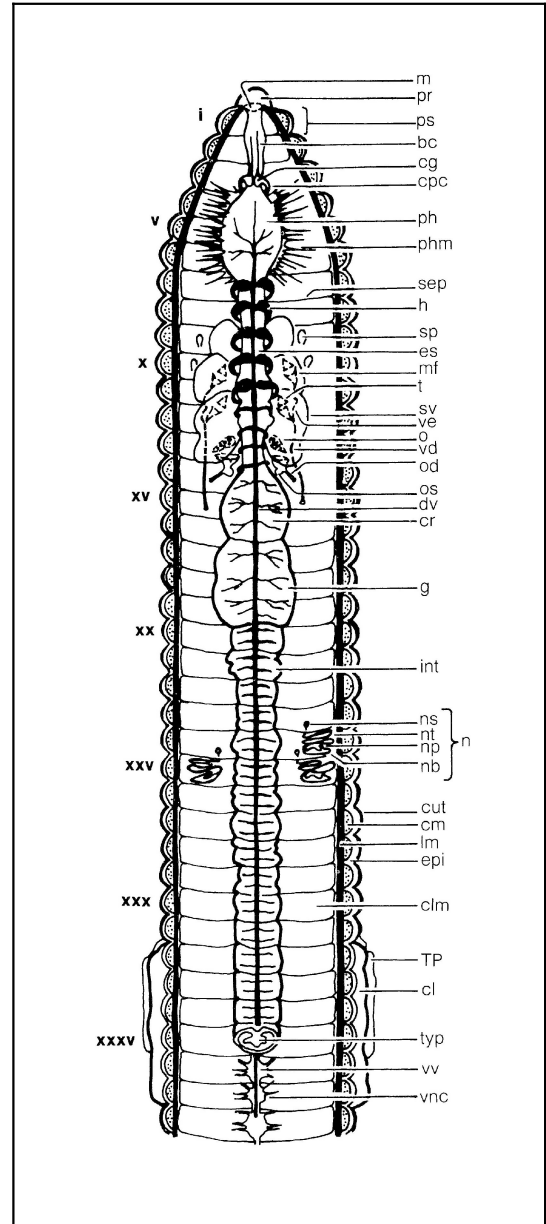


Fig. 2. Diagrammatic longitudinal section of a lumbricid earthworm showing internal organs (from Reynolds, 1977a).

Sperm are transferred via the sperm funnel and sperm ducts to a vas deferens that may traverse several segments before opening to a male gonopore. The female gonads are represented by a pair of gonads found in segment xiii. Ripe oocytes pass through the coelomic fluid into ovisacs which lead *via* an oviduct to the female genital pore. In each of segments ix and x there is a pair of sac-like organs, opening ventrally, that receive the sperm during copulation. These are the spermathecae.

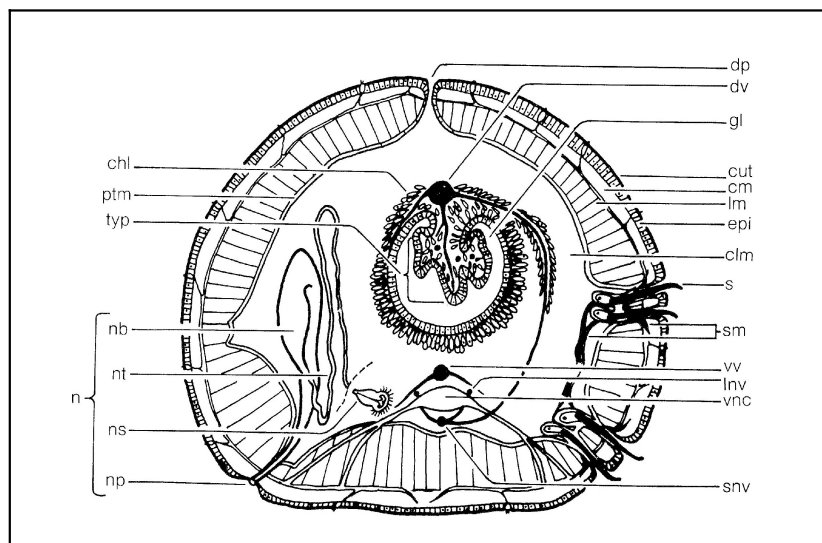


Fig. 3. Diagrammatic cross section of a lumbricid earthworm (from Reynolds, 1977a).

In recent years the inadequacies and inconsistencies of reproductive characters in taxonomy have been discussed (Reynolds *et al.*, 1974; Reynolds, 1974a; Gates, 1974b). Unfortunately, statements such as "Oligochaetes are hermaphrodite, and have more complicated genital systems than unisexual animals" (Edwards and Lofty, 1972) are true only in the broadest sense (*cf.* Reynolds, 1974a). In this study, six of the 26 lumbricids are parthenogenetic (or unisexual). In megadriles, only the clitellum, ovaries, oviducts, and possibly ovisacs are essential to reproduction (*cf.* Gates, 1974a; Reynolds, 1974a). Therefore, when reproduction is parthenogenetic all of the following are no longer required: testes, seminal vesicles, seminal receptacles, vas deferens, copulatory chambers, copulatory penes, prostates and ducts, genital markings, spermathecae, tubercula pubertates, genital and penial setae.

The external position and morphology of the genital apertures, setae and tumescences, clitella, and tubercula pubertates have been widely used in lumbricid identification. If these characters are constant for a given species, they are excellent simple characters that non-specialists can use with reliability.

Scientific and common names (modified from Grimm *et al.*, 2009)

In the preceding sections I have already used two names for species. In Zoology, formal names of animals follow rules established by the International Commission on Zoological Nomenclature (ICZN, 1999). The primary unit of biological entities ("kinds" of animals) are species, and while there are different ways to define what a species is, the traditional definition is that a species is a group of individuals capable of breeding in natural conditions with each other but not with other such groups (Blackwelder, 1967). In practice, this determination is difficult and zoologists usually use differences in morphology – both of the genital and somatic characters – as a reflection of reproductive and evolutionary isolation.

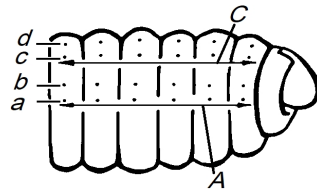
Names of species of earthworms (and all animals) are formed by two words in combination: the genus names and the species epithet. Genera (plural of genus) are groups of related species and they may have hundreds, dozens, a few, or but a single species.

Consider the dewworm or night crawler, *Lumbricus terrestris*: this species name is composed of *Lumbricus*, the genus, and *terrestris*, the species epithet. Both genus and species names are italicized since they are based on, or treated as, Latin or Greek. Genera are always capitalized, while species epithets are not, even when derived from the name of a person (e.g., *gatesi*, for the American Dean of Oligochaetology) or place (*lusitana* from Lusitana, the Latin for the country of Portugal).

Glossary

! Exclamation mark is used in taxonomy to indicate the author has seen the type specimens, *vis-à-vis* a period (.) which indicates the author knows the types are there, but has not seen them (Sigovini *et al.*, 2016).

A, B, C, D These single capital letters refer to the meridians of longitude passing anteroposteriorly along the apertures of the respective setal follicles. Thus, *A* represents a line along the *a*, the most ventrally located setal follicles.



AA, BB, CC, DD See setal formula.

acinus (Fr. *acine* m.) A sac-like termination of a branched gland.

acitellate adults (Fr. *adultes sans clitellum, antéclitellienne* f.) These are prereproductive individuals without a clitellum but in which genital markings are obvious. The second number in the age classification formula (*q.v.*) refers to such individuals.

adiverticulate (Fr. *sans diverticule*) Without diverticula, and usually referring to spermathecae.

aestivation (Fr. *estivation, anhydrobiose*) A period of inactivity, or dormancy, resulting from unfavourable moisture conditions.

age classification formula (Fr. *formule de classification par âge* m.) A series of numbers following a binomen (usually three or four numbers) separated by dashes indicating the number of: juveniles - acitellate adults - clitellate adults - postclitellate adults in a collection. If there are no postclitellate adults in the collection the final zero is omitted from the formula. See juveniles, acitellate adults, clitellate adults, postclitellate adults.

amphigony See amphimixis.

amphimixis (Fr. *amphimixie* f.) Reproduction involving fertilization of an ovum by a sperm. In megadriles the same as biparental reproduction. Cf. parthenogenesis.

anal segment See periproct.

anastomosis (Fr. *anastomose* f.) Cross connections of ducts, branches of organs, or, more usually, of blood vessels.

anthropochore (Fr. *anthropochore*) Transported by man, usually unintentionally. Cf. peregrine.

aortic arch See hearts.

asetal (Fr. *sans soies*) Without setae. *Cf.* peristomium, periproct.

atrial gland (Fr. *glande atriole* f.) Glandular tissue associated with a cleft or coelomic invagination containing the male pore.

bithecal (Fr. *bithécale*) A worm with two spermathecae.

blood glands (Fr. *glandes sanguines* f.) Follicles clustered in the pharyngeal region, supposed to function in the production of haemoglobin and blood corpuscles.

brain (Fr. *cerveau* m.) See cerebral ganglion.

buccal cavity (Fr. *cavité buccale* f.) (**bc**) The first region of the alimentary canal, between mouth and pharynx (Fig. 2, p. 11).

C. Abbreviation for circumference (in German publications replaced by U = Umfang). See setal formula.

caecum (Fr. *cæcum* m.) A blind diverticulum or pouch from the alimentary canal.

calciferous gland (Fr. *glande de Morren, glande calcifère* f.) (**cag**) Whitish gland that secretes calcium carbonate and opens into the gut via the esophageal pouches. In Lumbricidae, it is generally found in segments x–xiv. In Megascolecidae, it is generally found in segments xi–xiii, or lacking, depending on the genus. In Sparganophilidae, these are absent.

castings (Fr. *déjections de surface* f., *turricules* m.) Feces, the voided earth and other waste matter that are commonly deposited on the surface of the ground. Not all species, however, form their casts above the ground.

cephalization (Fr. *céphalisation* f.) The loss of metameric uniformity at the anterior end of the body.

cerebral ganglion (Fr. *ganglion cérébral* m.) (**cg**) Concentrated nerve cells above the alimentary canal that function as a simple brain (Fig. 2, p. 11).

cf. (*confer*) Compare.

chaeta See seta.

chloragogen cells (Fr. *cellules chloragogues* f.) (**chl**) Cells surrounding the alimentary canal; their function is uncertain but is attributed to excretion and regeneration in the literature (Fig. 3, p. 12).

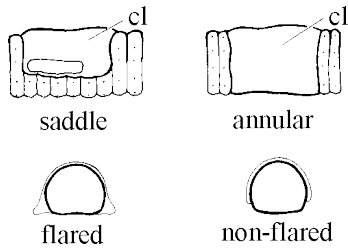
cingulum See clitellum.

circumpharyngeal connective (Fr. *connectif circumpharyngien* m.) (**cpc**) Nerve collar, between cerebral ganglion and ventral nerve ganglion (Fig. 2, p. 11).

clade (Fr. *clade* m.) Also known as a monophyletic group, is a group of organisms that consists of a common ancestor and all its lineal descendants.

clitellate adult (Fr. *adulte avec clitellum, clitellienne* f.) Those individuals with developed clitellum and genital markings. The third number in the age classification formula (*q.v.*) refers to these individuals.

clitellum (Fr. *clitellum* m.) (**cl**) A regional epidermal swelling where gland cells secrete material to form the cocoon. There are two types recognizable. An annular clitellum or cingulum (Fr. *anneau* m.) encircles the body whereas a clitellum that encompasses only the dorsal and lateral parts of the body is referred to as a saddle (Fr. *selle* f.). The convention xxvi, xxvii-xxxii, xxxiii means that the clitellum is generally found on segments xxvii-xxxii, but may in some individuals overlap onto segments xxvi and/or xxxiii.



In the case of *Aporrectodea rosea* the clitellum has been termed flared. This ventral flared condition is easily recognizable.

coelom (Fr. *cavité cœlomique, cœlome* f.) (**clm**) The body cavity between the body wall and the alimentary canal (Fig. 3, p. 12).

congeneric (Fr. *congenere*) Belonging to the same genus.

copulation (Fr. *accouplement* m., *copulation* f.) Sexual union, mating.

copulatory pouches (Fr. *poches copulatrices* f.) Copulatory pouches are invaginations of the ventral body wall surrounding the male pores. A copulatory pouch contains the primary male pore and its opening is the secondary male pore (frequently referred to as the "male pore"). A copulatory pouch can be quite shallow and confined within the body wall or large and penetrating into the coelom. Sometimes, recognition of a copulatory pouch may be more difficult than expected. A superficial male pore may look like it is within an invagination due to contraction (often the result of fixation or preservation) of muscles around the male pore during specimen preservation. In contrast, strong muscle contraction may cause a copulatory pouch to be fully everted and look like a cone-shaped superficial male pore. These deformations of the male pore area make the recognition of copulatory pouches sometimes challenging.

cosmopolitan (Fr. *cosmopolite*) Of a species with a large distribution (usually worldwide), when the distinction between peregrine, exotic and invasive is unknown.

crop (Fr. *jabot* m.) (**cr**) A widened portion of the digestive system that lacks the muscularity of the gizzard, in Lumbricidae anterior to the gizzard and posterior to the oesophagus (Fig. 2, p. 11).

cuticle (Fr. *cuticule* f.) (**cut**) A thin, non-cellular, colourless, transparent outer layer of the body wall. See iridescence 2.

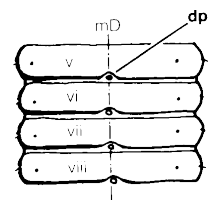
diapause (Fr. *diapause* f.) An obligatory resting stage in development.

digitiform (Fr. *digitiforme*) Finger-shaped.

dorsal pore (Fr. *pore dorsal* m.) (**dp**) Small single intersegmental apertures in the mid-dorsal line (mD) leading to the coelomic cavity (Fig. 3, p. 12). The convention first dorsal pore 5/6 means that the dorsal pore is found in the intersegmental furrow between segments v and vi.

dorsal vessel (Fr. *vaisseau dorsal* m.) (**dv**) A major blood vessel located above the dorsal surface of the alimentary canal (Figs. 2, 3, pp. 11, 12).

ectal (Fr. *ectal*) Outer, external, toward the body wall.



e.g. (*exempli gratia*) *E.g.* is used before an item or list of items that serve as examples for the previous statement.

egg sac See ovisac.

endemic (Fr. *endémique*) Restricted to a certain region or part of a region, native. *Cf.* exotic, indigenous.

endogean (Fr. *endogé*) Are environments which are the parts of caves that are in communication with surface soils through cracks and rock seams, groundwater seepage, and root protrusion.

ental (Fr. *ental*) Inner, internal, away from the body wall.

epidermis (Fr. *épiderme*) (**epi**) The outer cellular layer of the body wall, which secretes a protective cuticle (Fig. 3, p. 12).

epilobic (Fr. *épilobique*) See prostomium.

eq. Equatorial (Fr. *équatorial m.*, *équatoriale f.*), see mL.

esophagus (Fr. *œsophage m.*) (**es**) The portion of the gut between the pharynx (anterior) and crop (posterior), ending in an esophageal valve (Fig. 2, p. 11).

etc. (*et cetera*) (pl. *etceteras*) Is used to indicate unspecified additional items.

euryoecious (Fr. *euryoeciques*) Having a wide range of habitat tolerance.

exoic (Fr. *exoique*) Opening to the exterior through the epidermis, referring to the excretory system.

exonephridia (Fr. *exonéphridie f.*) Integumentary nephridia lie scattered on the entire inner or parietal surface of body wall in each segment, except the first two. Their terminal duct opens on body surface independently through minute openings, known as nephridiopore. They are thus known as exonephric.

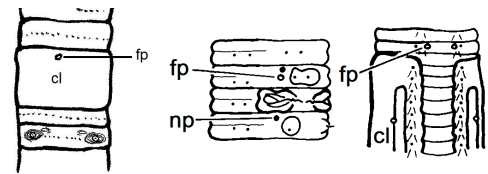
exotic (Fr. *exotique*) Introduced, foreign. *Cf.* endemic, indigenous; species found outside their native ranges, mainly transported and introduced by humans, and generally found in disturbed habitats.

facultative (Fr. *facultatif*) Conditional, having the power to live under different conditions. *Cf.* obligatory.

female ducts Gonoducts. See oviducts.

female pores (Fr. *pores femelles m.*) (**fp**) 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.

Megascolecidae - left
Lumbricidae - centre
Sparganophilidae - right



fide On the authority of, or with reference to publication, to a cited published statement.

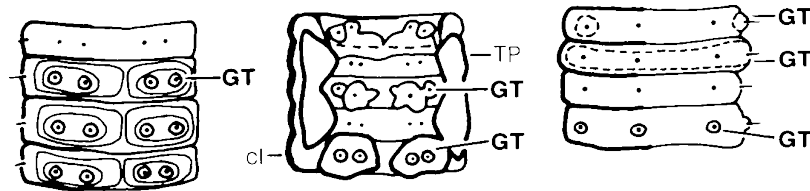
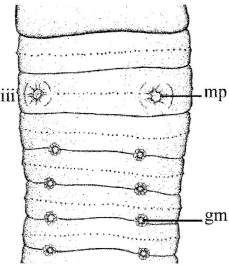
flared clitellum (Fr. *clitellum évasé m.*) See clitellum.

genital characters (Fr. *caractères génitaux* m.) Those taxonomic structures associated with the reproductive system. See somatic characters.

genital markings (Fr. *mamelons antiarrheniques, mamelons périarrheniques* m.) (**GM**) Glandular swellings, pits or grooves of the epidermis in the Megascolecidae. See genital tumescences Jamieson and Ferraguti (2006).

genital setae (Fr. *soies génitales* f.) (**GS**) See setae.

genital tumescences (Fr. *papille puberculienne* f.) (**GT**) In Lumbricidae, areas of modified epidermis (glandular swellings) without distinct boundaries and through which follicles of genital setae open.



giceriate (Fr. *gicériate*) An organism having one or more gizzards.

girdle See clitellum.

gizzard (Fr. *gésier* m.) (**g**) The muscularized portion of the digestive system, in Lumbricidae, anterior to the intestine and posterior to the crop (Fig. 2, p. 11).

gonopore (Fr. *gonopore* m.) See male pores, female pores.

hearts (Fr. *cœurs* m.) (**h**) The enlarged, segmental, pulsating connectives of the blood system between the ventral and one or two other longitudinal trunks (*e.g.*, dorsal and/or supra-esophageal) (Fig. 2, p. 11)

hemerobiont (Fr. *hémérobiont* m., f.) A species dependent on human culture.

hemerodiaphore (Fr. *hémérodiphore* m., f.) A species indifferent to the influence of human culture.

hemerophile (Fr. *hémérophile* m., f.) A species favoured by human culture.

hemerophobe (Fr. *hémérophobe* m., f.) A species averse to the influence of human culture.

hibernation (Fr. *hibernation* f.) A period of inactivity or dormancy resulting from unfavourable temperature conditions.

holandric (Fr. *holandrique*) The condition where the testes are restricted to segments x and xi, or a homoeotic equivalent.

holoic (Fr. *holonéphridique*) The condition of having a pair of stomate, exoic nephridia in each segment of the body except the first and last.

holonephric see holic.

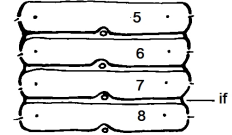
homoeotic (Fr. *homoéotique*) The condition of having glands or organs in a segment(s) where they do not normally occur. Refers principally to intraspecific variation.

i.e. (*id est*) *I. e.* is an abbreviation for the phrase *id est*, which means "that is." *i.e.* is used to restate something said previously in order to clarify its meaning.

indigenous (Fr. *indigène*) Belonging to a locality, not imported, native. *Cf.* endemic, exotic.

in litt. (*In litteris*) In correspondence. See pers. comm.

intersegmental furrow (Fr. *sillon intersegmentaire* m.) (**if**) The boundary between two consecutive segments; the area where the epidermis is thinnest and where, in pigmented species, colour is lacking.



invasive (Fr. *envahissante*) Of a species introduced deliberately or unintentionally (usually transported by humans) outside its native range, that successfully establishes itself in, and then modifies (possibly outcompeting native species, if present) otherwise intact native ecosystems.

iridescence (Fr. *irisation, iridescence* f.) In the context of earthworm biology this refers to 1) the appearance of sperm aggregated on the male funnels (*q.v.*), or 2) the appearance of cuticular colour as a result of refracted light.

juveniles (Fr. *larves* f.) Those individuals with no recognizable genital markings such as the clitellum, tubercula pubertatis, tumescences, *etc.*, *i.e.*, in the life stage between hatching and the appearance of genital markings. The first number in the age classification formula (*q.v.*) refers to these individuals.

lamella (Fr. *lamelle* f.) Any thin plate- or scale-like structure.

lumbricin arrangement (Fr. *arrangement lumbricin*) Having eight setae per segment. (See setal pairings)

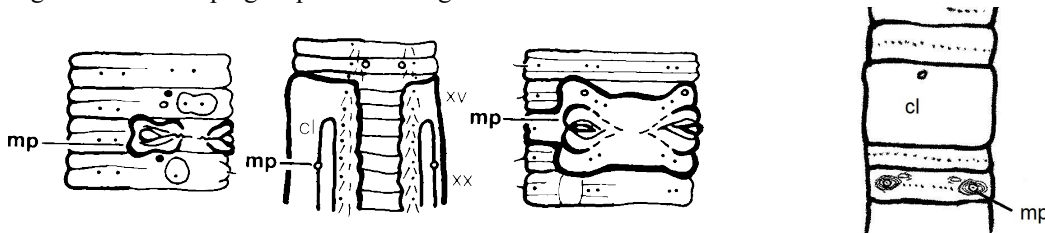
mD (Fr. *médio-dorsales*) Mid-dorsal line.

mL (Fr. *médio-latérale*) Mid-lateral line.

mV (Fr. *médio-ventrale*) Mid-ventral line.

male funnel (Fr. *entonnoir mâle* m.) (**mf**) The enlargement of the ental end of a sperm duct with a central aperture through which sperm pass into the lumen of the duct on their way to the exterior. Sperm may temporarily aggregate on the funnels, prior to entering the ducts, their presence being indicated by iridescence (*q.v.*).

male pores (Fr. *pores mâles* m.) (**mp**) The external paired openings for the male ducts through which sperm are liberated during copulation. In Lumbricidae they are usually conspicuous near the mL on segment xv; any variation is noted in the diagnosis, *i.e.* on xiii in most forms of *Eiseniella tetraedra*. In Megascolecidae on segment xviii. In Sparganophilidae in segment xix.



Lumbricidae,

Sparganophilidae,

Lumbricidae,

Megascolecidae

male sterility (Fr. *stérilité mâle* f.) Often cited as evidence for parthenogenesis (*q.v.*) and may be indicated by the following: 1) adult retention of juvenile testes, 2) adults with juvenile seminal vesicles and no evidence of sperm, 3) the absence at maturity of iridescence on the male funnels, indicating that there are no mature

sperm aggregations, 4) the absence of similar iridescences in the male ducts and/or spermathecae, and 5) the absence of externally adhesive spermatophores. These criteria will only suggest male sterility in any given individual and many cases of repeated evidence are required before a species can be considered male sterile or parthenogenetic.

megadrile (Fr. *mégadrile* m.) *Sensu* Gates (1972a: 29) and Reynolds and Cook (1977), this term is synonymous with terrestrial oligochaetes. There is some morphological basis for the megadrile/microdrile division of the Oligochaeta (*cf.* Gates, 1972a). Brinkhurst (*in* Brinkhurst and Jamieson, 1971: 104) employs microdrile as a major heading when discussing the aquatic oligochaetes. In general, these old terms are used to describe terrestrial and aquatic oligochaetes without any systematic judgments.

mesial (Fr. *médial*) In the middle vertical or longitudinal plane.

metamere (Fr. *métamère* m.) A segment.

moniliform (Fr. *moniliforme*) Arranged like a string of beads.

monotypy (Fr. *monotypie* f.) The situation arising when a genus-group taxon is established with only one originally included species; or when a family-group taxon is established with only one originally included genus.

morph (Fr. *forme* f., *morph* f.) A group of individuals that share a common anatomy resulting from degradations, deletions, or other changes from structure of the ancestral amphimictic population caused by reproductive isolation. Such isolation usually comes about as a result of parthogenesis.

Morren's gland See calciferous gland.

mouth (Fr. *bouche* f.) (**m**) The anterior opening to the alimentary canal located in the peristomium.

mouth cavity See buccal cavity.

muscular tube See nephridial bladder.

nearctic (Fr. *néarctique*) A zoogeographical region including Canada, the United States, Greenland, and northern Mexico.

neotype (Fr. *neotype* m.) A single specimen designated as the type specimen of a nominal species- group taxon of which the holotype (or lectotype), and all paratypes or all syntypes are lost or destroyed. Neotypification is the act of selecting a neotype. (For nominal taxon, see taxon.)

nephridial bladder (Fr. *vesicule de la néphridie* f.) (**nb**) The extended portion of the nephridial tube connected to the nephropore (Fig. 3, p. 12).

nephridial pore See nephropore.

nephridial reservoir See nephridial bladder.

nephridiopore See nephropore.

nephridium (pl. nephridia) (Fr. *néphridie* f.) (**n**) The organ for nitrogenous excretion (Figs. 2, 3, pp. 11, 12).

nephropore (Fr. *néphridiopore* m.) (**np**) The external opening of a nephridium (Fig. 3, p. 12).

nephrostome (Fr. *néphrostome* m.) (**ns**) The ciliated funnel at the ental end of the nephridium (Fig. 3, p. 12).

obligatory (Fr. *obligatoire*) Limited to one mode of life or action. *Cf.* facultative.

octothecal (Fr. *octothécal* m.) A worm with eight spermathecae.

esophagus (Fr. *œsophage* m.) (**es**) The portion of the gut between the pharynx (anterior) and crop (posterior), ending in an esophageal valve (Fig. 2, p. 11).

omnivorous (Fr. *omnivore*) Eating both animal and plant tissue.

op. cit. (*opere citato*) In the work or article previously cited for this writer (no page cited).

ovary (Fr. *ovaire* m.) (**o**) The organ for ova (egg) production (Fig. 2, p. 11).

oviducal pores See female pores.

oviduct (Fr. *oviducte* m.) (**od**) The duct carrying the ova from the coelomic funnel to the exterior (Fig. 2, p. 11).

ovisac (Fr. *ovisac* m.) (**os**) An egg-capsule or receptacle (Fig. 2, p. 11); in *Amyntas* none.

ovum (pl. ova) (Fr. *ovule, œuf* m.) The female germ cell, matured egg-cell.

palaeartic (Fr. *paléoarctique* m.) A zoogeographical region including all of Europe and the U.S.S.R. to the Pacific Ocean, Africa north of the Sahara Desert, and Asia north of the Himalaya Mountains.

papilla (Fr. *papille* f.) A protruding dermal structure.

parietes (Fr. *pariètes* m.) Walls or sides of structures.

parthenogenesis (Fr. *parthénogénèse* f.) Uniparental reproduction in which the ova develop without fertilization by spermatozoa. *Cf.* amphimictic.

penial setae (Fr. *soies de la verge* m.) See seta.

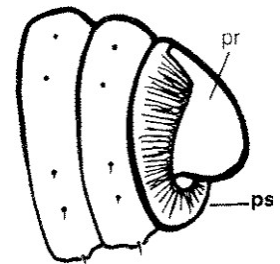
peregrine (Fr. *périgrin*) Widely distributed, not necessarily involving man; species that may be native to a country but have colonized areas outside their native range. A species can be peregrine but not exotic neither invasive.

perichaetin arrangement (Fr. *disposition périchaétine* f.) The location of setae, when more than eight per segment, in a more or less complete circle around the equator of a segment. (See setal pairings)

periproct (Fr. *pygidium* m.) (**Pp**) The terminal (last, caudal) "segment" of the body, without coelomic cavity, asetal.

pers. comm. Personal communication orally as opposed to *in litt.*

peristomium (Fr. *péristomium* m.) (**ps**) The first body segment, asetal, and containing the mouth (Fig. 2, p. 11).



pH (Fr. *pH* m.) An indication of acidity or alkalinity measured as the negative logarithm of the hydrogen-ion concentration, and expressed in terms of the pH scale (0–14) where pH 7 is neutral, less than 7 is acidic, and more than 7 is alkaline. Previously, North American studies employed an aqueous solution to make soil pH

readings, and these are the figures given in the text, but variations can occur when the amount of water present in the soil changes as well as when the amount of dissolved gases in this water, *e.g.*, CO₂, changes. To overcome these variations in the pH readings, one of several salt solutions of differing strengths may be employed instead of water, *e.g.*, KCl or CaCl₂• (For details, see Peech, 1965.)

pharynx (Fr. *pharynx* m.) (**ph**) The portion of the gut between the buccal cavity (anterior) and the oesophagus (posterior) (Fig. 2, p. 11).

pinnate (Fr. *penné*) Divided in a feathery manner.

polymorphism (Fr. *polymorphisme* m.) Occurrence of different forms of individuals within the same species.

poropore (Fr. *poropore* m.) Any area, protuberance or special structure bearing a pore, usually that of a spermatheca, oviduct or sperm/male-duct.

postclitellate adult (Fr. *adulte après clitellum, postclitellienne* f.) Postreproductive individuals without a clitellum but with areas of discolouration in the regions of the clitellum, and with genital markings. If these discolourations disappear (which is not abnormal), differentiation between acitellate adults and postclitellate adults may be impossible even after dissection. These individuals have reverted to an acitellate state and in the future may become clitellate again and be reproductive. The fourth number in the age classification formula refers to these individuals, but if such individuals are not present in the sample then this fourth figure is omitted instead of using a zero.

proandric, proandry (Fr. *proandrique*) A classical term that now means only, testes restricted to x or a homoeotic equivalent, the state of being such

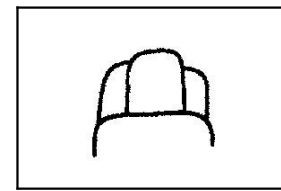
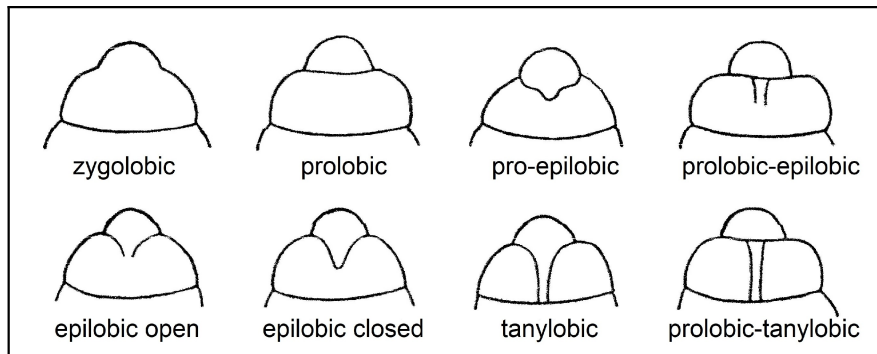
prolobic (Fr. *prolobique*) See prostomium.

prostate glands (Fr. *glandes prostatiques* f.) Amphimictic individuals have one pair of large, racemose prostate glands in 18, usually extending anteriorly and posteriorly for several segments. The ducts of prostate glands are always in 18, where they meet with sperm ducts (*vas deferens*) and connect to the male pores. The shape of the glands and the size of the glands relative to the body are important species identification characters. The relative size is usually indicated using the numbers of segments the prostate gland covers (*e.g.*, 17–19). This range, as well as the shape, varies to some degree within a species.

prostates (Fr. *prostates* f.) In Lumbricidae, without stalks are characterized as atrial glands, and of unknown function. They are more or less associated with the male pores.

prostatic pores (Fr. *pores prostatique* m.) See male pores.

prostomium (Fr. *prostomium* m.) (**pr**) 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 (*zygobolique*): prostomium not demarcated in any manner. 2) prolobic (*prolobique*): prostomium demarcated from the peristomium without a tongue. 3) pro-epilobic (*pro-épilobique*): an epilobic prostomium with an open tongue, the beginning of the tongue is divided by a transverse groove. 4) prolobic-epilobic (*prolobique-épilobique*): prostomium demarcated from the peristomium as in the prolobic type but with an open tongue. 5) epilobic open (*épilobique ouvert*): tongue of the prostomium partly divides the peristomium, tongue not delimited posteriorly by a transverse groove. 6) epilobic closed (*épilobique fermé*): tongue of the prostomium partly divides the peristomium, tongue delimited posteriorly by a transverse groove. 7) tanylobic (*tanylobique*): with a tongue that completely divides the peristomium. 8) prolobic-tanylobic (*prolobique-tanylobique*): with a tongue that completely divides the peristomium, the beginning of the tongue is divided by a transverse groove (see diagram top of following page).



Broad tanylobic prostomium.

pseudogamy (Fr. *pseudogamie*) The activation of ova by a sperm without nuclear fusion and thus without true fertilization.

pygidium (Fr. *pygidium* m.) See periproct.

pygomere See periproct.

pyriform (Fr. *pyriforme*) Pear-shaped.

quadrithecal (Fr. *quadrithécale*) A worm with four spermathecae.

quiescence (Fr. *quiescence* f.) A period of inactivity, or dormancy, resulting from an unfavourable environment; cf. aestivation and hibernation.

q.v. (*quod vide*) (Fr. *voir cela*) Which see.

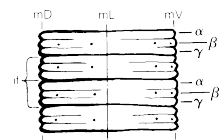
racemose (Fr. *racémiforme*) from Latin *racemus*, bunch.

ridge of puberty (Fr. *crêtes de puberté* f.) See tubercula pubertatis.

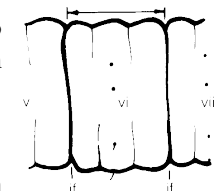
sacculate (Fr. *sacculé* m.) Provided with sacculi, small sacs or pouches.

saddle (Fr. *selle* f.) See clitellum.

secondary annulation (Fr. *sillons transversaux* m.) (**sa**) The furrows which occur between the intersegmental furrows (q.v.). These demarcations are only external and are labelled α , β or γ .



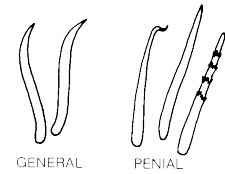
segment (Fr. *segment* m.) A portion of the body, along the anteroposterior axis, between two consecutive intersegmental furrows and the associated septa. Segments are numbered with lower case Roman numerals, i, ii, iii, etc., beginning anteriorly with the peristomium as i. The older system and some microdrile workers used upper case numerals, I, II, III, etc.



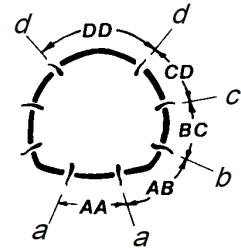
seminal vesicles (Fr. *vesicules seminales* f.) (**sv**) The storage sacs for an earthworm's own sperm until copulation.

septum (pl. septa) (Fr. *cloison* f.) (**sep**) The internal partition at intersegmental furrows. Also acts as a supporting membrane for internal organs (Fig. 2, p. 11).

seta (Fr. *soie* f.) (**s**) A solid rod or bristle secreted by cells at the ental end of a tubular epidermal ingrowth, the setal follicle. Setae are of several types: 1) general: sigmoid shape with pointed outer tip; 2) genital: associated with genital tumescences and/or gonopores, and not sigmoid; 3) penial: associated with the male pores and not sigmoid. Individual setae are referred to as *a*, *b*, *c*, *d*, as shown in the first diagram of this glossary, *a* being the most ventral and *d* the most lateral or dorsal of the setae on a particular segment.



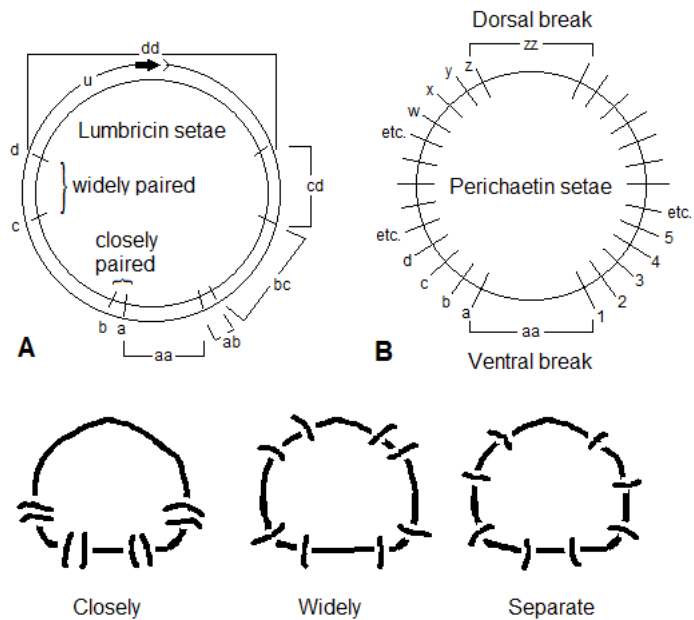
setal formula (Fr. *formule des soies* f.) The distance between the setae, usually measured on segments *x* and/or *xxx*, and being an estimate of the space between the *A*, *B*, *C*, and *D* meridians (*q.v.*). The data can be expressed as a ratio (e.g., $AA:AB:BC:CD:DD = 9:3:6:2:30$), as groupings (e.g., $AA > BC < DC$, $AA = BC$) or in terms of the circumference, *C*, (e.g., $DD = \frac{1}{2}C$). See also setal pairings.



setal pairings (Fr. *schéma de la disposition des soies* m.) Setae may be closely paired (Fr. *soies étroitement géminées*), widely paired (Fr. *soies distantes*), or separate (Fr. *soies écartées*, *soies séparées*).

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) $AB \approx CD$, $AA > BC$, $DD \approx \frac{1}{2}C$; *Amyntas agrestis* (perichaetine) 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.



sexthecal (Fr. *sexthécale*) A worm with six spermathecae.

somatic characters (Fr. *caractères somatiques*) Referring to any portion of the anatomy except the reproductive organs.

sperm (Fr. *spermatozoïdes* m., *sperme* m.) The male germ cells, fertilizing agent.

sperm ducts See vas deferens. **sperm funnel** See male funnel. **sperm sacs** See seminal vesicles.

spermathecae (Fr. *spermathèque* f.) (**sp**) 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.

spermathecal pores (Fr. *pores de spermathèque* m.) The opening in the epidermis leading to the spermathecae.

spermatophore (Fr. *spermatophore* m.) A capsule of albuminous matter containing a number of sperm.

spermatozoa See sperm.

spermiducal pores See male pores.

stomate (Fr. *stomate*) Referring to open nephridia, *i.e.*, with funnel.

tanylobic (Fr. *tanylobique*) See prostomium.

taxon (pl. taxa) (Fr. *taxon* m.) Any taxonomic unit such as a particular family, genus, or species. Nominal taxon: The taxon, as objectively defined by its type, to which any given name whether valid or invalid applies.

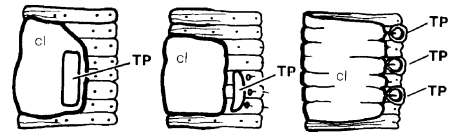
testis (pl. testes) (Fr. *testicules* m.) (**t**) The organs for sperm production.

testis sac (Fr. *sac du testicule* m.) Usually a closed off coelomic space containing one or both testes and male funnels of a segment.

trabeculate (Fr. *trabéculaire*) Seminal vesicles that develop as connective tissue proliferations from a septum so as to have numerous irregular spaces that remain inconsiderable until spermatogonia (primitive sperm cells) begin to enter.

troglophile (Fr. *troglophile* m.) Any organism that is able to live its entire life in a cave.

tubercula pubertatis (Fr. *puberculum* m.) (**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.



typhlosole (Fr. *typhlosolis* m.) (**typ**) Any longitudinal fold in the gut wall projecting into the gut lumen, usually at mD or mV (Figs. 2, 3, pp. 11, 12).

vas deferens (Fr. *canal déférent* m.) (**vd**) The ducts that carry sperm from the male funnels to the exterior (Fig. 2, p. 11).

ventral vessel (Fr. *vaisseau ventral* m.) (**vv**) A major blood vessel, located ventral to the alimentary canal and dorsal to the ventral nerve cord (Fig. 2, p. 11).

vesiculate (Fr. *vesiculeux*) Having a vesicle or small bladder-like sac.

vesticles (Fr. *vessie* f., *sac* m., *kyste* m., *vacuole* f.) A small fluid-filled bladder, sac, cyst, or vacuole within the body.

viz. (*videlicet*) Namely.

zygobolic (Fr. *zygoblique*) See prostomium.

1-1-1-1 See age classification formula.

$\frac{1}{2}$ See first dorsal pore.

i, ii, iii See segment.

Identification of the earthworms of Canada

The identification of local earthworms is not as difficult as most people suspect. The following key, which should be used in conjunction with the glossary and diagnoses, has been designed to facilitate identification of the 33 species recorded in Canada, without the necessity of dissecting the specimens. The exception would be the Megascolecidae where dissection may be necessary to determine the species. At this time, they are very rare in Canada only being obtained from a single site in Ontario. Generally speaking, mature specimens are essential for a definitive identification by the non-specialist.

The most useful characters of the key are the nature of the prostomium (zygolobic only in *Sparganophilus tamesis*, tanylobic in species of the genus *Lumbricus*, and epilobic in all others), the segmental position of the clitellum and tuberculata pubertatis (remembering that the prostomium is not numbered), the arrangements of the setae, and the presence or absence of pigment. These characters are all readily visible in fresh material. The Megascolecidae have an annular clitellum, while the Lumbricidae and Sparganophilidae have a saddle clitellum.

If only preserved material is available, some difficulty may be experienced in those parts of the key (couplet 10) that rely on assessments of colour. In these circumstances it may be necessary at the appropriate point to refer to the detailed diagnoses of several species before proceeding further. At couplet 10, for example, if the colour cannot be assessed confidently, it will be necessary to refer separately to the diagnoses of *Dendrobaena octaedra*, *Dendrodrilus rubidus*, and *Eisenia fetida*. If the preserved specimen at hand definitely is not one of these three species then one continues through the key on the assumption that there is no red pigment present.

There are 15 species that are so rare or only one specimen has been collected that it is highly unlikely you are going to encounter in your collecting: Lumbricidae: *Bimastos lawrenceae*, *Dendrobaena attemsi*, *Dendrobaena lusitana*, *Eisenia hortensis*, *Satchellius mammalis*, and Megascolecidae: *Amyntas agrestis*, *Amyntas hilgendorfi*, and *Arctiostrotus fontinalis*. That being said, with the advent of climate change, the oriental megascolecids may become more common in Canada in the years to come (Moore *et al.*, 2019; see discussion p. 139).

The study of the characters used in the key requires no more than a good hand lens or a low-power binocular microscope. The key itself is strictly dichotomous. The numbers in parentheses after the main couplet numbers indicate the couplet from which that particular point in the key was reached. They are inserted to make it easier to retrace one's steps through the key in the event that an obviously incorrect alternative has been reached.

Identification of most earthworms requires dissection of specimens. Reference to a genus and to a family is possible only after some knowledge of internal anatomy. The late James Joyner is one of many biologists who abandoned the study of earthworms after realizing that dissection was usually necessary to identify specimens accurately. (Gates, pers. comm., 12 July 1977). Obviously, in some circumstances, when the internal anatomy already has been studied to some extent, and with adequate knowledge of the various species, it does of course become possible to recognize an already described species, by or from its external characteristics/structures (Gates and Reynolds, 2017).

Occasionally, there may be need for earthworm identification without time for dissection. Therefore, I began various projects with my late mentor Gordon Gates, to determine how far a key could be based on the externalia (= external characteristics) without requiring dissection.

Taxonomic keys cannot always provide consistent resolution for the unique challenges associated with the accurate identification of specimens. For instance, the occasional misidentification of *Aporrectodea trapezoides* as *Lumbricus terrestris* when using available keys cannot necessarily be attributed solely to those keys. A key is intended as an aid to a solution of the problem and when a name has been obtained by its use, the description of the species should be checked, carefully. Publications in which the original description for the species discussed in this book are found in the Literature Cited section and annotated in brackets [] using the currently accepted nomenclature (pp. 140–172). Note, however, that revisions to the descriptions of some of these genera and species, published in recent literature should be consulted (Gates and Reynolds, 2017).

Key to sexually mature earthworms found in Canada

To help with identification of the earthworm species, a new key is provided. This key uses external morphological characters of both somatic and genital structures. It is based on Canadian species, but additional characters are employed from elsewhere, when only one or a few specimens have been reported. The primary character is placed first in the couplet, and additional characters may be included to help confirm the identification.

In the classical earthworm literature, external characters use Roman numerals for segments number and Arabic numbers for internal segments. Today, most people are not familiar or comfortable with Roman numerals, so that I am only using Arabic numbers in this key. Those species in **bold** text are very rare and unlikely to be encountered often at this time in Canada. They have only been reported from one or a couple of sites and only one or a very few specimens.

- | | | |
|-----|--|-----------------------------------|
| 1. | Clitellum annular | 2 |
| 1'. | Clitellum saddle | 7 |
| 2. | Setae perichaetine arrangement | 3 |
| 2'. | Setae lumbricine arrangement (separate) | 4 |
| 3. | Sexthecal pores, 3 pairs or fewer, minute and superficial in 5/6–7/8, <i>ea.</i> 1/3 C apart; in spring reddish-brown, but seasonally changes to greenish-blue iridescence in autumn | <i>Amyntas agrestis</i> |
| 3'. | Quadrithecal pores, 4 pairs, minute and superficial in 6/7–7/8, <i>ea.</i> 1/2 C apart | <i>Amyntas hilgendorfi</i> |
- A. *agrestis* A. *hilgendorfi*
- | | | |
|-----|---|--|
| 4. | Genital tumescences present on 19, 20 | 5 |
| 4'. | Genital tumescences lacking | 6 |
| 5. | Prostomium epilobic 1/2 open, medium to large earthworm 113–121 segments; male pore 18; unpigmented. | <i>Toutellus oregonensis</i> |
| 5'. | Prostomium tanylobic, broad, moderately large earthworm 147–204 segments; male pore 18; unpigmented or purple-brown | <i>Arctiostrotus vancouverensis</i> |
| 6. | Sexthecal pores in 6/7, 7/8, and 8/9 in line B; number of segments 67–102; male pore 18; small earthworm; Unpigmented | <i>Arctiostrotus fontinalis</i> |
| 6'. | Octothecal pores in 5/6, 6/7, 7/8, and 8/9 in line B; number of segments 135–170; male pore 18; large earthworm; unpigmented | <i>Arctiostrotus perrieri</i> |
| 7. | Prostomium zygaloblic, thin earthworm; number of segments 150–200; clitellum 15–25; TP 17–22; dorsal pores and genital tumescences lacking; male pore 19; unpigmented | <i>Sparganophilus tamesis</i> |
| 7'. | Prostomium not zygaloblic | 8 |
| 8. | Male pores on 13; clitellum 22, 23–26, 27; TP 23–25, 26; yellowish-brown | <i>Eiseniella tetraedra</i> (part.) |
| 8'. | Male pores on 15 | 9 |
| 9. | Tubercula pubertatis small, sucker-like on 31, 33, 35; clitellum 28, 29–37, colour usually green; small earthworm 80–138 segments | <i>Allolobophora chlorotica</i> |
| 9'. | Tubercula pubertatis not sucker-like | 10 |

10.	Colour red or purple.....	11
10 ² .	Colour not red or purple.....	25
11.	Setae closely paired.....	12
11 ² .	Setae widely paired or separate.....	20
12.	Prostomium epilobic.....	13
12 ² .	Prostomium tanylobic.....	17
13.	Tubercula pubertatis 28–30; clitellum 24, 25, 26–32; sometimes striped (alternate transverse dark and light bands); prostomium ½ open; 1st DP 4/5, but could be 3/4 or 5/6.....	<i>Eisenia fetida</i>
13 ² .	Tubercula pubertatis lacking/absent.....	14
14.	Clitellum begins on or before segment 24.....	15
14 ² .	Clitellum begins after segment 24.....	16
15.	Clitellum 24–31; small earthworm; 66–95 segments.....	<i>Bimastos beddardi</i>
15 ² .	Clitellum 23, 24–30; small earthworm; 65–110 segments.....	<i>Bimastos parvus</i>
16.	Clitellum 25–34, 35; small earthworm; 103–134 segments.....	<i>Bimastos lawrenceae</i>
16 ² .	Clitellum 26–31; small earthworm; 50–120 segments.....	<i>Dendrodrilus rubidus</i> (part.)
17.	Clitellum begins before segment 30.....	18
17 ² .	Clitellum begins after segment 30.....	19
18.	Clitellum 26, 27–31, 32; Tubercula pubertatis 28–31; medium to large earthworm.....	<i>Lumbricus rubellus</i>
18 ² .	Clitellum 28–33; Tubercula pubertatis 29–32; small earthworm.....	<i>Lumbricus castaneus</i>
19.	Clitellum 31, 32–37; Tubercula pubertatis 33–36; large earthworm.....	<i>Lumbricus terrestris</i>
19 ² .	Clitellum 33, 34–39; Tubercula pubertatis 35–37, 38; large earthworm.....	<i>Lumbricus festivus</i>
20.	Setae widely paired.....	21
20 ² .	Setae separate.....	24
21.	First dorsal pore at 5/6.....	22
21 ² .	First dorsal pore not at 5/6.....	23
22.	1st dorsal pore 5/6; clitellum 24, 25, 26, 27–31, 32, 32; Tubercula pubertatis 30–31; prostomium epilobic ½ open or tanylobic; small earthworm; 50–114 segments.....	<i>Eisenia hortensis</i>
22 ² .	1st dorsal pore 5/6; clitellum 26, 27–31, 32; Tubercula pubertatis 28, 29–30; prostomium epilobic open; small earthworm; 50–120 segments.....	<i>Dendrodrilus rubidus</i> (part.)
23.	1st dorsal pore at 5/6; clitellum 30, 31–36, 37; Tubercula pubertatis 33–34; epi ½ open.	<i>Satchellius mammalis</i>
23 ² .	23 ¹ . 1st dorsal pore at 21/22; clitellum 21–27; Tubercula pubertatis may or may not be present.	<i>Dendrobaena lusitana</i>
24.	Clitellum 28, 29–33,34; Tubercula pubertatis 29, 30–32, 33; 1st dorsal pore at 17/18; pale reddish	<i>Dendrobaena attemsi</i>
24 ² .	Clitellum 27, 28, 29–33, 34; Tubercula pubertatis 31–33; 1st dorsal pore at 4/5–6/7; red-purple	<i>Dendrobaena octaedra</i>
25.	Setae widely paired at least posteriorly.....	26
25 ² .	Setae closely paired.....	27

26.	Clitellum 29–34; Tubercula pubertatis 30–33; 1st dorsal pore at 7/8; large worm; blue-grey	<i>Octolasion cyaneum</i>
26 ¹ .	Clitellum 30–35; Tubercula pubertatis 31–34; 1st dorsal pore at 9/10–13/14; small worm; whitish-grey	<i>Octolasion tyrtaeum</i>
27.	Pigment present; dorsoventrally flattened posteriorly.....	28
27 ¹ .	Unpigmented or pigment lacking; body cylindrical.....	29
28.	Clitellum 27, 28–34, 35; Tubercula pubertatis 33–34; no genital tumescence on 28; prostomium epilobic ½ closed, large worm; 80–150 segments; colour grey-brown.....	<i>Aporrectodea longa</i>
28 ¹ .	Clitellum 27, 28–33, 34; Tubercula pubertatis 31–33; genital tumescence on 28; prostomium epilobic ½ closed; large worm; 93–169 segments; colour reddish brown.....	<i>Aporrectodea trapezoides</i> (part.)
29.	First dorsal pore at 4/5; small to medium worms.....	30
29 ¹ .	First dorsal pore at 11/12–13/14, medium to large worms.....	33
30.	Prostomium epilobic ⅓–½ closed.....	31
30 ¹ .	Prostomium epilobic ⅓–½ open.....	32
31.	Clitellum 25–½32 not flared; Tubercula pubertatis 29–½30; genital tumescence on c, d of 12	<i>Aporrectodea bowcrowensis</i>
31 ¹ .	Clitellum 25, 26–32 flared; Tubercula pubertatis 29–31; genital tumescence on a, b of 13, 14, 16, 17	<i>Aporrectodea rosea</i>
32.	Clitellum ½28, 29–35, 36; Tubercula pubertatis 33–34; genital tumescence on a, b of 9–12	<i>Aporrectodea limicola</i>
32 ¹ .	Clitellum 33, 34–42, 43; Tubercula pubertatis 34, 35–41, 42, 43; genital tumescence on c, d 34, 35–41, 42, 43.....	<i>Aporrectodea icterica</i>
33.	Genital tumescence lacking in 33, and often present in 26; clitellum 27–34; TP 30, 31–33, 34	<i>Aporrectodea tuberculata</i>
33 ¹ .	Genital tumescences present in 33.....	34
34.	Genital tumescence present in 33 and in 27; clitellum 27, 28, 29–34, 35; Tubercula pubertatis in 31–33	<i>Aporrectodea turgida</i>
34 ¹ .	Genital tumescence present or lacking in some or all of 33–34 and present in 28; clitellum 27, 28–33, 34; Tubercula pubertatis 31–33; male sterile	<i>Aporrectodea trapezoides</i> (part.) (albino)

Systematic section

There are three levels of taxa reported in this section—families, genera, and species. For each family (Lumbricidae, Megascolecidae and Sparganophilidae), a diagnosis and the designation of the type genus are given. For each of the 12 genera occurring in Canada, there is presented a synonymy, the type species, a diagnosis, and a discussion.

The information for the 33 species reported from Canada is presented in the following order: common name (English and French), synonymy, diagnosis, external anterior illustrations (lateral and ventral views), discussion, biology (habitats, reproduction, *etc.*), range, Canadian, America and Mexican distribution. For the most complete information on the distribution of the species in North America, see the checklists and ecoregion summaries by Reynolds (2017b; 2019; 2020c). The customary usage by oligochaetologists is to use Roman numerals to number the segments for external structures and Latin or Arabic numerals for internal structures. For the purposes of this study, North American distribution includes Canada, the United States of America, and Mexico. It should be noted, that

unless otherwise, stated all biological notes for the species are compilations from the literature and my personal research. Very little work has been done on the biology of earthworms in Canada and most data are from Europe. The most thorough reviews to which reference may be made for further information are those of Bouché (1972), Gates (1972a), Fragoso (2001), Reynolds (1977a) and Edwards *et al.* (2013).

There have been four species which have been reported from Canada, *e.g.* DriloBASE Taxo, but are not included in this publication. There are two species which are included here, but not found in DriloBASE Taxo – *Aporrectodea bowcrowensis* and *Arctiostrotus fontinalis* (Reynolds and Clapperton, 1996; Reynolds *et al.*, 2019a, respectively).

Dichogaster bolau (Acanthodrilidae formerly in Octochaetidae), a tropical species, was a live collection I received from Ontario many years ago and brought to New Brunswick, but that collection became extinct long ago (Reynolds and Wetzel, 2008). *Eudrilus eugeniae* (Eudrilidae) has been imported and reared for fish-bait in Canada, but this African species is not able to overwinter in Canada in the wild. *Haplotaxis gordioides* (Haplotaxidae) was reported from Ontario by Brinkhurst (1986). This species is an aquatic microdrile and not covered in the scope of this book. *Perionyx excavatus* (Megascolecidae) is a tropical species which has been accidentally imported with species for vermi-composting and is not able to overwinter in Canada in the wild if it escapes from the worm bin.

Family LUMBRICIDAE Claus, 1880

- 1876 Lumbricidae (part.), Claus, Grundzüge der Zool. (3rd ed.) 1: 416. (Included only *Lumbricus* and *Helodrilus*.)
1880 Lumbricidae (part.), Claus, Grundzüge der Zool. (4th ed.) 1: 478. (Excluded *Criodrilus* and *Pontoscolex*.)
1959 Lumbricidae-Gates, Bull. Mus. Comp. Zool. Harvard College 121: 255.

Distribution: Family Lumbricidae is the youngest phylogenetic family in the subclass of Oligochaeta. The family originated perhaps in the Palearctic, but there is a well-supported clade native to Eastern North America. Several species of the family are invasive in numerous regions, such as North America, Australia, South Africa, Southern South America and New Zealand, and they can be found even in tropical countries in higher elevation (*e.g.*, Zicsi, 2007). The total number of earthworm species of the Lumbricidae family comprises some 700 species belonging to 42 genera (Csuzdi, 2012; Rota and de Jong, 2015), however the Lumbricidae genera system is highly controversial and not settled yet (Mršić, 1991, Qiu and Bouché, 1998, Csuzdi and Zicsi, 2003, Dominguez *et al.*, 2015, de Sosa *et al.*, 2019).

In North America, there are both native and non-native species and genera. The native genera are *Bimastos* and *Eisenoides*, with 12 and two species, respectively. There are 11 genera of non-native lumbricids in North America (Reynolds, 2018, 2019; Reynolds and Wetzel, 2004, 2008, 2012, 2021), and 10 genera of non-natives in South America (Fragoso and Brown, 2007). In Europe, centres of diversity of lumbricids are situated in the Pyrenees and the Balkan Peninsula, as well as in the Carpathians and the Caucasus (Rota and de Jong, 2015). The biodiversity of the Balkans is the largest in Europe (Mršić, 1991). The reason for this is the complex geological history, the specific geographical position with several biogeographical regions, each characterized by specific ecological, climatic and geomorphological conditions, as well as a great variety of habitats (EEA, 2002).

Today, most lumbricological scientists agree that the original lumbricid fauna was significantly destroyed during the glacial period in much of Europe. The elements of today's lumbricid fauna come from various elements both in their historical age and in their origins. Namely, the present faunal elements are fragments of modified fauna from the Tertiary Period, that are thought to have originated in the Paleocene or Eocene. These are archaic (old) species that, with their adaptability to specific conditions, have survived to this day. Archaic species are now present in the Balkans, the Pyrenees and the Apennine peninsula, the northwestern part of Africa (Maghreb), the southern part of France, Sardinia, Corsica, the southern parts of Switzerland and the Czech Republic, Turkey and the central parts of Asia (Omodeo 1952, 1956, 1961, 1988; Bouché 1972, 1983; Mršić and Šapkarev 1988; Mršić 1991). In addition to archaic species, there are also "modern" species that are thought to have appeared in Miocene and later. A greater expansion of new "modern" species occurred during interglacial and postglacial periods, mainly in the Holocene (last 4 K years) (Mršić, 1991).

On the Balkan Peninsula there are 90 endemic species, with the largest share of the genus *Dendrobaena* (25) and *Allolobophora* (24) (Trakić *et al.*, 2016), while 39 endemic species in the basin of the Carpathians have been discovered with the dominant share of Dacian endemics. Of the total of 20 Dacian endemics, 12 species are of the genus *Octodrilus* whose distribution center is located in the Apuseni Mountains in the southern part of the Carpathians (Csuzdi *et al.*, 2011).

This relatively small but ecologically very important group of invertebrates from the Lumbricidae has been explored using various tools by a large number of researchers. Despite significant molecular research, there are still many species that do not have a stable taxonomic status, most of which relate to archaic species with specific taxonomic characteristics and disjunctive distribution. The answers to some of these questions are expected in the near future, which will certainly lead to a better understanding of many concerns regarding the origin and dynamics of the development of the Lumbricidae family as a whole.

Diagnosis (after Gates, 1972a: 61–62)

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. Ova, not yolky, Prostates, none.

Type genus

Lumbricus Linnaeus, 1758 (neotypification by Sims (1973)).

Genus *Allolobophora* Eisen, 1873

- 1873 *Allolobophora* Eisen, Öfv.-Akad. Förh. Stockholm 30(8): 46.
1975 *Allolobophora*-Gates, Megadrilogica 2(1): 3.
1977 *Allolobophora*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 35.
1980 *Allolobophora*-Gates, Megadrilogica 3(11): 177.

Type species

Lumbricus riparius Hoffmeister, 1843 (= *Enterion chloroticum* Savigny, 1826)

Diagnosis (after Gates, 1972a: 68; 1975a: 3)

Calciferous gland, opening into gut through a pair of vertical sacs posteriorly in x. Calciferous lamellae continued along lateral walls of sacs. Gizzard, mostly in xvii. Extrasophageal vessels, passing to dorsal trunk in xii. Hearts, in vi–xi. Nephridial bladders, J-shaped, closed end laterally, ducts passing into parieties near B. Nephropores, inconspicuous, behind the clitellum irregularly alternating between levels slightly above B and above D. Setae paired. Prostomium, epilobic. Longitudinal musculature, pinnate. Colour variable.

Discussion

Allolobophora was erected by Eisen (1873) without the designation of a type species and this situation was not corrected by Michaelsen (1900a) in his revision of the Lumbricidae. Typification of the genus was by Omodeo (1956) who selected *chlorotica* to be the type. Additional species that Eisen included in his *Allolobophora* were: *arborea*, *fetida*, *mucosa*, *norvegica*, *subrubicunda*, and *turgida*, none of which is now referable to this genus (Gates, 1975b: 7).

Allolobophora chlorotica (Savigny, 1826)

Green worm — Ver vert
(Fig. 4)

- 1826 *Enterion chloroticum* + *E. virescens* Savigny, Mém, Acad. Sci. Inst. Fr. 5: 183. Type species are missing (Reynolds and Cook, 1976).
1828 *Lumbricus anatomicus* Dugès, Ann. Sci. Nat. 15(1): 289.
1837 *Lumbricus chloroticus*-Dugès, Ann. Sci. Nat. (2), 8: 17, 19.
1843 *Lumbricus riparius* Hoffmeister, Arch. Naturg. 9(1): 189.
1845 *Lumbricus communis luteus* Hoffmeister, Regenwürmer, p. 29.
1865 *Lumbricus iridis* Johnston, Cat. British non-paras. worms, p. 60.
1873 *Allolobophora riparia*-Eisen + *A. mucosa* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 46, 47.
1882 *Allolobophora neglecta* Rosa, Atti Acc. Torino 18: 170.
1892 *Allolobophora cambrica* Friend, Essex Nat. 6: 31.
1896 *Allolobophora curiosa* Ribaucourt + *A. waldensis* Ribaucourt + *A. morganensis* Ribaucourt + *A. nusbaumi* Ribaucourt + *A. cambria* (laps.) Ribaucourt, Rev. Suisse Zoo1. 4: 46, 47, 83, 94.
1972 *Allolobophora chlorotica postepheba* Bouché, Inst. Natn. Rech. Agron., p. 269.
1975 *Allolobophora chlorotica kosovensis* Šapkarev, Ann. Fac. Sci. Université Skopje 27: 43.
1977 *Allolobophora chlorotica*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 36.
1998 *Allolobophora chlorotica eutypica* Qiu and Bouché, Doc. pédozool. intégral. 4: 86.

Diagnosis (after Reynolds *et al.*, 1974: 16; Reynolds, 1977a: 36)

Small earthworm, length 30–70 mm, diameter 3–5 mm, segment number 80–138, prostomium epilobic ½ closed, first dorsal pore 4/5. Clitellum saddle on xxviii, xxix–xxxvii. Tubercula pubertatis small, sucker-like discs on xxxi, xxxiii and xxxv. Setae closely paired, $AA > BC$, $DD = \frac{1}{2} C$ anteriorly, and $DD < \frac{1}{2} C$ posteriorly. Setae *c* and *d* on x often on white genital tumescences. Male pores in xv with large elevated glandular papillae extending over xiv and xvi. Female pores on xiv. Seminal vesicles, four pairs in 9–12. Spermathecae, three pairs opening on level *cd* in 8/9, 9/10 and 10/11. Colour variable, frequently green but sometimes yellow, pink, or grey. Body cylindrical.

Biology

This species has been found in a wide variety of soil types, with a pH of 4.5–8.0, including gardens, fields, pastures, forests, clay and peat soils, lake shores and stream banks, estuarine flats, and among all sorts of organic debris. It has been found in caves in Europe and North America and also in botanical gardens and greenhouses in these same continents. Eaton (1942) reported the habitat preference of this species as "wet and usually highly organic or polluted soil." It has been found in caves in Slovenia by Novak (2005).

In appropriate conditions, activity, including breeding, possibly occurs all year. In the northern part of the range there may be a single period of activity in the summer. There are records of active specimens occurring 300 mm below the soil surface, although the species generally is characterized as shallow-burrowing.

This species has been reported as the secondarily-preferred host of the cluster fly, *Pollenia rudis* (Fabr.) (Yahnke and George, 1972; Thomson and Davies, 1973b); otherwise it is of minimal economic importance. It seems not to be preferred by fish, and anglers have found little use for it as bait.

Climatic zone

Boreal, temperate, mediterranean, sub-tropical.

Ecological type

Allolobophora chlorotica in an endogeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis and considered a peregrine species, *A. chlorotica* is known from Europe, Iran, North America, South America, North Africa, and New Zealand (Reynolds, 1977a). It is also known from Bermuda (Reynolds and Fragoso, 2004), Isle of Man (Reynolds, 1996b), Tristão da Cunha Islands (Pickford, 1932) and Turkey (Mısırlıoğlu *et al.* 2018).

Reproduction

Allolobophora chlorotica is obligatorily amphimictic (Reynolds, 1974a). Defecation occurs below the soil surface as does copulation.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, Ontario, Quebec.

United States: Alaska, Arkansas, Arizona, California, Colorado, Connecticut, District of Columbia, Delaware, Georgia, Idaho, Illinois, Indiana, Kentucky, Maryland, Maine, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nevada, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Tennessee, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Mexico: Distrito Federal, México, Puebla states (Fragoso, 2001).

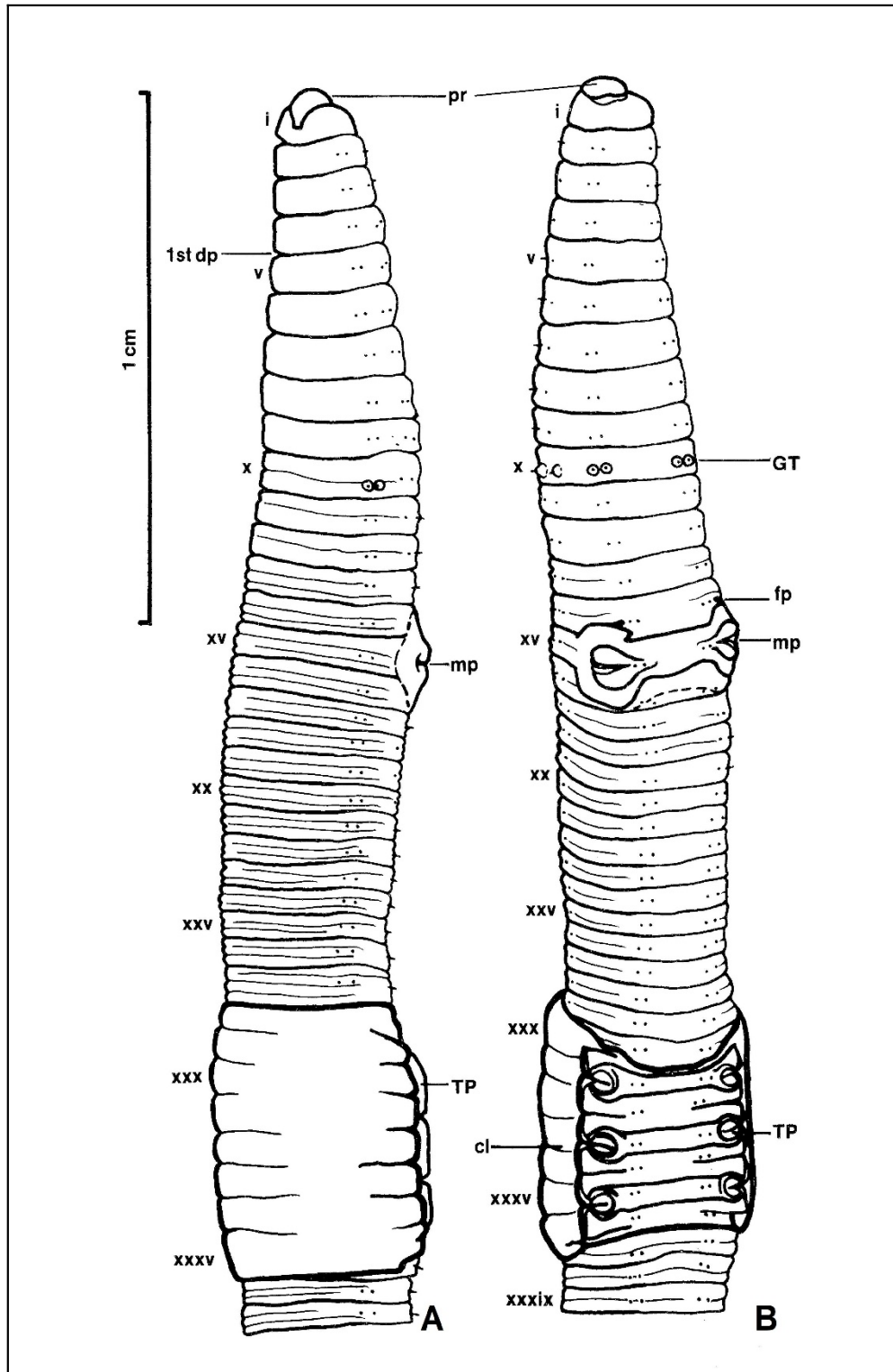


Fig. 4. External longitudinal views of *Allolobophora chlorotica* showing taxonomic characters. A. Dorsolateral view. B. Ventrolateral view (from Reynolds, 1977a).

Genus *Aporrectodea* Örley, 1885

- 1885 *Aporrectodea* Örley, Ertek. Term. Magyar Akad. 15(18): 22.
1900 *Allolobophora* (part.)-Michaelsen, Das Tierreich, Oligochaeta 10: 480.
1930 *Allolobophora* (part.)-Stephenson, Oligochaeta, p. 905, 906, 907, 908.
1941 *Allolobophora* (part.)-Pop, Zool. Jb. Syst. 74: 20.
1956 *Allolobophora* (part.)-Omodeo, Arch. Zool. Italiano 41: 180.
1972 *Allolobophora* (part.)-Gates, Trans. Amer. Philos. Soc. 62(7): 68, 69.
1972 *Allolobophora*-Gates, Bull. Tall Timbers Res. Stn. 12: 2.
1972 *Nicodrilus* Bouché, Inst. Natn. Rech. Agron., p. 315.
1975 *Aporrectodea*-Gates, Megadrilogica 2(1): 4.
1977 *Aporrectodea*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 40.

Type species

Lumbricus trapezoides Dugès, 1828.

Diagnosis (after Gates, 1975a: 4)

Calciferous gland, opening into gut through a pair of vertical sacs equatorially in x. Calciferous lamellae continued onto posterior walls of sacs. Gizzard, mostly in xvii. Extraesophageal vessels, passing to dorsal trunk in xii. Hearts, in vi–xi. Nephridial bladders, U-shaped, ducts passing into parieties near *B*. Nephropores, inconspicuous, irregularly alternating between levels slightly above *B* and above *D*. Setae, paired. Prostomium, epilobic. Longitudinal musculature, pinnate. Pigment, if present, not red.

Discussion

This forgotten genus originally included *Enterion chloroticum* Savigny, 1826 and *Lumbricus trapezoides* Dugès, 1828. Since Omodeo (1956) designated the former as the type species of *Allolobophora*, the latter automatically becomes the type for *Aporrectodea*. Bouché (1972) erected a new genus *Nicodrilus* with *Enterion caliginosum* Savigny, 1826 as the type and included *Lumbricus trapezoides* Dugès, 1828 in this new genus. Since *Aporrectodea* is a valid and available genus, *Nicodrilus* must be considered the junior synonym of *Aporrectodea*.

***Aporrectodea bowcrowensis* Reynolds and Clapperton, 1996**

Bowcrow worm — Ver de Bowcrow

(Fig. 5)

- 1996 *Aporrectodea bowcrowensis* Reynolds and Clapperton, *Megadrilogica* 6(8): 77. Type species are in the Canadian Museum of Nature (Aylmer, Quebec), cat. No. 1996-0052-53! (Reynolds and Wetzel, 2020).
2011 *Aporrectodea bowcrowensis*-Reynolds and Damoff, *Megadrilogica* 14(8): 165.
2018 *Aporrectodea bowcrowensis*-Reynolds, *Megadrilogica* 23(1): 5, 10.

Diagnosis (after Reynolds and Clapperton, 1996: 77)

Small earthworm, length 24–43 mm; width 2.15–2.85 mm; segment number 82–136. Prostomium epilobic. Setae, closely paired, beginning in ii. Setal formula $AA > AB < BC > CD < DD > \frac{1}{2}C$ anterior to clitellum, $DD < \frac{1}{2}C$ posterior to clitellum. Clitellum, saddle, not flared, reaching almost to *B*, usually on xxv– $\frac{1}{2}$ xxxii. Tubercula pubertatis, continuous elevated band, generally on xxix– $\frac{1}{2}$ xxx. First dorsal pore in 4/5. Genital tumescences, obvious, most often on *c* and *d* of xii. Male pores, minute, equatorial at bottom of deep cleft on elevated papillae in xv, usually midway between band *c*. Female pores, minute, equatorial but not elevated in xiv, slightly dorsal to *b*. Spermathecal pores, minute near mD at 9/10–10/11. Nephropores, inconspicuous, above *d* near mD in the *y* area of secondary segmentation. Calciferous sacs opening vertically into equator of esophagus in x. Gizzard, mainly in xvii. Intestinal origin, in xv. Nephridial vesicles (bladders), U-shaped, ducts passing into parieties near *B*. Spermathecae, two pairs with short ducts. Seminal vesicles, four pairs in 9–12. Typhlosole, beginning in region of xxi–xxiii. Colour, unpigmented but greyish when preserved. Additional details can be found in the original description.

Biology

In the unglaciated region of the Porcupine Hills in the Bow Crow Forest *Aporrectodea bowcrowensis* was collected under aspen (*Populus tremuloides*), grass under logs, rocks near a stream, digging in sandy soil on a recently flooded stream bank [cottonwood poplar (*Populus deltoides*) and white spruce (*Picea glauca*)] and, digging under logs and rocks on stream bank and bottom recently flooded (Reynolds and Clapperton, 1996). In Colorado, *Ap. bowcrowensis* was collected in a residential garden and a lake shore (Reynolds and Damoff, 2011).

Reproduction

Aporrectodea bowcrowensis is considered amphimictic until there is evidence to the contrary (Reynolds and Clapperton, 1996).

Climatic zone: Temperate.

Ecological type: *Aporrectodea bowcrowensis* is an endogeic species (Reynolds, 2018).

Origin, range: *Aporrectodea bowcrowensis* may be a native species in North America, since it is currently known only from Canada and the United States.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Rare in North America

Canada: Alberta.

United States: Colorado.

Mexico: none.

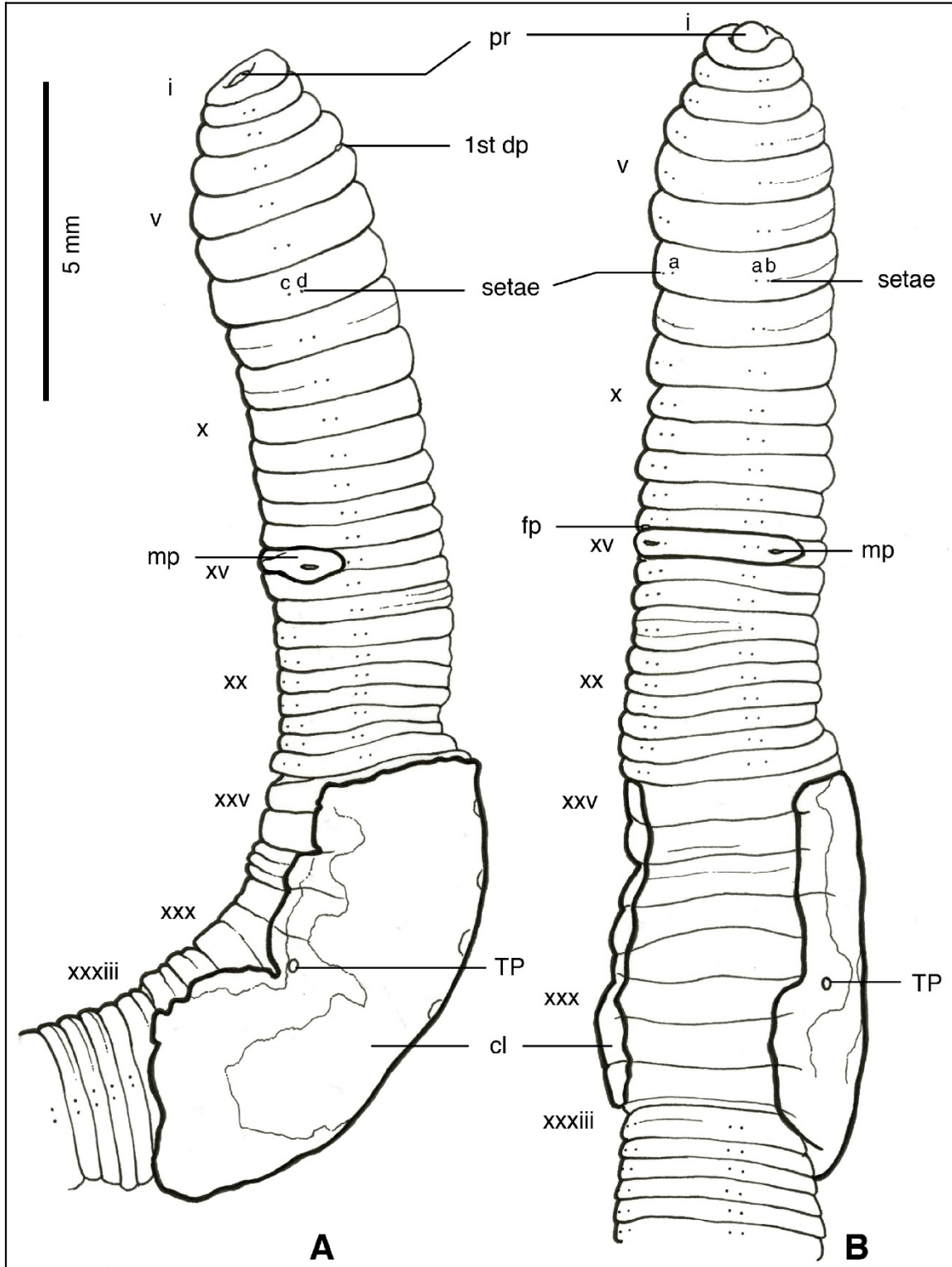


Fig. 5. External longitudinal views of *Aporrctodea bowcrowensis* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

Aporrectodea icterica (Savigny, 1826)

Mottled worm — Ver marbré

(Fig. 6)

- 1826 *Enterion ictericum* Savigny, Mém. Acad. Sci. Inst. France 5: 183. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1837 *Lumbricus ictericus*-Dugès, Ann. Sci. Nat. (2), 8: 17.
- 1886 *Allolobophora icterica*-Rosa, Atti Ist. Veneto, ser. 6, 4: 685.
- 1896 *Allolobophora claparedi* Ribaucourt, Rev. Suisse Zool. 4: 85
- 1900 *Helodrilus ictericus*-Michaelsen, Das Tierreich, Oligochaeta 10: 500.
- 1926 *Bimastus tenuis*-Pickford, Ann. Mag. Nat. Hist. (9), 17: 96.
- 1938 *Eophila icterica*-Tétry, Contr. Étude Faune Est France, p. 269.
- 1972 *Allolobophora icterica*-Bouché, Inst. Natn. Rech. Agron., p. 273.
- 1976 *Aporrectodea icterica*-Reynolds, Megadrilogica 2(12): 3.
- 1977 *Aporrectodea icterica*-Schwert, Canadian J. Zool. 55(1): 245.

Diagnosis (after Reynolds, 1977: 42)

Small to medium sized earthworm, length 55–135 mm, diameter 3–5 mm, segment number 140–190, prostomium epilobic $\frac{1}{2}$ – $\frac{3}{4}$ closed, first dorsal pore 4/5. Clitellum saddle on xxxiii, xxxiv–xlii, xliii. Tubercula pubertatis in the form of a band xxxiv, xxxv–xli, xlii, xliii. Setae closely paired, posteriorly $AA:AB:BC:CD = 45:5:25:4$; c and d in form of genital tumescences in ix and a and b in xi–xvii, xxix–xxxiv, and xlii–xlv. Male pores on xv, minute, about at mid BC , with tumescences small and restricted to xv. Female pores in xiv. Seminal vesicles, four pairs in 9–12, the anterior two pairs smaller. Spermathecae, three pairs with ducts opening on level C in 8/9–10/11, sometimes an anterior pair opening in 7/8. Colour, lacking. Body cylindrical.

Biology

In Europe, Černosvitov and Evans (1947), Gerard (1964), and Tétry (1938) reported the species from garden soil, meadows, and orchards. With the exception of Bouché's (1972) study in France, *Ap. icterica* has been reported infrequently and in low numbers in Europe. In Canada, the sole site was in the University of Guelph Arboretum and a sole site in a park in Rochester, New York (Reynolds, 1976: 3). *Ap. icterica* is not known to have any economic importance.

Climatic zone: Temperate, mediterranean.

Ecological type: *Aporrectodea icterica* is an epi-endogeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis and considered a peregrine species, *Ap. icterica* is now known from western Europe and North America (Reynolds, 1976c; Schwert, 1977).

Reproduction:

Aporrectodea icterica is obligatorily amphimictic (Gates, 1968).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Very rare in North America.

Canada: Ontario.

United States: New York.

Mexico: none.

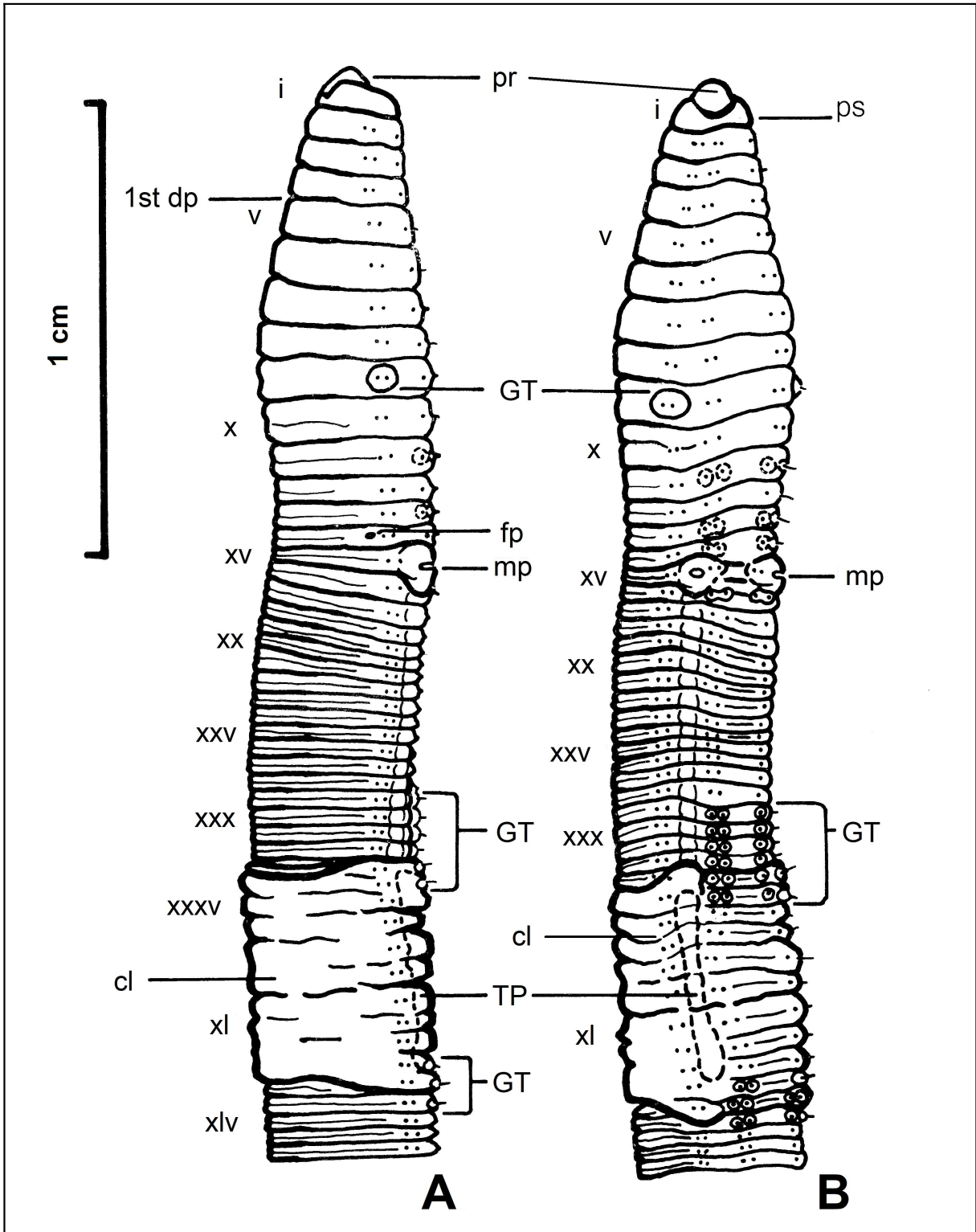


Fig. 6. External longitudinal views of *Aporectodea icterica* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Aporrectodea limicola* Michaelsen, 1890**
European mud worm — Ver de boue européen
(Fig. 7)

- 1890 *Allolobophora limicola* Michaelsen, Jb. Hamburg. Wiss. Anst. 7: 10. Type species is in the Zoologisches Museum Hamburg, Universität Hamburg, cat. no. 124! (Reynolds and Cook, 1976).
1972 *Allolobophora limicola*-Gates, Bull. Tall Timbers Res. Stn. No. 12, p. 113.
2007 *Aporrectodea limicola*-Marshall and Fender, Megadrilogica 11(4): 33.
2018 *Aporrectodea limicola*-Reynolds, Megadrilogica 23(1): 3, 4, 5, 6, 7, . . . 33.

Diagnosis (after Michaelsen, 1900: 484, translated from German by JWR)

Small to medium sized earthworm, length 42–90 mm, diameter 3–4 mm, segment number 103–127, prostomium epilobic, ½ open, first dorsal pore 4/5. Clitellum saddle on ⅓ xxviii, xxix–xxxv, xxxvi. Tubercula pubertatis, 2 pairs on xxxiii, xxxiv. Genital tumescences including a and b, in one or more of the following: ix, x, xi, xii, xvii, xxix, xxx, xxi, xxxii, xxxv, xxxvi. Setae closely paired, $AA > BC$, $DD = \frac{1}{2} C$. Male pores on xv, large elevated papillae on xiv and xvi. Female pores in xiv. Seminal vesicles, four pairs in 9–12. Spermathecae, two pairs opening on level *cd* in 9/10 and 10/11, which are preseptal and differing from the other species in the *trapezoides* group. Colour, unpigmented, live material appears flesh coloured.

Biology

Since publication of Michaelsen's (1900a) monograph, *Ap. limicola* is known to have been identified occasionally as *A. caliginosa*. Other unadmitted or unrecognized misidentifications of the taxon may have been made (Gates, 1972b). This species has been reported from peat bogs at the Arnold Arboretum in Boston and the Calloway Gardens in Pine Mountain, Georgia. In British Columbia, at Grice Bay under western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and in soil near a boat ramp, as well in silt under skunk cabbage (*Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton) near Long Beach (Marshall and Fender, 2007). *Ap. limicola* has been recorded from soils with a pH range of 3.7–7.0.

Reproduction: *Aporrectodea limicola* is obligatorily amphimictic (Reynolds, 1974a).

Climatic zone: Temperate.

Ecological type: *Aporrectodea limicola* is an endogeic, acidophilic species occurring in grasslands and forests with a preference for moist habitats.

Origin, range

A native of Palaearctis and considered a peregrine species, but original home is unknown. In Europe it has been reported from Austria, Belgium, Czech Republic, England, France, Germany, Ireland, Scotland, Sweden, Switzerland (Gates, 1972a; Sims and Gerrard, 1999).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Relatively rare in North America.

Canada: British Columbia.

United States: Georgia, Hawaii, Maryland, Massachusetts, New Jersey, Oregon, Pennsylvania, Washington, Wyoming.

Mexico: none.

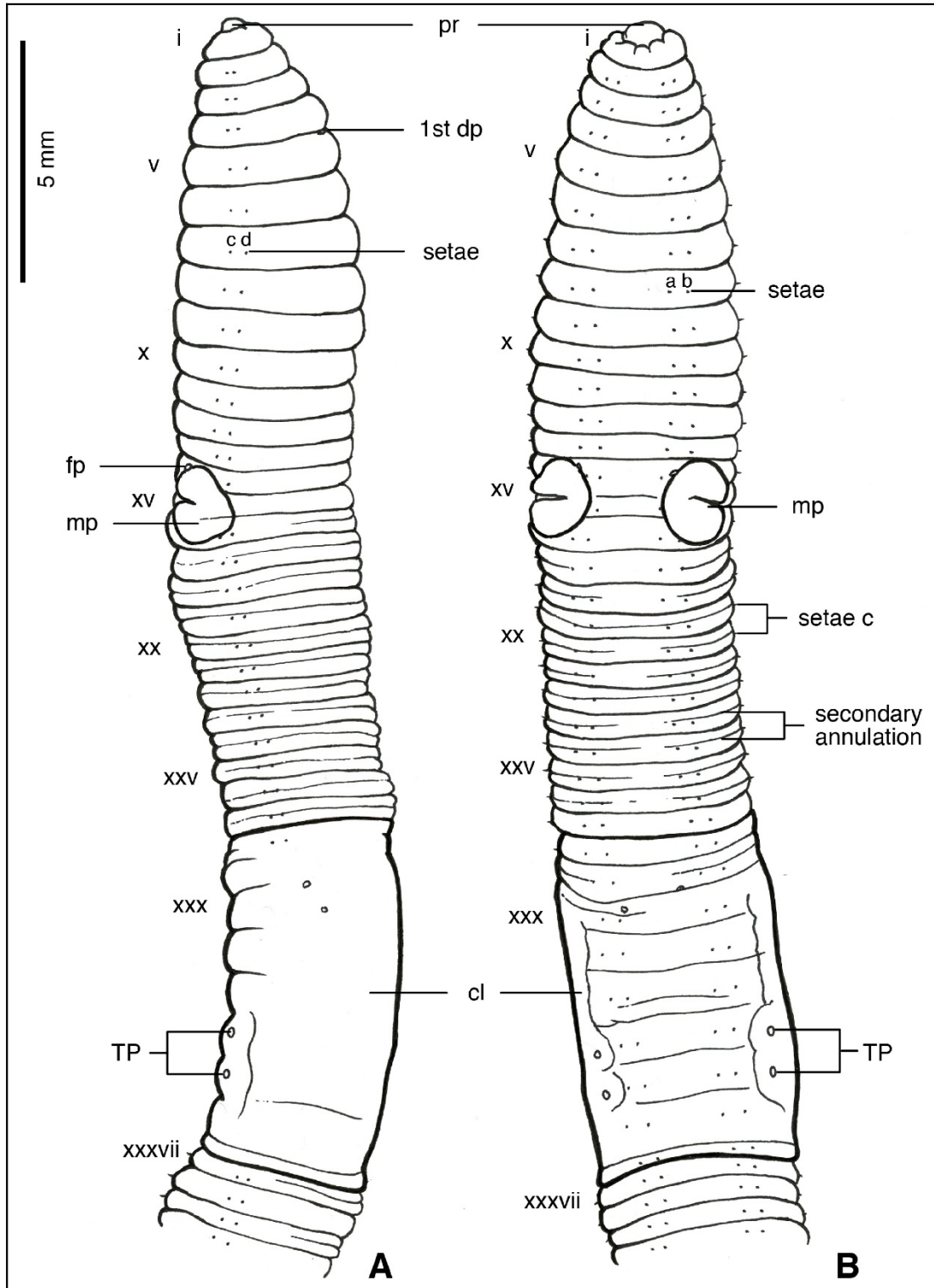


Fig. 7. External longitudinal views of *Aporrectodea limicola* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

***Aporrectodea longa* (Ude, 1885)**
Black head worm — Ver à tete noire
(Fig. 8)

- 1826 *Enterion terrestre* (non 1820) Savigny, Mém. Acad. Sci. Inst. France 5: 180.
1837 *Lumbricus terrestris*-Dugès, Ann. Sci. Nat. (2), 8: 17, 18.
1845 *Lumbricus agricola* (non 1842) (part.) Hoffmeister, Regenwürmer, p. 5.
1885 *Allolobophora longa* Ude, Zeit. Wiss. Zool. 57: 57. Type species are unknown (Reynolds and Cook, 1976).
1893 *Allolobophora terrestris*-Rosa, Mem. Acc. Torino (2), 43: 424.
1900 *Helodrilus (Allolobophora) longus*-Michaelsen, Das Tierreich, Oligochaeta 10: 483.
1972 *Nicodrilus longus longus*-Bouché, Inst. Natn. Rech. Agron., p. 322.
1977 *Aporrectodea longa*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 43.
1982 *Allolobophora terrestris longa*-Zicsi, Acta Zool. Hung. 28: 432.
1988 *Aporrectodea (Aporrectodea) longa*-Mršić and Šapkarjev, Acta Mus. Macedonici Sci. Nat. 154 (1): 29.

Discussion

Previously, and perhaps especially in Britain, the species seems to have been confused with *Lumbricus terrestris*. *Aporrectodea longa* was placed by Rosa (1893) in the synonymy of *A. terrestris* (Savigny, 1826). Michaelsen (1900a) reversed the synonymy and at the same time put *Allolobophora* in *Helodrilus* as a subgenus. Savigny's name, *terrestris*, still is in use today in spite of the fact that it has been known for at least 70 years to be preoccupied by *Enterion terrestre* Savigny, 1820.

Worms called by Europeans *A. terrestris* probably were often of Ude's species but how frequently and when cannot be determined without examination of the specimens involved. Also required is a more adequate characterization of *non-longa* material. Some Europeans have referred to the two taxa as *A. terrestris* subsp., var., or *A. t. f. typica* and *longa*. Specimens of *f. typica* have not been available to this author. If unpigmented material, now mainly distinguished by a bipartite origin of tubercula and location of genital tumescences in x–xii, xxx, xxxi, xxxiii, is specifically distinct from *Aporrectodea longa*, it obviously must have another name than *Lumbricus terrestris*.

Diagnosis (after Reynolds *et al.*, 1974: 18; Reynolds, 1977a: 43)

Large earthworm, length 90–150 mm, diameter 6–9 mm, segment number 150–222, prostomium, epilobitic ½ closed, first dorsal pore 12/13. Clitellum saddle on xxvii, xxviii–xxxiv, xxxv. Tubercula pubertatis xxxii–xxxiv. Setae closely paired, posteriorly AA:AB:BC:CD = 60: 7:28:5; *a* and *b* in form of genital setae on genital tumescences in ix, x, xi, xxxi, xxxiii, xxxiv, and sometimes xii. Male pores on xv with elevated glandular borders, sometimes extending to xiv and xvi. Female pores on xiv. Seminal vesicles, four pairs in 9–12, the anterior pairs smaller. Spermathecae, two pairs with short ducts opening on level *c* in 9/10 and 10/11. Colour, grey or brown with slight iridescence dorsally. Body cylindrical and dorsoventrally flattened posteriorly.

Biology

Aporrectodea longa often has been studied in Europe, since it is a relatively rare species in North America. In Europe, Černosvitov and Evans (1947) and Gerard (1964) reported the species from cultivated soil, gardens, pastures, and woodlands, and found it to be abundant in soils bordering rivers and lakes. According to Gates (1972b), *Ap. longa* is found in soils with a pH of 4.5 to 8.0, in greenhouses and botanical gardens, lawns, peat bog, in compost and under manure, including chicken yards and cow yards, and in many other types of soils. The species is known from caves in Europe.

In appropriate circumstances, year-round activity is possible. Feeding, which takes place nocturnally on the surface of the soil, seems to be selective and leaves occasionally are dragged into the burrows. Activity is maintained in winter below the frost line. Casts are deposited on the surface and *Ap. longa*, together with *Ap. nocturna* (Evans, 1946), are believed responsible for the surface castings in England that Darwin studied so intensively (Reynolds *et al.*, 1974). Exposure to -2° to -50° C for 12 hours, is not fatal. Critical heat death temperature is 25.7° C (Gates, 1972b).

Reproduction

Aporrectodea longa is obligatorily amphimictic with copulation, under ground (Reynolds, 1974a). Incubation, 10–15 weeks, one hatching per cocoon. Maturity, reached in 38–71 weeks.

Climatic zone: Temperate, mediterranean.

Ecological type

Aporrectodea longa is an anecic species (Reynolds, 2018).

Origin, range

Aporrectodea longa is a native of Palaearctis and is known from Europe, North America, Central America, Africa and Australasia (Reynolds, 1977a). A study which I recently found reported it from Bangladesh (Makin *et al.*, 2014), which was a surprise, because in my four working trips to that country and two papers I never encountered any lumbricids and only Oriental species (Reynolds, 1994c; Reynolds *et al.*, 1995).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, Quebec.

United States: Alabama, California, Colorado, Connecticut, Indiana, Maine, Maryland, Massachusetts, Michigan, Montana, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, South Dakota, Tennessee, Vermont.

Mexico: Distrito Federal, México states (Fragoso, 2001).

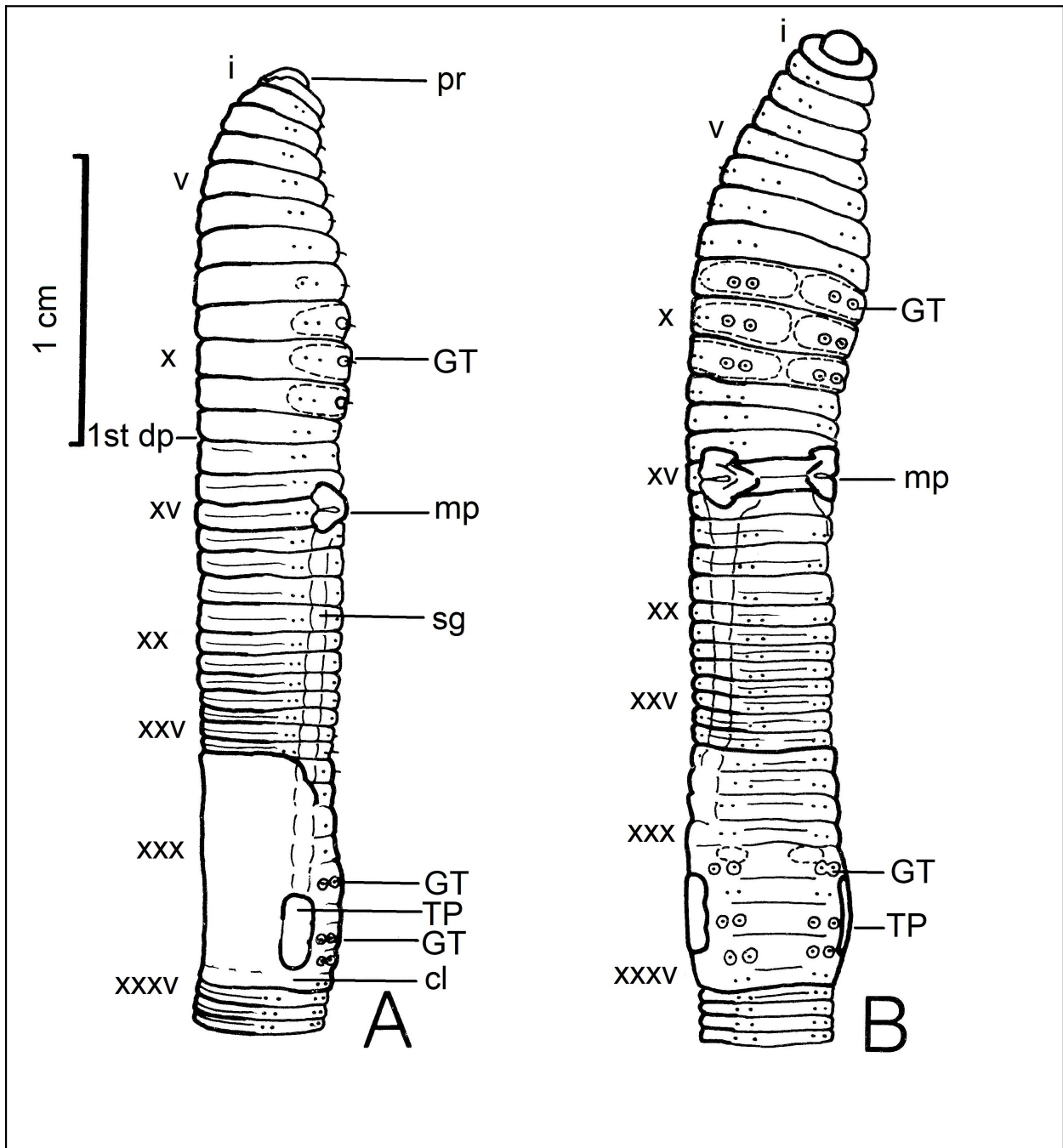


Fig. 8. External longitudinal views of *Aporrectodea longa* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Aporrectodea rosea* (Savigny, 1826)**

Pink soil worm — Ver rose du sol

(Fig. 9)

- 1826 *Enterion roseum* Savigny, Mém. Acad. Sci. Inst. France 5: 182. Type species missing (Reynolds and Cook, 1976).
- 1837 *Lumbricus roseus*-Dugès, Ann. Sci. Nat. (2), 8: 17, 20.
- 1845 *Lumbricus communis anatomicus* (part.) Hoffmeister, Regenwürmer, p. 28.
- 1873 *Allolobophora mucosa* (part.) Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 47.
- 1875 *Lumbricus aquatilis* Vejdovský, SB Bohm. Ges., p. 199.
- 1879 *Lumbricus muscosus*-Tauber, Annul. Danmark, p. 68.
- 1882 *Lumbricus carneus* (err. non *Enterion carneum* Savigny, 1826)-Vejdovský, Brunnenw. Prague, p. 51.
- 1884 *Allolobophora carnea*-Vejdovský, Syst. Morph. Oligochäten, p. 61.
- 1885 *Allolobophora aquatilis*+ *A. aquatilis*-Örley, Ertek. Term. Magyar Akad. 15(18): 24, 28.
- 1893 *Allolobophora rosea*-Rosa, + *A. r. macedonica* Rosa, Mem. Acc. Torino (2), 43: 424, 427.
- 1896 *Allolobophora danieli rosai*-Ribaucourt, Rev. Suisse Zool. 4: 39.
- 1900 *Eisenia rosea*-Michaelsen, Das Tierreich, Oligochaeta 10: 478.
- 1903 *Helodrilus (Bimastus) bimastoides* Michaelsen, Mitt. Naturh. Mus. Hamburg 19: 13.
- 1907 *Helodrilus (Bimastus) indicus* Michaelsen, Mitt. Naturh. Mus. Hamburg 24: 188.
- 1917 *Helodrilus (Eisenia) roseus*-Smith, Proc. United States Natn. Mus. 52(2174): 165, 166.
- 1922 *Helodrilus (Allolobophora) prashadi* Stephenson + *A. (Bimastus) indica*-Stephenson, Rec. Indian Mus. 22: 440, 441.
- 1940 *Eisenia rosea* f. *typica* + *E. r. f. macedonica* + *Allolobophora hataii* + *A. harbinensis* + *A. dairensis* + *A. jeholensis* Kobayashi, Sci. Rep. Tôhoku Imp. Univ. (4), 15: 285-287, 288-289, 290-291, 291-293, 293-295.
- 1949 *Eophila kulagini* Malević, Dokl. Akad. Nauk SSSR (Biol.) 47: 400.
- 1967 *Allolobophora rosea* var. *alpina* Vedovini, Bull. Soc. Zool. France 92: 793.
- 1972 *Allolobophora rosea*-Edwards and Lofty, Biol. earthworms, p. 217.
- 1972 *Allolobophora rosea rosea*-Bouché + *A. r. vedovinii* Bouché, Inst. Natn. Rech. Agron., p. 418, 423.
- 1974 *Eisenia rosea*-Reynolds, Clebsch and Reynolds, Bull. Tall Timbers Res. Stn., no. 17, p. 35.
- 1976 *Aporrectodea rosea*-Gates, Megadrilogica 2(12): 4.
- 2006 *Eisenia hataii* Huang, Xu, Wang and Zhen, J. China Agric. Univ. 11(3): 18.

Diagnosis (after Reynolds *et al.*, 1974: 36; Reynolds, 1977a: 78)

Small earthworm, length 25–85 mm, diameter 3–5 mm, segment number 120–150, prostomium epilobic $\frac{1}{2}$ – $\frac{2}{3}$ closed, first dorsal pore 4/5. Clitellum, saddle, somewhat flared ventrally xxv, xxvi–xxxii. Tubercula pubertatis xxxiv–xxxvi. Setae closely paired, usually $AA > BC < DD$, $AB > CD$, anteriorly $DD = \frac{1}{2}C$, posteriorly $DD = \frac{1}{2}C$. Male pores with elevated glandular papillae in xv with male tumescences extending over xiv and xvi. Female pores in xiv. Seminal vesicles, four pairs in 9–12. Spermathecae, two pairs with short ducts opening near mD line or halfway between mL and MD in 9/10 and 10/11. Body cylindrical, except in clitellar region. Unpigmented, but colour appears rosy or greyish when alive, and white when preserved.

Biology

Černosvitov and Evans (1947) and Gerard (1964) recorded *Ap. rosea* in soil, fields, gardens, pastures, and forests, under leaves and stones, and frequently on river and lake banks. Gates (1972a) mentioned soils of pH 4.9–8.0 and recorded that it is found often enough in conditions that were thought to justify characterization as "amphibious". Murchie (1956) states, "*Ap. rosea*, although showing considerable adaptability in habitat requirements, is to be regarded primarily as a true soil species". The results of this survey would tend to confirm Murchie's statement. In soil under logs was the most common habitat of this species in Ontario. *Aporrectodea rosea* is one of the cosmopolitan species that have been introduced by Europeans into all parts of the world. It is known also from caves in Europe, Asia, and North America, as well as from botanical gardens and greenhouses. It has been found in caves in Slovenia by Novak (2005). It is the only species widely distributed in the virgin steppes of Russia and the mountains of the Caucasus (Gates, 1972a).

In suitable conditions activity, including breeding, is possible the year round. But in northern parts of the range there is a resting stage during winter cold and summer drought in which both hibernation and aestivation are spent tightly coiled in a small pink ball (Gates, 1972a). According to Thomson and Davies (1974), *Aporrectodea rosea* produces surface casts, despite some contrary statements in the literature.

Aporrectodea rosea is the primary host of the cluster fly, *Pollenia rudis* (Fabr.) (Yahnke and George, 1972; Thomson and Davies, 1973a).

Climatic zone: Boreal, temperate, mediterranean.

Ecological type

Aporrectodea rosea is an endogeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis and considered peregrine, *Ap. rosea* is now known from Europe, North America, South America, Africa, Asia, and Australasia. It also occurs in Bermuda (Reynolds and Fragoso, 2004), Iceland (Backlund, 1949), Tristão da Cunha Islands (Pickford, 1932) and Turkey (Reynolds and Misirlioğlu, 2018). Generally, therefore, it is a cosmopolite although apparently absent from tropical lowlands (Gates, 1972a).

Reproduction

The species is parthenogenetic and biparental reproduction of anthropochorous morphs is unknown (Gates, 1974, Reynolds, 1974a). Černosvitov (1930) reported degeneration, phagocytosis, and reabsorption of sperm and Tuzet (1946) recorded atypical spermatogenesis. Evans and Guild (1948) reared isolated individuals to sexual maturity which then produced fertile cocoons.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan.

United States: Arkansas, Arizona, California, Colorado, Connecticut, Delaware, Florida, Georgia, Hawaii, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wyoming.

Mexico: Baja California, Distrito Federal, Hidalgo, México, Nuevo León (Reynolds and Reynolds, 2004b), Puebla, San Luis Potosi, Tamaulipas states (Fragoso and Reynolds, 1997; Fragoso, 2001).

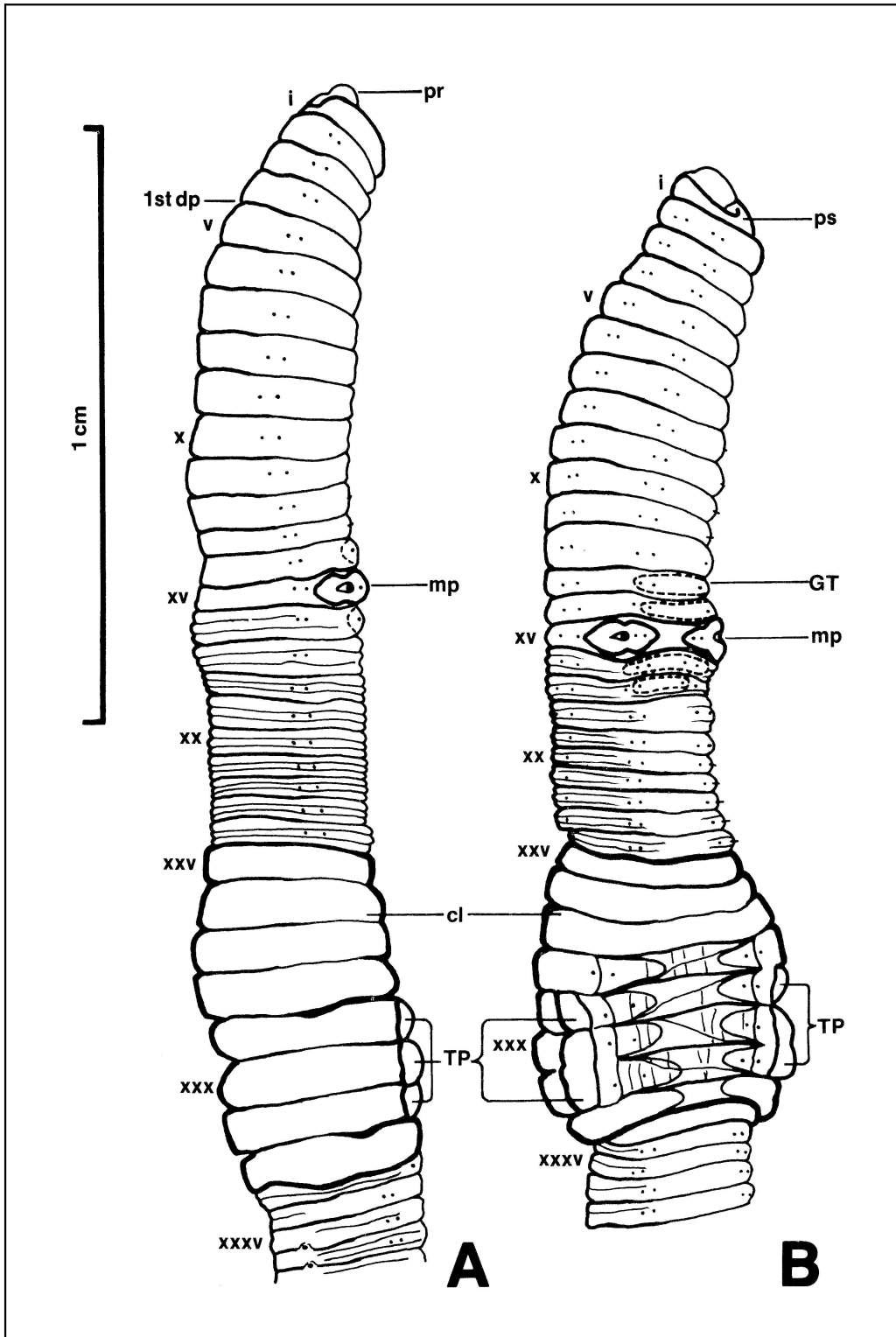


Fig. 9. External longitudinal views of *Aporrectodea rosea* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Aporrectodea trapezoides* (Dugès, 1828)**

Southern worm — Ver méridional

(Fig. 10)

- 1828 *Lumbricus trapezoides* Dugès, Ann. Sci. Nat. 15(1): 289. Type species are missing (Reynolds and Cook, 1976).
- 1899 *Allolobophora inflata* Michaelsen, Zool. Jb. Syst. 12: 124.
- 1917 *Helodrilus (Helodrilus) mariensis* Stephenson, Rec. Indian Mus. 13: 414.
- 1923 *Allolobophora (Eophila) mariensis*-Stephenson, Fauna British India, Oligochaeta, p. 504.
- 1931 *Allolobophora caliginosa trapezoides*-Chen, Cont. Biol. Lab. Sci. Soc. China (Zool.) 7(3): 168.
- 1938 *Dendrobaena samarigera* var. *graeca* Černosvitov, Zool. Anz. 123: 192.
- 1941 *Allolobophora caliginosa* f. *trapezoides*-Gates, Proc. California Acad. Sci. (4), 23: 452.
- 1942 *Allolobophora caliginosa* (part.)-Eaton, J. Wash. Acad. Sci. 32(8): 246.
- 1948 *Allolobophora iowana* Evans, Ann. Mag. Nat. Hist. (11), 14: 515.
- 1956 *Allolobophora (Microeophila) mariensis*-Omodeo, Arch. Zool. Italiano 41: 184.
- 1969 *Allolobophora longa* (part.)-Reinecke and Ryke, Rev. Écol, Biol. Sol. 6: 515.
- 1972 *Nicodrilus (Nicodrilus) caliginosus meridionalis* Bouché, Inst. Natn. Rech. Agron., p. 334.
- 1972 *Allolobophora trapezoides*-Gates, Bull. Tall Timbers Res. Stn. No. 12: 2.
- 1973 *Allolobophora caliginosa* f. *trapezoides*-Plisko, Fauna Polski, no. 1, p. 108.
- 1975 *Aporrectodea trapezoides*-Reynolds, Megadrilogica 2(3): 3.

Diagnosis (after Reynolds *et al.*, 1974: 36; Reynolds, 1977a: 78)

Medium to large earthworm, length 80–140 mm, diameter 3–7 mm, segment number 93–169, generally > 130, prostomium epilobic $\frac{1}{2}$ – $\frac{3}{4}$ closed, first dorsal pore 12/13, usually. Clitellum saddle on xxvii, xxviii–xxxiii, xxxiv. Tubercula pubertatis xxxi–xxxiii. Setae closely paired, posteriorly $AA > AB$, $DD < \frac{1}{2}C$. Genital tumescences including *a* and *b* setae only, in ix–xi, xxxii–xxxiv, often in xxviii and occasionally in the region of xxvi–xxix. Male pores on xv. Female pores in xiv. Seminal vesicles, four pairs in 9–12. Spermathecae, two pairs opening in 9/10 and 10/11. Colour variable and often lighter behind the clitellum until near the hind end, then deeper, slate, brown, brownish, reddish brown, and occasionally almost reddish, but not purple. Body dorsoventrally flattened posteriorly so that a cross section is nearly transversely rectangular with setal couples at the corners.

Biology

This species is found in a wide variety of habitats, according to the material examined by Gates (1972a). Similar statements have been made by Smith (1917), Olson (1928), Eaton (1942), Gates (1967), Reynolds (1973a-c), and Reynolds *et al.* (1974). According to Gates (1972b), *Ap. trapezoides* is found in the earth around the roots of potted plants, in gardens, cultivated fields, forest soils of various types, on the banks of streams, and sometimes in sandy soil. It has been recorded from caves in North America (Reeves and Reynolds, 1999; Holler *et al.*, 2020) and Afghanistan, and in California and Arizona may occur at elevations of 1525 m or more. Activity may be year round under suitable conditions, but it is not possible yet to make a similar statement concerning breeding.

This species is often found in earthworm culture beds and is one of the five species commonly sold and used for bait in North America (Gates, 1972a).

It should be noted that many literature records of this species must be treated with caution because of taxonomic confusion. For a long time *Aporrectodea trapezoides* was considered to be a variety of subspecies of *Aporrectodea caliginosa* but it is unlikely that all references to *Ap. caliginosa* subspecies, variety, or forma, *trapezoides* do in fact refer to *Ap. trapezoides* (*cf.* Gates, 1972b: 4).

Although *Aporrectodea rosea* and *Aporrectodea turgida* are considered the primary hosts for *Pollenia rudis*, recently there was the first report of *Aporrectodea trapezoides* as a host for the cluster fly (Reynolds *et al.*, 2020b).

Reproduction

Aporrectodea trapezoides is parthenogenetic, sometimes with pseudogamy, and male sterility is also common (Gates, 1972a; Reynolds, 1974a).

Origin, range

A native of Palaearctis and considered a peregrine species, *Aporrectodea trapezoides* is now known from Europe, North America, South America, Africa, and Australia

Climatic zone: Boreal, temperate, mediterranean, sub-tropical.

Ecological type

Aporrectodea trapezoides is an endogeic species (Reynolds, 2018).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan.

United States: Alaska, Alabama, Arkansas, Arizona, California, Colorado, Connecticut, District of Columbia, Delaware, Florida, Georgia, Hawaii, Iowa, Idaho, Illinois, Indiana, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, North Carolina, North Dakota, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Virginia, West Virginia, Wyoming.

Mexico: Baja California Sur, Distrito Federal, Durango, Hidalgo, México, Michoacán, Nuevo León (Reynolds and Reynolds, 2004b), Puebla, Tamaulipas, Tlaxcala states (Fragoso and Reynolds, 1997).

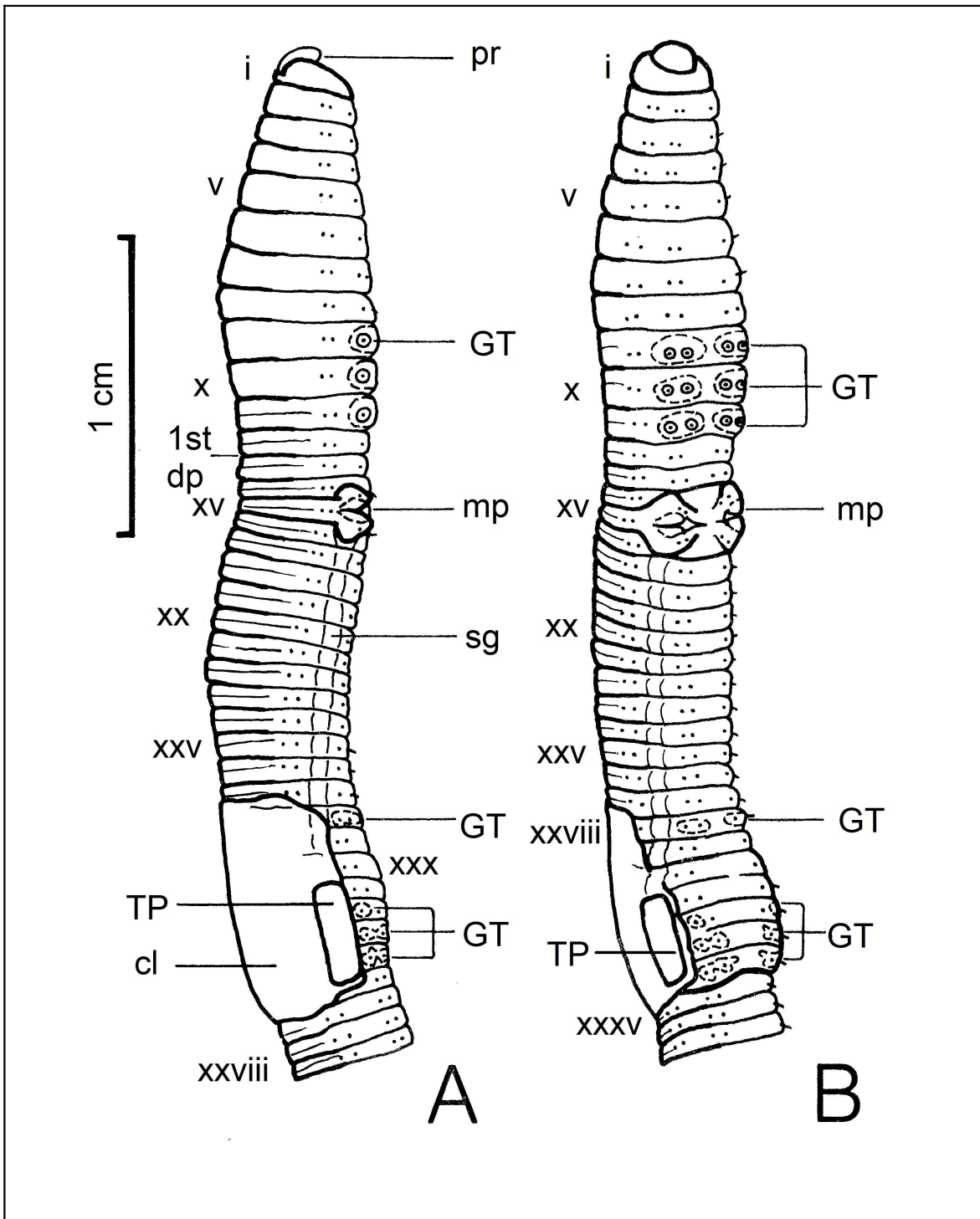


Fig. 10. External longitudinal views of *Aporrectodea trapezoides* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Aporrectodea tuberculata* (Eisen, 1874)**

Canadian worm — Ver canadien

(Fig. 11)

- 1874 *Allolobophora turgida* f. *tuberculata* Eisen, Öfv, Vet-Akad. Förh. Stockholm 31(2): 43. Types species not designated (Reynolds and Cook, 1976).
- 1986 *Allolobophora waldensis* Ribaucourt + *A. nusbaumi* Ribaucourt, Rev. Suisse Zool. 4: 46.
- 1910 *Allolobophora similis* Friend, Gardener's Chron. 48: 99.
- 1911 *Aporrectodea similis*-Friend, Zoologist (4), 15: 144.
- 1927 *Helodrilus caliginosus trapezoides*-Blake, Illinois Biol. Monogr. 10(4): 63.
- 1930 *Allolobophora turgida* (part.) + *Allolobophora trapezoides* (part.)-Bornebusch, Forstl, Førsegs. Danmark 11:94
- 1942 *Allolobophora caliginosa* (part.)-Eaton, J. Washington Acad. Sci. 32(8): 246.
- 1952 *Allolobophora arnoldi* Gates, Breviora, no. 9: 1.
- 1962 *Allolobophora arnoldi* + *A. nocturna*-Omodeo, Mem. Mus. Civ. Sto. Nat. Verona 10: 92.
- 1963 *Lumbricus terrestris*-Cameron and Fogal, Canadian J. Zool. 41: 753.
- 1972 *Allolobophora chlorotica postepheba* Bouché, Inst. Natn. Rech. Agron., p. 269.
- 1972 *Nicodrilus (Nicodrilus) caliginosus alternisetosus* Bouché, Inst. Natn. Rech. Agron., p. 333.
- 1972 *Allolobophora tuberculata*-Gates, Bull. Tall Timbers Res. Stn. 12: 44, 45.
- 1973 *Allolobophora caliginosa* f. *typica* (part.)-Plisko, Fauna Polski, no. 1, p. 107.
- 1975 *Aporrectodea tuberculata*-Reynolds, Megadrilogica 2(3): 3.
- 1975 *Allolobophora chlorotica kosovensis* Šapkarev, Ann. Fac. Sci. Univ. Skopje 27: 43.
- 1998 *Allolobophora chlorotica eutypica* Qiu and Bouché, Doc. pédozool. intégrol. 4: 86.

Discussion

Aporrectodea tuberculata was described by Eisen in 1874 with specimens obtained from Niagara County (then Welland County), Ontario. Scandinavian specimens of *Ap. tuberculata* seem to have first been identified by Eisen as *Allolobophora cyanea* (fide Hoffmeister) (Gates, 1972b). Eisen recorded no Type Locality for *Ap. tuberculata*; but subsequently this has been designated as Niagara Region, Ontario.

Diagnosis (after Reynolds *et al.*, 1974: 36; Reynolds, 1977a: 78)

Medium sized earthworm, length 90–150 mm, diameter 4–8 mm, segment number 146–194, prostomium epilobic, closed $\frac{1}{3}$, first dorsal pore 11/12 or 12/13. Clitellum saddle on xxvii–xxxiv. Tubercula pubertatis xxx, xxxi–xxxiii, xxxiv. Setae closely paired, $AB \approx CD$, $AA > BC$, $DD \frac{1}{2}C$. Genital tumescences absent in xxxi and xxxiii, present in xxx, xxxii, and xxxiv and frequently in xxvi. Male pores in xv between *b* and *c*. Female pores on xiv. Seminal vesicles, four pairs in 9–12. Spermathecae, two pairs opening on level *c* in 9/10 and 10/11. Colour, unpigmented, almost white or greyish or sometimes with light pigmentation on the dorsum. Body cylindrical.

Biology

Gerard (1964) reported this species' habitat as pastureland. In the western United States, Gates (1967) found it in wet areas near streams and springs where there was a large concentration of organic matter. In east Tennessee (Reynolds *et al.*, 1974) *Aporrectodea tuberculata* was recorded 75% of the time from ditches, or under logs or debris such as lumber. Gates (1972a) records it from soils of pH 4.8–7.5 including turf, compost, peat, bogs, and rarely manure. In Ontario, this species was found primarily under logs and rocks in all but four eastern counties (Reynolds, 1977a). This was also the situation in Quebec (Reynolds and Reynolds, 1992; Reynolds, 2010a).

Under favourable conditions activity, including breeding, can be year round. However, Gates (1972a) states that probably throughout northern United States and Canada aestivation and hibernation are climatically imposed with breeding restricted to spring and late autumn.

Aporrectodea tuberculata has been obtained from culture beds on earthworm farms and, being so common in gardens and fields, is the species most likely to be dug for fish bait in much of Canada.

Reproduction

Reproduction in this species is obligatorily amphimictic with copulation beneath the soil surface (Reynolds, 1974a).

Origin, range

A native of Palaearctis and considered a peregrine species, *Ap. tuberculata* is now known from Europe, North America, South America, Asia, and Australia (Gates, 1972a), also from Iceland (Backlund, 1949), and Falkland Islands (Reynolds and Jones, 2006).

Climatic zone: Boreal, temperate, sub-tropical.

Ecological type

Aporrectodea tuberculata is an endogeic species (Reynolds, 2018).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, Nunavut, Ontario, Prince Edward Island, Quebec, Saskatchewan.

United States: Alaska, Arkansas, Arizona, California, Colorado, Connecticut, Delaware, Florida, Georgia, Iowa, Idaho, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, New Hampshire, New Jersey, New York, Nevada, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Utah, Vermont, Virginia, West Virginia, Wisconsin, Wyoming.

Mexico: Distrito Federal, México states (Fragoso, 2001).

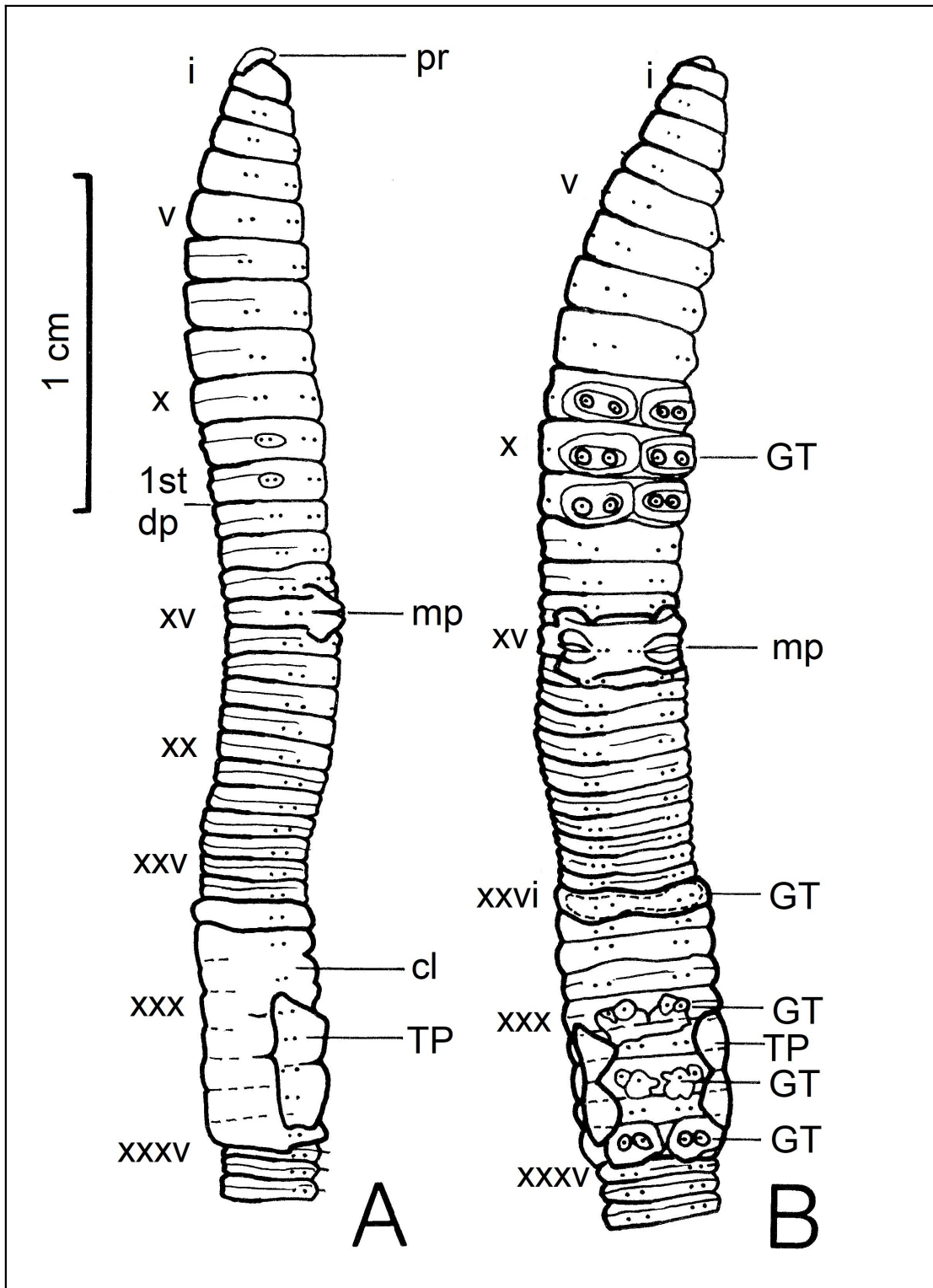


Fig. 11. External longitudinal views of *Aporrectodea tuberculata* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Aporrectodea turgida* (Eisen, 1873)**

Pasture worm — Ver du pâturage

(Fig. 12)

- 1873 *Allolobophora turgida* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 46. Type species in the United States National Museum–Smithsonian Institution cat. no. 1157 (Reynolds and Cook, 1976).
- 1874 *Allolobophora turgida* (part.)–Eisen, Öfv. Vet.-Akad. Förh, Stockholm 31(2): 43.
- 1946 *Allolobophora caliginosa*–Evans, Ann. Mag. Nat. Hist. (11), 13: 100, 101.
- 1947 *Allolobophora caliginosa*–Černosvitov and Evans, Linn. Soc. London, Syn. British Fauna, no. 6: 13.
- 1952 *Allolobophora caliginosa* + *A. molita* Gates, Breviora, no. 9: 1, 3.
- 1959 *Allolobophora caliginosa*–Zicsi, Acta Zool. Hungary 5(1-2): 172.
- 1964 *Allolobophora caliginosa* (*in toto*)–Gerard, Linn. Soc. London, Syn. British Fauna, no. 6: 27.
- 1969 *Allolobophora caliginosa* (part.)–Støp-Bowitz, Nytt. Mag. Zool. 17(2): 191.
- 1970 *Allolobophora caliginosa*–Zajonc, Biol. Prace 16(8): 23.
- 1972 *Allolobophora caliginosa* f. *typica* (part.) + *A. c.* f. *trapezoides* (part.)–Edwards and Lofty, Biol. earthworms, p. 217.
- 1972 *Nicodrilus caliginosus caliginosus*–Bouché, Inst. Natn. Rech. Agron., p. 326.
- 1972 *Allolobophora turgida*–Gates, Bull. Tall Timbers Res. Stn. 12: 89.
- 1973 *Allolobophora caliginosa* f. *typica* (part.)–Plisko, Fauna Polski, no. 1, p. 107.
- 1975 *Aporrectodea turgida*–Reynolds, Megadrilogia 2(3): 3.
- 2014 *Allolobophora caliginosa*–Makin, Miah, Yadav and Khan, Adv. Zool. Botany 2(4): 65.

Discussion

Aporrectodea turgida, along with the previous two species, has given oligochaetologists great difficulty until a publication by Gates (1972b). This species was first recorded from Ontario (Niagara Region) by Eisen in 1873. Four specimens labelled *Ap. turgida* from Niagara were sent by Eisen to the United States National Museum (cat. no. 1157). One specimen may be an aberrant individual of *Ap. turgida*, but the other three appear to be *Ap. tuberculata* (Gates, 1972b). I have subsequently examined these specimens and confirm this report.

Diagnosis (after Reynolds *et al.*, 1974: 36; Reynolds, 1977a: 78)

Medium sized earthworm, length 60–85 mm, diameter 3.5–5.0 mm, segment number 130–168, prostomium epilobic, first dorsal pore 12/13 or 13/14. Clitellum saddle on xxvii, xxviii, xxix–xxxiv, xxxv. Tubercula pubertatis xxxi–xxxiii. Setae closely paired, $AA:AB:BC:CD:DD = 3:1:2:\frac{3}{2}:10$. Genital tumescences contain *a* and *b* only in xxx, xxxii–xxxiv, and frequently in xxvii. Male pores on xv between *b* and *c*. Female pores on xiv. Seminal vesicles, four pairs in 9–12. Spermathecae, two pairs, with short ducts opening at level *cd* in 9/10 and 10/11. Colour, unpigmented with the region anterior to the crop flesh pink and the remaining segments pale grey, or occasionally with light pigmentation on the dorsal surface. Body cylindrical.

Biology

Gates (1972b) records this species from a variety of habitats, including gardens, fields, turf, forest humus, compost, banks of springs and streams, wasteland and city dumps, and from a cave in West Virginia. The widespread distribution and variety of utilized habitats for *Ap. turgida* were recorded also by Eaton (1942), Černosvitov and Evans (1947), Murchie (1956), and Gerard (1964). The amazing water tolerance of this species was reported by Guild (1951) and Reynolds *et al.* (1974), in Scotland and the United States, respectively. The variety of habitats utilized by *Ap. turgida* in Ontario can be seen from the collection data. On Tristan da Cunha, I reported it from open bush in grasses and ferns and cultivated crop land (Reynolds and Hänel, 2005).

Reproduction

Aporrectodea turgida is an amphimictic species (Reynolds, 1974a).

Climatic zone: Boreal, temperate, mediterranean, sub-tropical.

Ecological type

Aporrectodea turgida is an endogeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis and considered a peregrine species, *Aporrectodea turgida* is now known from Europe, South America, Asia, north Africa, Bermuda (Reynolds and Fragoso, 2004), Tristão da Cunha Islands (Pickford, 1932) and Turkey (Reynolds and Mısırlıoğlu, 2018). A study which I recently found reported it from Bangladesh (Makin *et al.*, 2014), which was a surprise, because in my four working trips to that country and two papers, I never encountered any lumbricids and only Oriental species (Reynolds, 1994c; Reynolds *et al.*, 1995).

North American distribution – complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, Ontario, Prince Edward Island, Quebec.

United States: Alaska, Arkansas, Arizona, California, Colorado, Connecticut, Delaware, Florida, Georgia, Hawaii, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, New Hampshire, New Jersey, New York, Nevada, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Mexico: Distrito Federal, México, Puebla, Veracruz States (Fragoso and Reynolds, 1997).

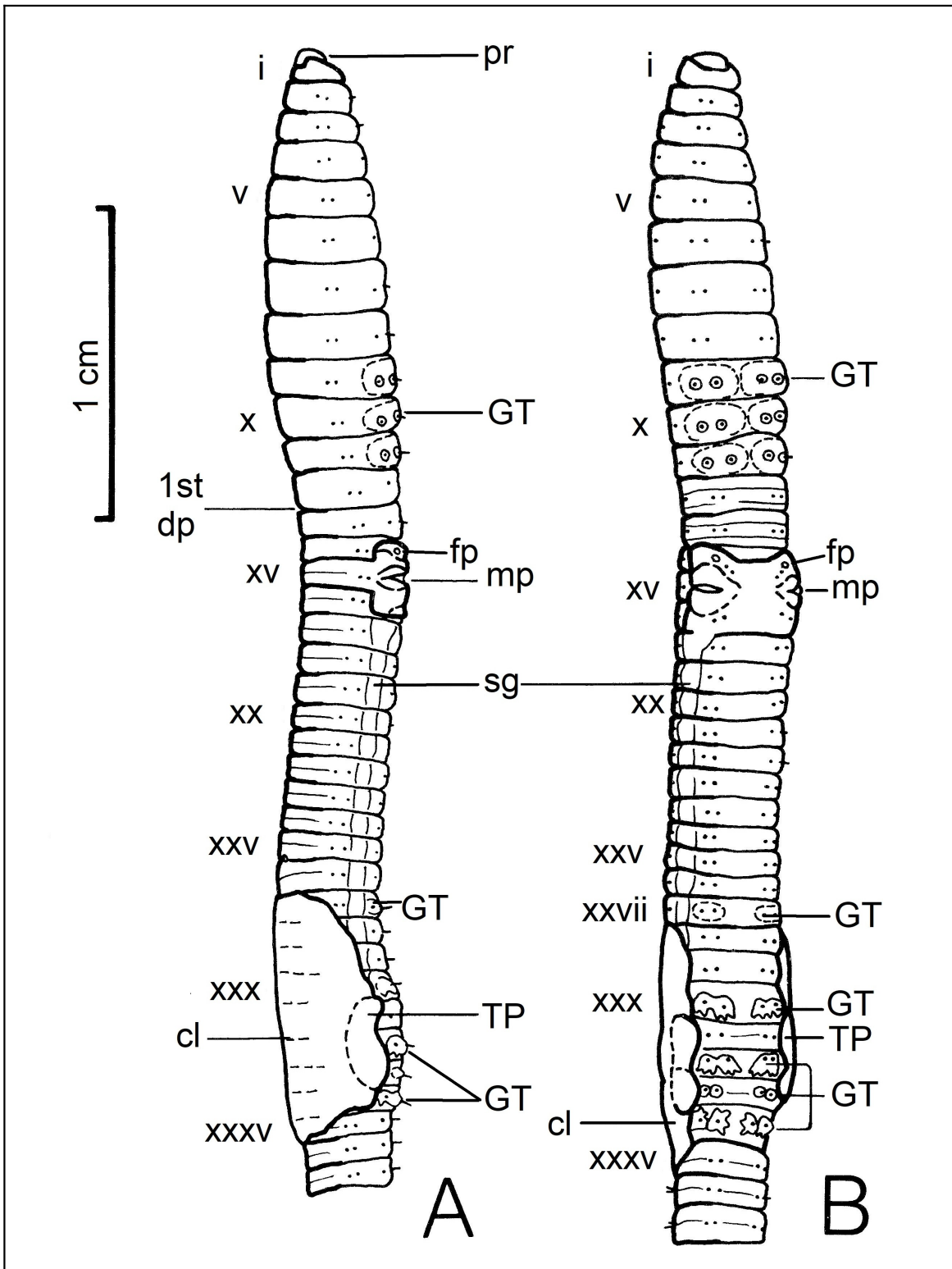


Fig. 12. External longitudinal views of *Aporectodea turgida* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

Genus *Bimastos* Moore, 1893

- 1893 *Bimastos* Moore, Zool. Anz. 16: 333.
1895 *Bimastos*-Moore, J. Morph. 10(2): 473.
1900 *Helodrilus* (*Bimastos*)-Michaelsen, Das Tierreich, Oligochaeta 10: 501.
1930 *Bimastos*-Stephenson, Oligochaeta, p. 913.
1969 *Bimastos*-Gates, J. Nat. Hist. London 9: 306.
1972 *Bimastos*-Gates, Trans. American Philos. Soc. 62(7): 86.
1975 *Bimastos*-Gates, Megadrilogica 2(1): 4.
1976 *Bimastos*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 61.

Type species

Bimastos palustris Moore, 1895.

Diagnosis (after Gates, 1972a: 86; 1975a: 4)

Calciferous gland, without marked widening in xi–xii, opening into gut in x through paired vertical sacs. Calciferous lamellae continued onto posterior walls of sacs. Gizzard, mainly in xvii. Extraesophageal trunks, joining dorsal trunk in xii. Hearts, in vii–xi. Nephridial bladders, U-shaped, closed ends laterally, ducts passing into parietes near *B*. Nephropores, inconspicuous, irregularly alternating (and with asymmetry), between levels somewhat above Band well above *D*. Setae, closely paired. Dorsal pores, present from region of 5/6. Male pores, equatorial in xv, in atrial chambers invaginated deeply into the coelom and bearing acinous glands. Female pores, equatorial on xiv, shortly above *B*. Holandric, seminal vesicles in xi–xii. Spermathecae, Tubercula pubertatis and Tuberculata pubertatis glands, lacking. Prostomium epilobic. Pigment red.

Discussion

This nearctic genus does not normally occur in Canada. The first collection of four specimens was from an accidental introduction to the National Arboretum in Ottawa (*cf. B. parvus*) (Reynolds, 1972a). The second report was by Berman and Marusik (1994) from the Yukon. The most recent and third report was also from the Yukon (Reynolds *et al.*, 2019b). Over the years there has been confusion over the spelling of this and other generic names (*cf. Octolasion*, p. 99). Much of the confusion dealt with changing between Greek and Latin spellings and declensions by authors who were not familiar with Greek and/or Latin.

***Bimastos beddardi* Michaelsen, 1894**

Beddard's worm — Ver de Bédard

(Fig. 13)

- 1894 *Allolobophora beddardi* Michaelsen, Zool. Jb. Syst. 8: 182. Type species is in the Zoologisches Museum Hamburg, Universität Hamburg, cat. no. 153! (Reynolds and Cook, 1976).
1897 *Allolobophora constricta* var. *geminata* (part.) Friend, Zoologist (4), 1: 459
1900 *Allolobophora (Bimastos) beddardi*-Michaelsen, Abh. Ver. Hamburg 16: 10, 13.
1900 *Helodrilus (Bimastos) beddardi*-Michaelsen, Das Tierreich Oligochaeta 10: 502.
1974 *Bimastos beddardi*-Reynolds, Clebsch and Reynolds, Bull. Tall Timbers Res. Stn., no. 17: 24.
1995 *Bimastos beddardi*-Reynolds, Earthworm Ecology and Biogeography, p. 11.

Diagnosis (after Reynolds *et al.*, 1974: 24)

Small earthworm, length 17–46 mm, diameter 1.5–3.0 mm, segment number 66–95, prostomium epilobic, first dorsal pore 5/6. Clitellum saddle on xxiv–xxxi. Setae closely paired, $aa:ab:bc:cd:dd = 26:4:20:3:80$. Male pores on xv between *b* and *c*. Female pores on xiv slightly dorsad of *b*. Seminal vesicles in 11 and 12. Spermathecae absent. A revision of the nearctic genus *Bimastos* Moore by Gates (1969) includes the following: "nephridial vesicles, elongately hairpin-(U) shaped, and a pair of vertical calciferous sacs present in 10." Colour reddish dorsally and yellowish ventrally.

Biology

Bimastos beddardi was reported for the first time from Tennessee in 1974. In Tennessee, *B. beddardi* was obtained from: logs (64; 83)¹, unknown (27; 9) and dumps (9; 8) (Reynolds *et al.* (1974). Smith (1917) collected it from *wet* situations and decaying logs, stumps or moss. Smith and Green (1916) recorded it from moss on the shore of a brook. A similar occurrence was reported by Reynolds (1972d). Causey's (1952) collections were from wooded areas. Harman (1952) reported this species from damp decaying logs and leaf mould. Murchie (1956) stated, "*Bimastos beddardi* is a woodland species which is also successful in the wetter habitats, such as along stream banks and in seepage zones."

Reproduction: *Bimastos beddardi* is a parthenogenetic species (Reynolds, 1974a).

Climate zone: Temperate.

Ecological type

Bimastos beddardi is a corticole-epigeic species (Reynolds, 2018).

Origin, range

Bimastos beddardi is a native species of North America and has not been recorded outside the United States, except for one Canadian record which was taken from a single site at a fishing camp in Quebec owned by residents of Pennsylvania, USA (Reynolds, 2010a, p. 34).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Not currently believed to be present in Canada.

Canada: Quebec (single isolated record; see above).

United States: Arkansas, California, Florida, Illinois, Indiana, Louisiana, Michigan, Montana, North Dakota, Ohio, South Carolina, Tennessee, Virginia, Washington.

Mexico: none.

¹ The first value = % of collections from a given habitat; the 2nd value = % of specimens obtained in that habitat.

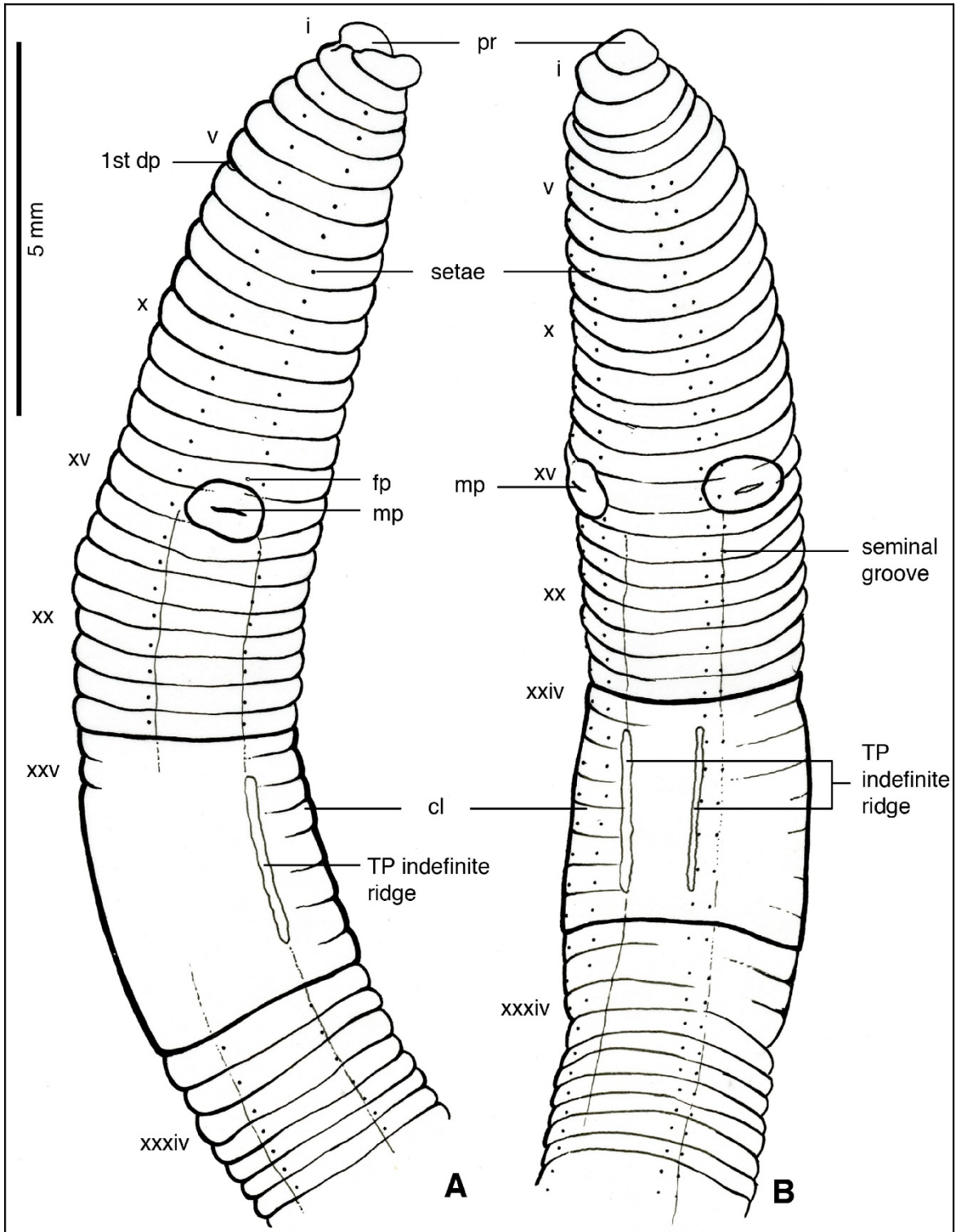


Fig. 13. External longitudinal views of *Bimastos beddardi* showing taxonomic characters. A. Dorsolateral view. B. Ventrolateral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

***Bimastos lawrenceae* Fender, 1994**
Mount Hood worm — Ver de mont hood
(Fig. 14)

- 1994 *Bimastos lawrenceae* Fender, Canadian J. Zool. 72: 1338. Type species in the Canadian Museum of Nature, cat no. 1994-0052-53.
2007 *Bimastos lawrenceae*-Marshall and Fender, Megadrilogica 11(4): 34.
2018 *Bimastos lawrenceae*-Reynolds, Megadrilogica 23(1): 6.

Diagnosis (after Fender, 1994: 1338)

Small to medium sized earthworm, length \approx 80 mm, diameter \approx 5 mm (size not given in original description), segment number 103, 113, 133, and 134 in paratypes, 133 in holotype. Dorsal pores prominent 5/6 et seq. in all specimens, but a rudimentary pore is present in 4/5 on one paratype. Prostomium broad, epilobous, open. Dorsal pores prominent 5/6 et seq. in all specimens, but a rudimentary pore is present in 4/5 on one paratype. Clitellum saddle on xxv–xxxiv (glandular but not thickened on xxxv in holotype, which is the specimen with the thickest clitellum), absent or very thin across ventrum (saddle-shaped). Tuberculata pubertatis, absent. Male pores, mL in xv. Nephropores easily visible on anterior soma at anterior edge of segments, in the first few segments between setal lines *C* and *D*, thereafter irregularly alternating between two strict levels, one just above *B* and one just above *D*, 1–10 pores in a series in one of those levels, the one side maintaining no pattern with respect to the other, this irregular alternation continuing to extreme posterior \approx $\frac{1}{2}$ *DD*. Nephridial vesicles in clitellar region very long, hairpin-shaped, extending from below an entally to nearly the mid-dorsal line before recurving and entering body wall at *B*, the ental portion of the loop anterior of the ectal portion. Septa 12/13 to 14/15 stronger than those posterior, slightly stronger than those anterior, but none especially strong. Calciferous gland very well developed in xi–xii, rudimentary in xiii but tissues appear much the same as in xi–xii, calciferous sacs transverse in x, opening by a transverse slit into esophagus. Gut of xiv valvular, constricted, that of xv–xvi much larger, thin-walled. Gizzard in xvii–xviii. Typhlosole begins very gradually as a pad on the roof of the intestine in xxii–xxiii, becoming bifurcate in cross section at about xxvii. Intestinal contents all fine-grained organic fragments, except a large (1 mm) chunk of soft, iron-oxide coated rock found in gizzard of holotype. Seminal vesicles postseptal in xi and xii only. Pigment reddish, pigment present in circular muscle in extreme anterior and posterior soma, especially dorsally, in life appearing pale reddish and transparent.

Biology

The data for this species are based on the only five clitellate adults specimens which have been collected of this species. All of the collections of *B. lawrenceae* are from a small area about 20 km southwest of Port Alberni, British Columbia. The Douglas Peak site is at high altitude, about 1200 m, and still remote, while the Museum Junction site is at an elevation of about 200 m along a heavily travelled forest road. Douglas Peak, in Ah layer, subalpine - mountain hemlock (*Tsuga mertensiana*) forest, Vancouver Island, Douglas Peak, same locality as holotype (within 100 m), under Rocky Mountain fir (*Abies lasiocarpa*) in drainage channel, steep slope, along a thin log in moist humus with arrowleaf ragwort (*Senecio triangularis*), and in mosses and matted vegetation in steep, cold (4°C) stream in recent clear-cut; 0.5 km S of Museum Junction on Franklin Main, McMillan Bloedel lands, mosses and muck of skunk-cabbage (*Lysichiton americanus*) swamp.

All of the paratypes were collected from moist humus and matted vegetation in wet situations. The holotype was obtained from a soil and vegetation sample brought back to the laboratory and so we are not sure of the precise site, but intensive digging in the area produced only the one paratype from a very moist site.

Remarks

Species have usually been based on one or few characters, partly because the American species are a relatively uniform group morphologically. *Bimastos lawrenceae* is very similar to *Bimastos zeteki* Smith and Gittins 1915, in somatic morphology, but is distinguishable by the more anterior position of its clitellum (xxv–xxxiv in *B. lawrenceae*, xxvii–xxxvii in *B. zeteki*). It is also a slightly smaller species. Despite the similarity in somatic morphology, the combination of a different clitellar position, different habitat, and range disjunction argue for *B. lawrenceae* and *B. zeteki* being separate species. *Bimastos welchi* Smith 1917, has a similar clitellar position but is unpigmented, has septum 14/15 essentially not thickened, and lives in soil.

The only lumbricid earthworm known to be native to Canada is *Bimastos lawrenceae*, which may be recognized from its clitellum covering segments xxv–xxxiv, male pores on segment xv, and total lack of other sexual markings.

The importance of *B. lawrenceae* to our understanding of the biogeography of North American earthworms can hardly be overestimated. All other known *Bimastos* species are either restricted to eastern North America or are widespread and extremely common adventives (Reynolds, 2010c, 2011a). *Bimastos lawrenceae* could be evidence of a preglacial distribution of *Bimastos* species across Canadian North America, something unknown for any other terrestrial earthworm genus (McKey-Fender *et al.*, 1994).

Reproduction

Bimastos lawrenceae is a parthenogenetic species (McKey-Fender *et al.*, 1994).

Climate zone: Temperate.

Ecological type

Bimastos lawrenceae is a corticole-epigeic species (Reynolds, 2018).

Origin, range

Bimastos lawrenceae is a North American native and known only from one site on Mount Hood in British Columbia.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This is a very rare earthworm in Canada.

Canada: British Columbia.

United States: none.

Mexico: none

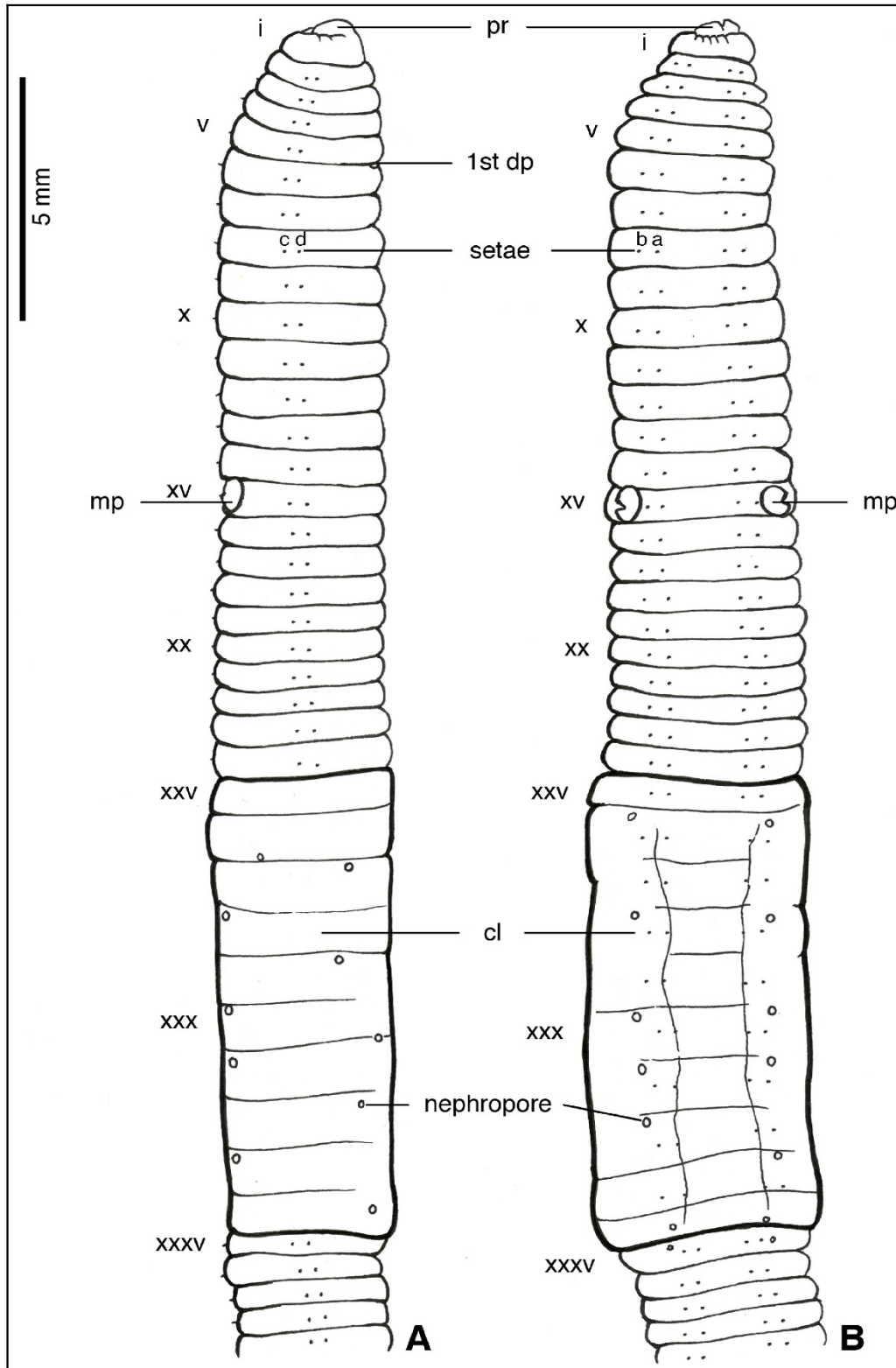


Fig. 14. External longitudinal views of *Bimastos lawrenceae* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

***Bimastos parvus* (Eisen, 1874)**
American bark worm — Ver américain de l'écorce
(Fig. 15)

- 1874 *Allolobophora parva* Eisen, Öfv. Vet-Akad. Förh. Stockholm 31(2): 46. Type species unknown (Reynolds and Cook, 1976).
- 1900 *Allolobophora (Bimastos) parvus*-Michaelsen, Abh. Nat. Verh. Hamburg 16(1): 10, 14.
- 1907 *Helodrilus (Bimastos) parvus*-Michaelsen, Reise in Ostafrika, p. 39.
- 1948 *Eisenia parvus* + *Bimastos beddardi*-Pop, Ann. Acad. Sect. Štiint. Geol. Geogr. Biol. (A), 1(9): 123.
- 1959 *Bimastos parvus*-Zicsi, Acta Zool. Hungary 5: 170.
- 1972 *Eisenia (sensu lato) parva*-Bouché, Inst. Nat. Rech. Agron., p. 386.
- 1973 *Bimastos parvus* (part. ?)-Plisko, Fauna Polski, no. 1, p. 99.
- 1974 *Bimastos parvus*-Reynolds, J. Tennessee Acad. Sci. 49(1): 17.
- 1977 *Bimastos parvus*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 61.
- 1979 *Allolobophora (Allolobophora) parva*-Perel, Nauka Moskva, p. 187.
- 1988 *Allolobophora parva*-Mršić and Šapkarev, Acta Mus. Macedonia Sci. Nat. 1(154): 23.
- 1991 *Allolobophora (Allolobophoridella) parva*-Mršić, Slovenska Akad. 31: 49.
- 2012 *Allolobophoridella parva*-Valchovski, Zootaxa 3458: 88.
- 2019 *Bimastos parvus*-Reynolds, Cameron, Sweeney, Bennett and Godin, Megadrilogica 25(1): 1, 7.

Diagnosis (after Reynolds *et al.*, 1974: 28; Reynolds, 1977a: 62–63)

Small earthworm, length 17–65 mm, diameter 1.5–4.0 mm, segment number 65–110, prostomium epilobed open $\frac{1}{2}$ – $\frac{2}{3}$. first dorsal pore 4/5 or 5/6. Clitellum saddle on xxiii, xxiv–xxx, xxxii. Tubercula pubertatis absent or in the form of indefinite ridges on xxiv, xxv, xxvi–xxx. Setae closely paired, $CD = AB$, AA slightly greater than BC , $DD = \frac{1}{2}C$. Male pores with small, slightly elevated papillae of a yellowish brown colour on xv. Calciferous glands in 10, 11 and 12. Seminal vesicles in 11 and 12. Spermathecae absent. Colour, reddish dorsally and yellowish ventrally.

Biology

Bimastos parvus, like all the members of the nearctic genus *Bimastos*, is found in close association with decaying logs and leaves, *i.e.*, habitats high in organic matter. This association has been reported by Černosvitov and Evans (1947), Causey (1952), Murchie (1956), and Reynolds *et al.* (1974). Gates (1972a) recorded it from soils with pH of 7.5 that were wetted with effluent from human habitations, and from forests, gardens, fields, humus, manure, dumps, and litter in caves.

Activity seems to be possible all year under favourable conditions (Gates, 1972a).

Reproduction

Bimastos parvus is obligatorily, or at least facultatively, parthenogenetic (Reynolds, 1974c). Sperm are rarely present, male sterility is apparent, and spermatophores are unknown (Gates, 1972a).

Climate zone: Temperate, mediterranean, sub-tropical, boreal.

Ecological type

Bimastos parvus is an epigeic and corticole species (Reynolds, 2018).

Origin, range

Bimastos parvus is the only known native North American anthropochore, but is also now known from Europe, North America, South America, Asia, South Africa, and Australia (Gates, 1972a).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This is a rare species in Canada.

Canada: Ontario, Northwest Territories, Yukon.

United States: Arkansas, California, Colorado, Florida, Hawaii, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Nebraska, Nevada, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, Washington, Wyoming.

Mexico: Distrito Federal, Sinaloa, Tamaulipas states (Fragoso, 2001).

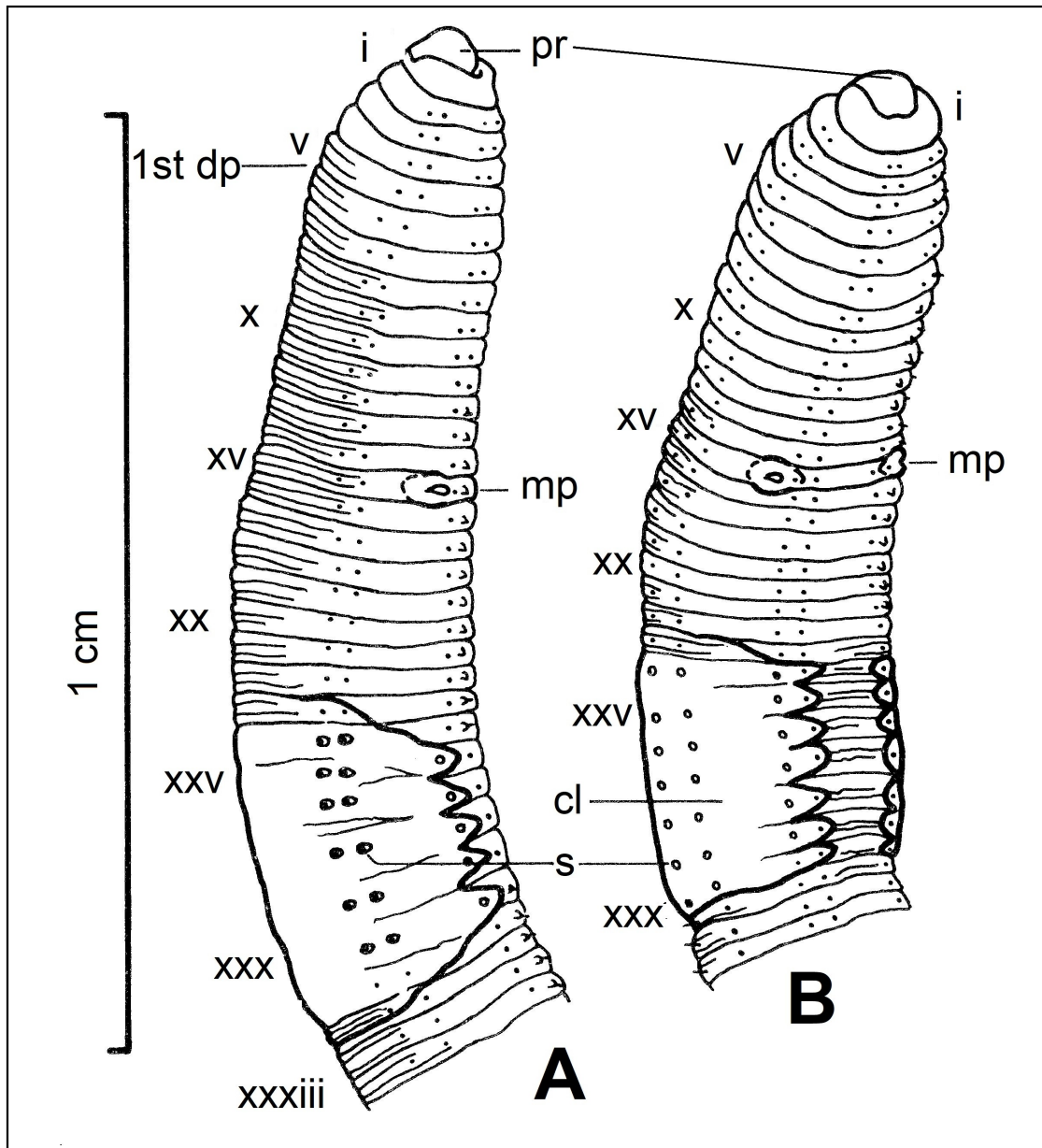


Fig. 15. External longitudinal views of *Bimastos parvus* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

Genus *Dendrobaena* Eisen, 1873

- 1873 *Dendrobaena* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 53.
1900 *Helodrilus (Dendrobaena)* (part.) + *Helodrilus (Bimastus)* (part.)-Michaelsen, Das Tierreich, Oligochaeta 10: 488, 501.
1930 *Dendrobaena* (part.)-Stephenson, Oligochaeta, p. 912.
1972 *Dendrobaena* (part.)-Gates, Trans. Amer. Philos. Soc. 62(7): 88.
1972 *Dendrobaena* (part.)-Bouché, Inst. Natn. Rech. Agron., p. 388.
1974 *Dendrobaena*-Gates, Bull. Tall Timbers Res. Stn. 15: 16.
1975 *Dendrobaena*-Gates, Megadrilogica 2(1): 3.
1976 *Dendrobaena*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 64.

Type species

Dendrobaena boeckii Eisen by monotypy in 1873 (= *Enterion octaedrum* Savigny, 1826).

Diagnosis (after Gates, 1972a: 88 and 1975a: 3)

Calciferous gland, without sacs opening into gut at vicinity of 10/11, markedly moniliform in xi–xii. Calciferous sacs, lacking. Gizzard, mainly in xvii. Extraesophageal trunks, passing to dorsal trunk in vicinity of 9/10. Hearts, in vii–ix. Nephridial bladders, ocarina-shaped, with bluntly rounded end laterally and pointed end mesially, ventral side funnel-shaped and narrowing to pass into parieties at *B*. Nephropores, obvious, behind first few segments in one rank on each side, just above *B*. Setae, not closely paired. Prostomium epilobic. Longitudinal musculature, pinnate. Pigment, red.

Discussion

The above diagnosis, after Gates (1972a and 1975a), is for a genus with *D. octaedra* as the type species. But another of Savigny's species, *Enterion rubidum*, has been congeneric with *D. octaedra* for decades, almost solely because of similarities in their genitalia. As a result of recent studies based on more conservative somatic anatomy, Omodeo's subgenus *Dendrodrilus* (1956) has been elevated to full genus status with *Enterion rubidum* as the type species (Gates, 1975a: 4).

Dendrobaena attemsi Michaelsen, 1902

Round-back worm — Ver rond-arrière

(Fig. 16)

- 1902 *Helodrilus (Dendrobaena) attemsi* Michaelsen, Mitt. Naturhist. Mus. Hamburg 19: 47. Type species missing (Reynolds and Cook, 1976).
1910 *Helodrilus (Eisenia) alpinus decipiens* Michaelsen, Ann. Mus. Zool. Acad. Imp. Sci. St.-Petersburg, 15: 26.
1948 *Dendrobaena octaedra* (part.) Pop, Compt. Rend. Zool. Cluj (A), 9: 108.
1952 *Dendrobaena attemsi*-Omodeo, Ann. Mus. Zool. Univ. Napoli 4: 10.
1972 *Dendrobaena (Dendrobaena) attemsi*-Bouché, Inst. Natn. Rech. Agron., p. 393.
1974 *Dendrobaena attemsi*-Gates, Bull. Tall Timbers Res. Stn. 15: 54.
1979 *Dendrobaena attemsi*-Perel, Nauka Moskva, p. 236.
1985 *Dendrobaena attemsi*-Fender, Megadrilogica 4(5): 115.
1991 *Dendrobaena attemsi*-Mršić, Slovenska Akad., p. 604.
2018 *Dendrobaena attemsi*-Reynolds, Megadrilogica 23(1): 6, 27, 35.

Diagnosis (after Bouché, 1972: 393; Fender, 1985:115; Mršić, 1991: 606)

Small earthworm, length 26–70 mm, diameter 2.5–3.0 mm, number of segments 94–145. Prostomium epilobic ½ open. Dorsal pores extremely variable. varying from obvious from 17/18, may also begin in segments 19/20, 20/21 and 23/24, or even lacking. None are found anterior to xvii. Setae, separate, $aa:ab:bc:cd:dd = 14:10:10:10:26$ ($DD=½ C$). Clitellum saddle on xxviii, xxix–xxxiii, xxxiv with Tubercula pubertatis in ridges or grooves on xxix, xxx–xxxii, xxxiii and the nephropores alternating with great regularity between levels *B* and *D*. Genital tumescences occur in the range of xxii, xxiii–xxiv, xxv, xxvi, xxix–xxxiii as a band in the clitellar ventrum, and as glandularity in the epaulets. Male pores in small prominent porophores in xv which extend part way onto xvi. Female pores minuscule on xiv. Seminal vesicles three pair, anteseptal in ix, postseptal in xi and xii. Nephropores alternate with great regularity between two levels in *B* and *D*, and asymmetrically on the two sides.

Internally, this species lacks hearts in x and xi. Calciferous gland opens in xi, swollen in posterior xi and xii, constricted at 11/12. Segment xiii has tubules in the gland wall, but these do not contain CaCO₃ spherules in life and this portion is not enlarged. Segments xii and posterior xi are swollen (constricted by 11/12) and this region in life is filled with CaCO₃ spherules. Calciferous sacs lacking. Typhlosole simply lamelliform, vertically oriented, and with a recurved ventral terminus rather like a J with the hooked end ventrad. This vesicle type is unique among the western Lumbricidae. Spermathecae are two pair in ix and x, opening in *D* in 9/10 and 10/11. Seminal vesicles three pair, anteseptal in ix, postseptal in xi and xii. Testis sacs are absent. Small worms, round in x-section, pale reddish dorsally, particularly in the anterior.

Biology

Dendrobaena attemsi has been found in two locations in the western USA. It was in moderate abundance under pots and wooden flats in a *Sphagnum* peat and vermiculite potting mix in a cool greenhouse in Dayton, Oregon and in association with *Dendrodrilus rubidus* f. *tenuis* (q.v.), and was abundant in bark mulch under and around established Mugo pines (*Pinus mugo*) in a garden in Auburn, Washington (Fender, 1982). In British Columbia, Marshall and Fender (2007) collected a single adult specimen in the Coastal Western Hemlock Zone Forest south of Tofino (Meindinger and Pojar, 1991). Graff (1953) reported this species' habitat as deciduous forest and also said that it is found in greenhouses and nursery operations and is restricted to these places in Germany. Geraskina and Shevchenko (2019) reported that *D. octaedra* and *D. attemsi* inhabited all of the examined forest types: coniferous-deciduous (*Picea orientalis*-*Acer* sp. + *Quercus* sp.), dark coniferous (*Abies nordmanniana*), beech, deciduous (*Carpinus betulus*), and pine, and were found in both the litter and deadwood. The results of the occurrence of these species in the different forest types showed that both species most often inhabited coniferous-deciduous forests.

Reproduction

Dendrobaena attemsi is considered amphimictic as spermatophores and sperm have been recorded (Gates, 1974b).

Climate zone: Temperate, mediterranean.

Ecological type

Dendrobaena attemsi is an epigeic species (Reynolds, 2018).

Origin, range

Dendrobaena attemsi is a native of Palaearctis whose geographical origin is Balkanic-Alpine (Rota and Erséus, 1997) and is found throughout Europe. Recently reported from Turkey (Mısrıoğlu and Stojanović, 2020). North American records are rare.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia.

United States: Alaska, Oregon, Washington.

Mexico: none.

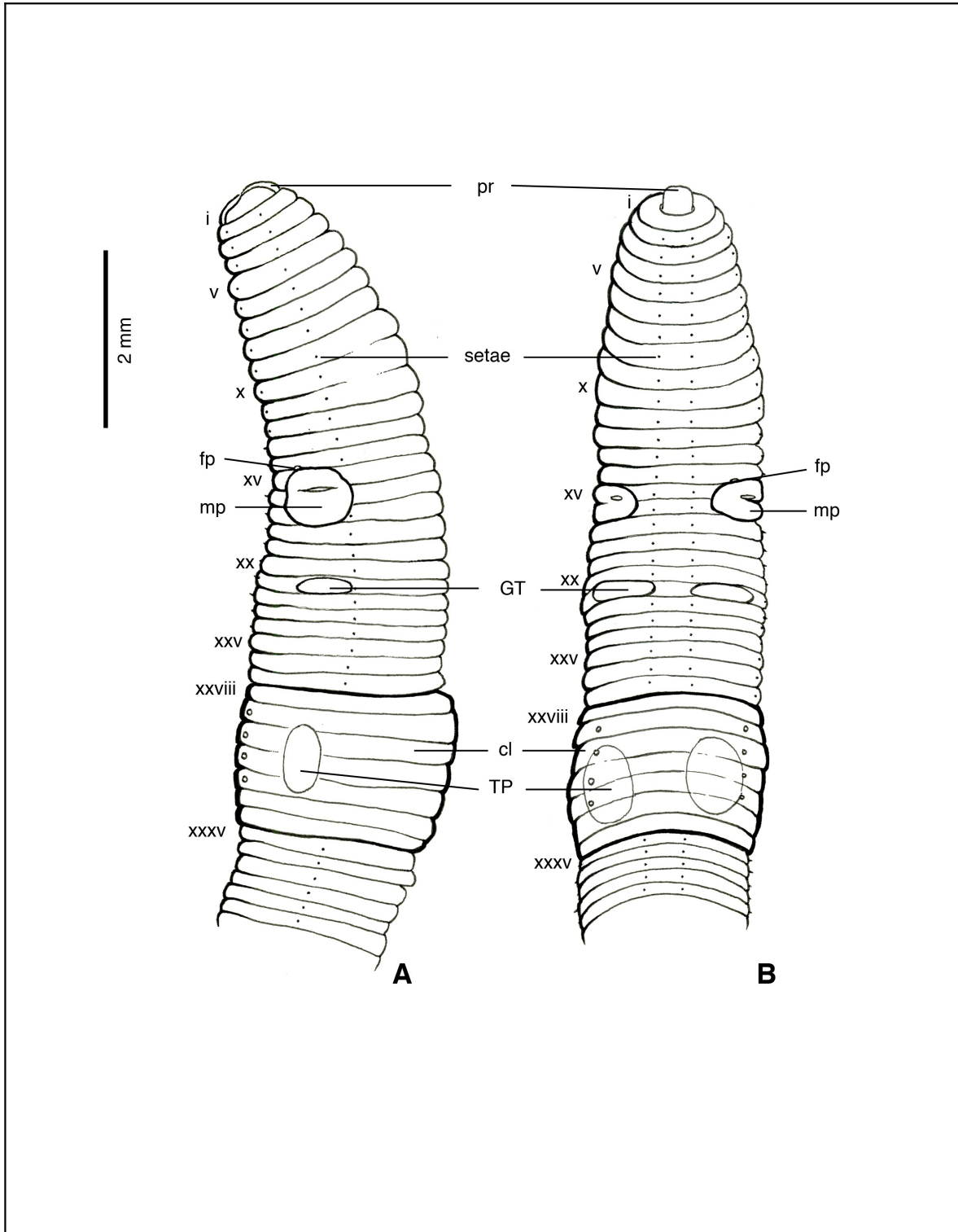


Fig. 16. External longitudinal views of *Dendrobaena attemsi* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the British Museum of Natural History, London, UK).

***Dendrobaena lusitana* Graff, 1957**

Portuguese worm — Ver portugais

(Fig. 17)

- 1957 *Dendrobaena lusitana* Graff, Agron. Lusitana 19(4): 303. Type species are in the Museu Nacional de Historia Nacional, Lisboa and Museo e Laboratorio Zoologico e Antropologico, Lisboa, cat. nos. unknown (Reynolds and Cook, 1976).
- 1987 *Dendrobaena carusoi* Omodeo and Martinucci, 1987: 240.
- 2018 *Dendrobaena lusitana*-Reynolds, Megadrilogica 23(1): 4.
- 2022 *Dendrobaena lusitana*-McAlpine, Reynolds, Graves and Sollows, Megadrilogica 26(11): 171.

Diagnosis (after Graff, 1957: 303, translated from Latin by JWR.)

Small earthworm, length 18+ mm, diameter 1–2 mm, segment number 60–70, secondary annulation lacking. Clitellum saddle on xxi–xxvii. Tuberculata pubertatis, may or may not be present, but generally lacking. Prostomium epilobic. Dorsal pores before the clitellum lacking. Male pores, small in xv. Female pores in xiv. Setae almost separate (widely spread), $aa > ab$, $bc = aa$, $ab = cd$, $dd = \frac{1}{4} C$. Typhosole fine. Calciferous glands large in x, and a small portion in xi?). Seminal vesicles in xi and xii. Seminal receptacles absent. Nephropores above B. Colour dorsum red, paler ventrally.

Biology

The original specimens were found under old leaves and debris (Graff, 1957). In New Brunswick, a single adult was collected at the Spednic Protected Natural Area in 2017 in leaf litter (McAlpine *et al.*, 2022; Reynolds, 2018).

Reproduction

Dendrobaena lusitana is considered an amphimictic species until evidence to the contrary.

Climatic zone: Mediterranean, temperate.

Ecological type

Dendrobaena lusitana is an epigeic species (Reynolds, 2018).

Origin, range

Dendrobaena lusitana is a native of Palaearctis (Portugal), but very limited distribution at this time. Currently known from Algeria and Morocco (Omodeo *et al.*, 2003), Canary Islands (Talavera, 1987), Madeira (Talavera, 1996), Portugal (Graff, 1957), Spain (Díaz Cosín *et al.*, 1992). The Canadian record is from the Spednic PNA in New Brunswick (McAlpine *et al.*, 2022).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This species is very rare in Canada.

Canada: New Brunswick.

United States: none.

Mexico: none.

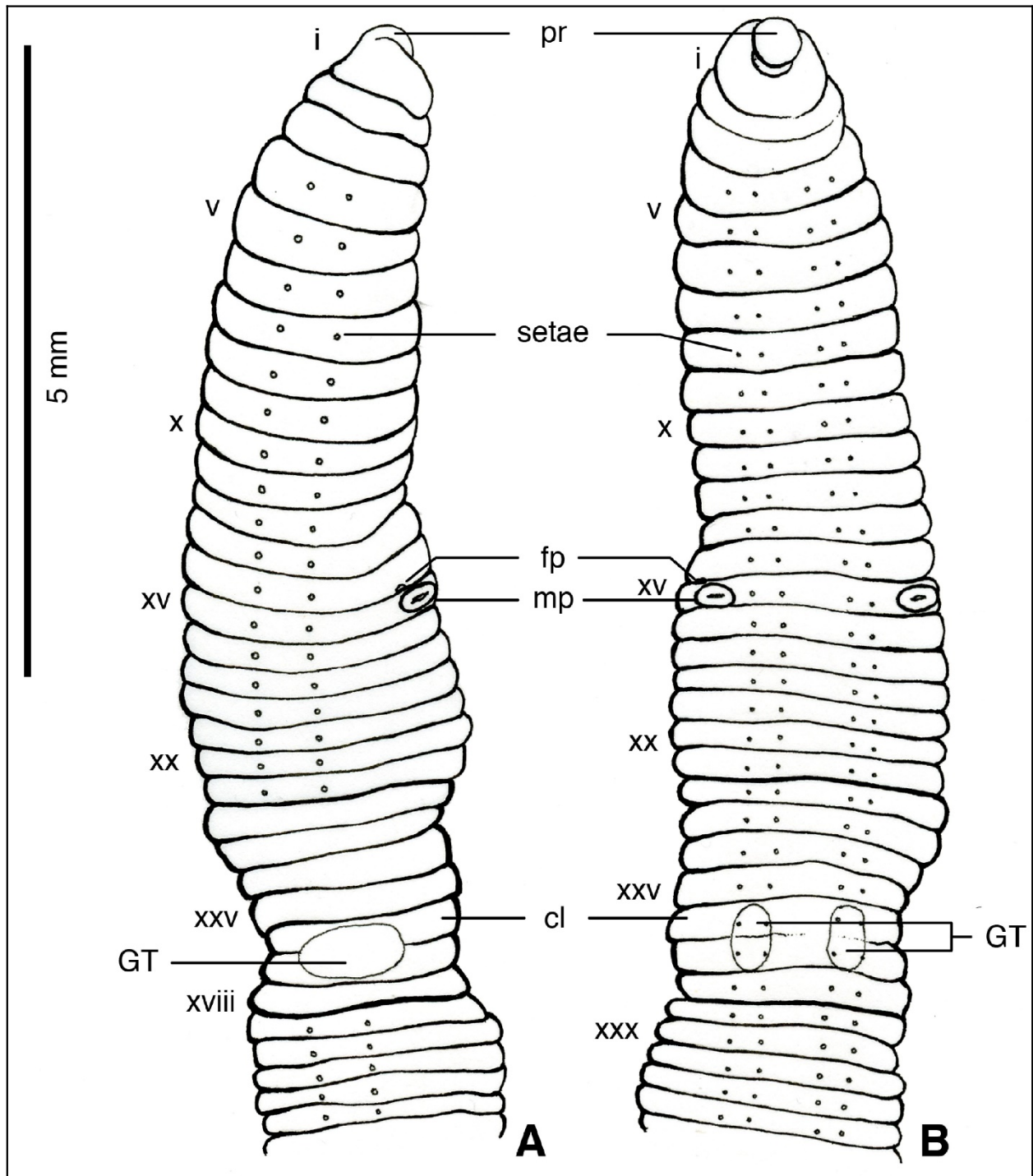


Fig. 17. External longitudinal views of *Dendrobaena lusitana* showing taxonomic characters. A. Lateral view, B. Ventral view (specimen graciously furnished by the New Brunswick Museum, Saint John, New Brunswick).

***Dendrobaena octaedra* (Savigny, 1826)**
Octagonal-tail worm — Ver à queue octogonale
(Fig. 18)

- 1826 *Enterion octaedrum* Savigny, Mém. Acad. Sci. Inst. France 5: 183. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1837 *Lumbricus octaedrus* + *L. vetaedrus* (laps.)-Dugès, Ann. Sci. Nat. (2), 8: 17, 24, 35.
- 1845 *Lumbricus riparius* (part.) Hoffmeister, Regenwürmer, p. 30.
- 1849 *Lumbricus fiaviventris* R. Leuckart, Arch. Naturg. 15(1): 159.
- 1871 *Lumbricus puler* (part.) Eisen, Öfv. Vet.-Akad. Förh. Stockholm 27(10): 959.
- 1873 *Dendrobaena boeckii* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 53.
- 1879 *Lumbricus boeckii*-Tauber, Annul. Danmark, p. 69.
- 1882 *Dendrobaena camerani* Rosa, Atti Acc. Torino 18: 172.
- 1885 *Octolasion boeckii*-Örley, Ertek. Term. Magyar Akad. 15(18): 20.
- 1887 *Allolobophora octaedra*-Rosa, Boll. Mus. Zool. Torino 2(31): 2.
- 1888 *Dendrobaena octaedra*-Vejdovský, Entwickgesch. Unters., p. 41.
- 1889 *Lumbricus (Dendrobaena) camerani* + *L. (D.) boeckii* + *L. (D.) octaedrus*-L. Vaillant, Hist. Nat. Annel. 3(1): 113, 118, 119.
- 1893 *Allolobophora (Dendrobaena) octaedra* (laps.)-Rosa, Mem. Ace, Torino, ser. 2, 43: 424, 437.
- 1896 *Allolobophora liliputiana* + *A. alpinula* Ribaucourt, Rev. Suisse Zool. 4: 32, 33, 37, 38.
- 1900 *Helodrilus (Dendrobaena) octaedrus*-Michaelsen, Das Tierreich, Oligochaeta 10: 494.
- 1948 *Dendrobaena octaedra* f. *typica* + *D. o.* var. *quadrivesiculata* Pop, Ann. Acad. Sect. Ştiint. Geol. Geogr. Biol. (A), 1(9): 104, 105, 106.
- 1964 *Dendrobaena octaedra* (laps.)-Langmaid, Canadian J. Soil Sci. 44: 34.
- 1972 *Dendrobaena (Dendrobaena) octaedra*-Bouché, Inst. Natn. Rech. Agron., p.388.
- 1974 *Dendrobaena octaedra*-Gates, Bull. Tall Timbers Res. Stn. 15: 16.
- 1977 *Dendrobaena octaedra*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 65.

Diagnosis (after Reynolds *et al.*, 1974: 31; Reynolds, 1977a: 65)

Small earthworm, length 17–60 mm, diameter 3–5 mm, segment number 60–100, prostomium epilobic closed, first dorsal pore 4/5–6/7. Clitellum saddle on xxvii, xxviii, xxix–xxxiii, xxxiv. Tubercula pubertatis usually on xxxi–xxxiii. Setae widely spread (separate), $AA = AB = CD$ and DD is slightly greater. On xvi setae *a* or *b* are found on small genital tumescences. Male pores on xv surrounded by small, often indistinct, glandular papillae. Seminal vesicles in 9, 11, and 12. Spermathecae, three pairs with long ducts on level with setae *d* opening in 9/10–11/12. Body cylindrical, with posterior portion octagonal. Colour, red, dark red to purple.

Biology

According to Gates (1972c), *Dendrobaena octaedra* is found in soils with a pH of 3.0–7.7, mostly in sites little affected by cultivation. Murchie (1956), from his studies in Michigan, characterized three types of habitat for the species: in sod or under moss on stream banks, under logs and leafy debris, or in cool, moist ravines and upland seepage areas. Gerard (1964) found it often under dung and in soil high in organic matter. These are the types of habitats in which it has been found in Ontario. In Europe, *D. octaedra* has been found on mountain tops and in caves, and it is known from botanical gardens and arboretums in Europe and North America. It has been recorded in caves in the United States by Reeves and Reynolds (1999), Holler *et al.* (2020), and in Slovenia by Novak (2005).

Under suitable conditions activity, including breeding, is possible the year round. In Maine, and therefore probably in Canada also, there are two breeding periods. The species is said to be surface living, the upper layers being abandoned only for aestivation and hibernation. Feeding is selective and sand and rock particles are rarely found in the intestine.

In Russia (Kursk), *D. octaedra* has been regarded as an important converter of leaf substances and it is believed mainly responsible for the decomposition of oak leaves (Gates, 1974b). In France, where these worms can be found crawling on bare mountain rocks, the viscous trails are held responsible for trapping lichens and thus initiating a lichen-moss-vascular plant succession (Ribaucourt and Combault, 1906). Geraskina and Shevchenko (2019) reported that *D. octaedra* and *D. attemsi* inhabited all of the examined forest types: coniferous-deciduous (*Picea orientalis*-*Acer* sp. + *Quercus* sp.), dark coniferous (*Abies nordmanniana*), beech, deciduous (*Carpinus betulus*), and pine, and were found in both the litter and deadwood. The results of the occurrence of these species in the different forest types showed that both species most often inhabited coniferous-deciduous forests.

Reproduction

Parthenogenetic polymorphism is widespread in *Dendrobaena octaedra*, probably more so than in any other lumbricid. A detailed discussion of the numerous morphs can be found in a paper by Gates (1974b).

Climatic zone: Boreal, temperate, mediterranean.

Ecological type

Dendrobaena octaedra is an epigeic species (Reynolds, 2018).

Origin, range

Dendrobaena octaedra is a native of Palearctis and is now known from Europe, North America, Chile, Colombia, Mexico, and Asia. This restriction of a peregrine lumbricid to the Northern Hemisphere is unusual (Gates, 1972a). It is also known from Iceland (Backlund, 1949), Tierra del Fuego, Argentina (Mischis, 2007) and Hawaii (Reynolds, 2015b).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Northwest Territory, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan, Yukon.

United States: Alaska, Arkansas, California, Colorado, Connecticut, Delaware, Georgia, Hawaii, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Mexico: Distrito Federal, Hidalgo, México, Michoacán, Puebla, Nuevo León, San Luis Potosí, Tamaulipas, Veracruz states (Fragoso and Reynolds, 1997; Fragoso, 2001).

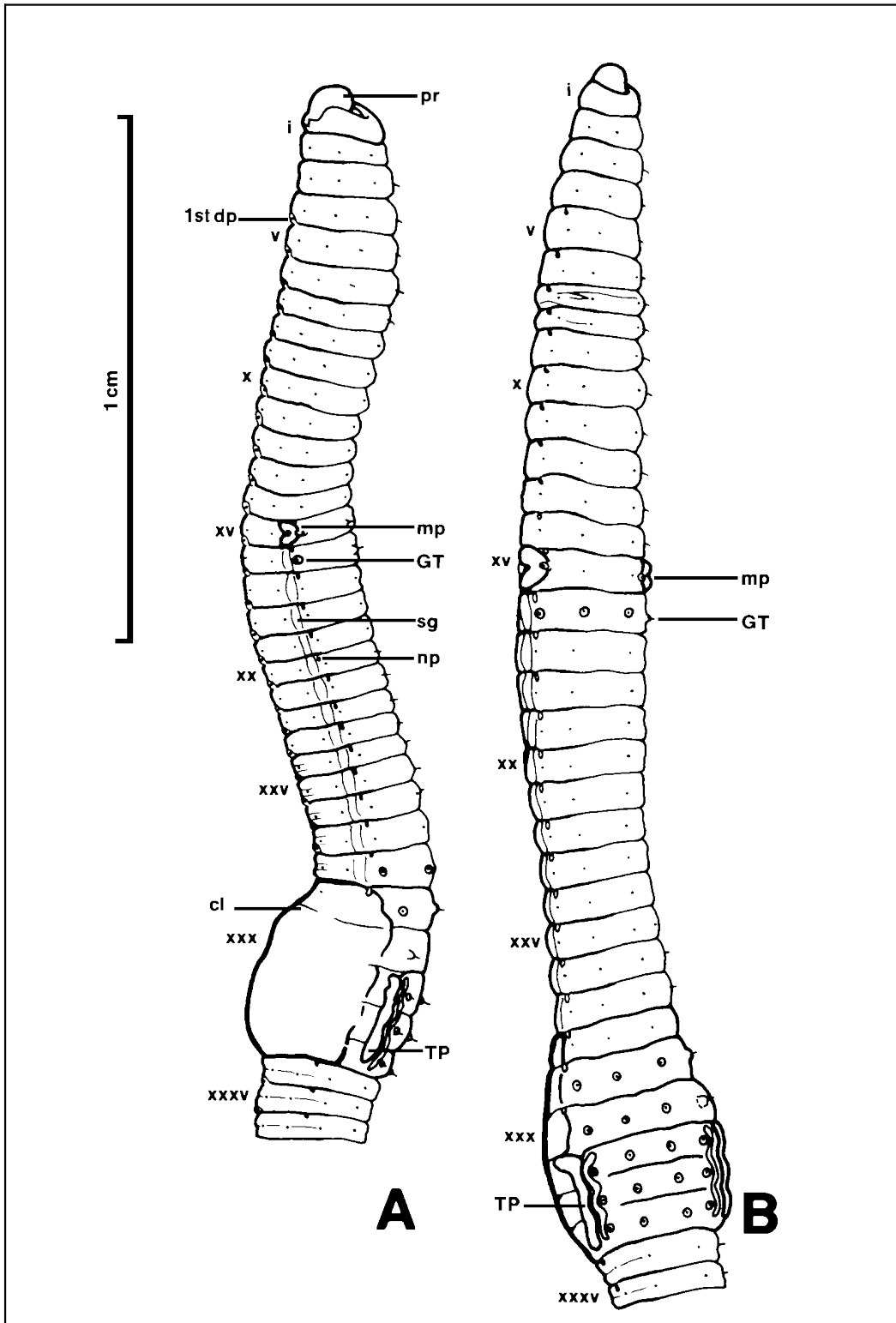


Fig. 18. External longitudinal views of *Dendrobaena octaedra* showing taxonomic characters. A Lateral view. B. Ventral view (from Reynolds, 1977a).

Genus *Dendrodrilus* Omodeo, 1956

- 1956 *Dendrobaena* (*Dendrodrilus*) Omodeo, Arch. Zool. Italiano 41: 175.
1969 *Dendrobaena* (part.)-Støp-Bowitz, Nytt. Mag. Zool. 17(2): 214.
1972 *Dendrobaena* (part.)-Gates, Trans. American Philos. Soc. 62(7): 88.
1972 *Dendrobaena* (part.)-Bouché, Inst. Natn. Rech. Agron., p. 388.
1973 *Dendrodrilus*-Plisko, Fauna Polski, no. 1, p. 78.
1975 *Dendrodrilus*-Gates, Megadrilogica 2(1): 4.
1976 *Dendrodrilus*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 69.
1979 *Dendrodrilus*-Gates, Megadrilogica 3(9): 153.

Type species

Enterion rubidum Savigny, 1826.

Diagnosis (after Gates, 1972a and 1975a)

Calciferous glands, opening into gut ventrally through a pair of sacs posteriorly just in front of insertion of 10/11. Calciferous lamellae continued along lateral walls of sacs. Gizzard, mainly in xvii. Extraoesophageal trunks, passing to dorsal trunk in xii. Hearts, in vii–xi. Nephridial bladders, U-shaped loop. Nephropores, inconspicuous, alternating irregularly and with asymmetry on each side between a level above *B* and one above *D*. Setae, not closely paired. Prostomium epilobic. Longitudinal musculature, pinnate. Pigment, red.

Discussion

Species of *Dendrodrilus* formerly congeneric with species in *Dendrobaena* because of similarities in genital anatomy are now separated on the basis of differences in their more conservative somatic anatomy (Reynolds, 1977a).

***Dendrodrilus rubidus* (Savigny, 1826)**
European bark worm — Ver européen de l'écorce
(Fig. 19)

- 1826 *Enterion rubidum* Savigny, Mém. Acad. Sci. Inst. France 5: 182. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1836 *Lumbricus xanthurus* R. Templeton, Ann. Mag. Nat. Hist. 9: 235.
- 1837 *Lumbricus rubidus*-Dugès, Ann. Sci. Nat. (2), 8: 17,23.
- 1849 ? *Lumbricus valdiviensis* E. Blanchard, Hist. Chile 3: 43.
- 1867 ? *Hypogeon havaicus* Kinberg, Öfv. Vet.-Akad. Förh. Stockholm 23: 101.
- 1873 *Allolobophora norvegica* + *A. arborea* + *A. subrubicunda* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 48, 49, 51.
- 1874 *Allolobophora tenuis* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 31(2): 44.
- 1881 *Allolobophora fraissei* Örley, Zool. Anz. 4: 285.
- 1881 ? *Dendrobaena puter* (part.)-Örley, Math. Term. Kozlem. Magyar Akad. 16: 586.
- 1884 *Allolobophora constricta* Rosa, Lumbric. Piemonte, p. 38.
- 1884 *Lumbricus subrubicunda* (part.)-Levinsen, Vidensk. Meddel. Naturhist. Forh. København, (4), 5: 242.
- 1885 *Octolasion constrictum* + *O. subrubicundum*-Örley, Ertek. Term. Magyar Akad. 15(18): 20, 21.
- 1888 *Allolobophora putra* (part.)-Vejdovský, Entwickgesch. Unters., p. 41.
- 1889 *Lumbricus (Allolobophora) constrictus*-L. Vaillant, Hist. Nat. Annel. 3(1): 113.
- 1891 *Allolobophora nordenskiöldii* (laps.) Michaelsen, Abh. Ver. Hamburg 11(2): 3.
- 1891 *Allolobophora rubicunda* (laps.)-Beddard, Proc. Roy. Phy. Soc. Edinburgh 10: 273.
- 1893 *Allolobophora putris arborea* (part. ?)-Rosa, Mem. Acc. Torino (2), 43: 433.
- 1893 *Dendrobaena constricta* (part.)-Friend, Naturalist, p. 19.
- 1896 *Allolobophora helvetica* + *A. darwini* Ribaucourt, Rev. Suisse Zool. 4: 18, 82.
- 1900 *Allolobophora (Bimastus) constricta*-Michaelsen, Abh. Nat. Ver. Hamburg 16(1): 10.
- 1900 *Helodrilus (Dendrobaena) rubidus*-Michaelsen, Das Tierreich, Oligochaeta 10: 490.
- 1908 *Helodrilus (Bimastus) constrictus*-Michaelsen, Denskschr. Med.-Naturew. Ges. Jena 13: 41.
- 1917 *Helodrilus (Bimastus) tenuis*-Smith, Proc. United States Natn. Mus. 52: 157, 182.
- 1958 *Dendrobaena rivulicola* Chandebois, Bull. Soc. Zool. France 83: 159.
- 1969 *Dendrobaena rubida* + *D. subrubicunda* + *D. tenuis*-Støp-Bowitz, Nytt. Mag. Zool. 17(2): 220, 224, 227.
- 1970 *Dendrobaena rubida* var. *typica*-Zajonc, Biol. Prace 16(8): 22.
- 1972 *Dendrobaena (Dendrodrilus) rubida rubida* + *D. (D.) rubida tenuis* + *D. (D.) subrubicunda*-Bouché, Inst. Natn. Rech. Agron., p. 410, 411, 414.
- 1972 *Dendrobaena subrubicunda* + *Bimastos tenuis* + *Dendrobaena rubida*-Edwards and Lofty, Biol. earthworms, p. 215, 216.
- 1973 *Dendrobaena (Dendrodrilus) rubida* + *D. (D.) r. f. typica* + *D. (D.) r. f. subrubicunda* + *D. (D.) r. f. tenuis*-Plisko, Fauna Polski, no. 1, p. 79, 84, 85, 87.
- 1975 *Dendrodrilus rubidus*-Reynolds, Megadrilogica 2(3): 3.
- 1979 *Dendrodrilus rubidus subrubicundus* + *D. r. tenuis*-Gates, Megadrilogica 3(9): 153, 158.

Diagnosis (after Reynolds *et al.*, 1974: 32–33; Reynolds, 1977a: 71)

Small earthworm, length 20–90 mm, diameter 2–5 mm, segment number 50–120, prostomium epilobitic open, first dorsal pore 5/6. Clitellum saddle on xxvi, xxvii–xxxi, xxxii. Tubercula pubertatis, if present, xxviii, xxix–xxx. Setae widely paired, present from ii in which all eight usually are there, widely paired, *AB* ca. = *CD*, *BC* ca. = *AA*, *DD* < ½*C*, *c* setae at or above *mL*. Genital tumescences, only including *a*, *b*, often approximated or even united mesially in xvi, frequently with a large translucent central area that includes both follicle apertures, in any of segments viii–xi, xiv, xvi–xviii, xx–xxvii, xxxi–xxxv of the clitellar region may be recognizable. Male pores on xv between *B* and *C*. Female pores, minute, just lateral to *B* and equatorial in xiv. Nephropores, minute, inconspicuous, very difficult to locate on strongly preserved material until the cuticular lining of an ectal portion of nephridial ducts is pulled out of them. Pores are at two levels on each side of the body, the lower slightly about *B*, the other above *D*. Seminal vesicles in 9, 11, and 12. Spermathecae, two pairs with short ducts on level with setae *c* opening in 9/10 and 10/11. Body rather compressed dorsoventrally behind the clitellum, the dorsum slightly convex, the ventrum usually rather flat or slightly arched upwards in *AA*. Colour, red and darker dorsally.

Biology

Dendrodrilus rubidus has been found in a wide range of habitats including gardens, cultivated fields, stream banks, in moss in running water and wells and springs, peat, compost, and sometimes in manure. It seems acid tolerant. The species is known from caves in Europe and North America, and in greenhouses, botanical gardens, and the culture beds of earthworm farms (Gates, 1972a). *Dd. rubidus* lives in the upper soil layers though on wet nights the worms have been seen wandering on the soil surface or climbing trees. Under experimental conditions it can withstand prolonged immersion in water (Roots, 1956). Černosvitov and Evans (1947) and Gerard (1964) reported it from under the bark of old trees, and under moss, leaf mould, or rotten wood in moist areas. In Ontario, *Dd. rubidus* was most frequently found under logs and bark of dead trees. In the southern USA, this habitat is exploited by various species of *Bimastos*. In Tristan da Cunha, I reported it from open bush with grass and ferns and drainage areas with ponds (Reynolds and Hänel, 2005). It was found in caves in New Brunswick by McAlpine and Reynolds (1977), the United States by Reeves and Reynolds (1999), Holler *et al.* (2020), in Slovenia by Novak (2005) and in Russia by Turbanov *et al.* (2016).

Although activity can be year round it is probable that in much of North America, including Canada, a winter rest is imposed by the climate. Copulation has not been properly studied but one published observation records an unusual position of ventral apposition, head to head and tail to tail (see Gates, 1972a).

Reproduction

Dendrodrilus rubidus is facultatively parthenogenetic with male sterility and absence of spermathecae common (Gates, 1972a; Reynolds, 1974a).

Climatic zone: Boreal, temperate, mediterranean, sub-tropical.

Ecological type

Dendrodrilus rubidus is a corticole and epigeic species (Reynolds, 2018).

Origin, range

Dendrodrilus rubidus is a native of Palaearctis and was known from Europe, North America, South America, Asia, Africa, and Australasia (Gates, 1972a). It is now known from Bermuda (Reynolds and Fragoso, 2004), Falkland Islands (Reynolds and Jones, 2006), Greenland (Blakemore, 2007), Iceland (Backlund, 1949), Tristão da Cunha Islands (Reynolds and Hänel, 2005) and Turkey (Mısırlıoğlu *et al.*, 2018).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan, Yukon.

United States: Alaska, Alabama, Arkansas, Arizona, California, Colorado, Connecticut, Delaware, Florida, Georgia, Hawaii, Iowa, Idaho, Illinois, Indiana, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, New Hampshire, New Jersey, New Mexico, Nevada, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wyoming.

Mexico: Distrito Federal, México, Michoacán, Nuevo León, San Luis Potosí, Tamaulipas, Veracruz (Fragoso and Reynolds, 1997; Fragoso, 2001).

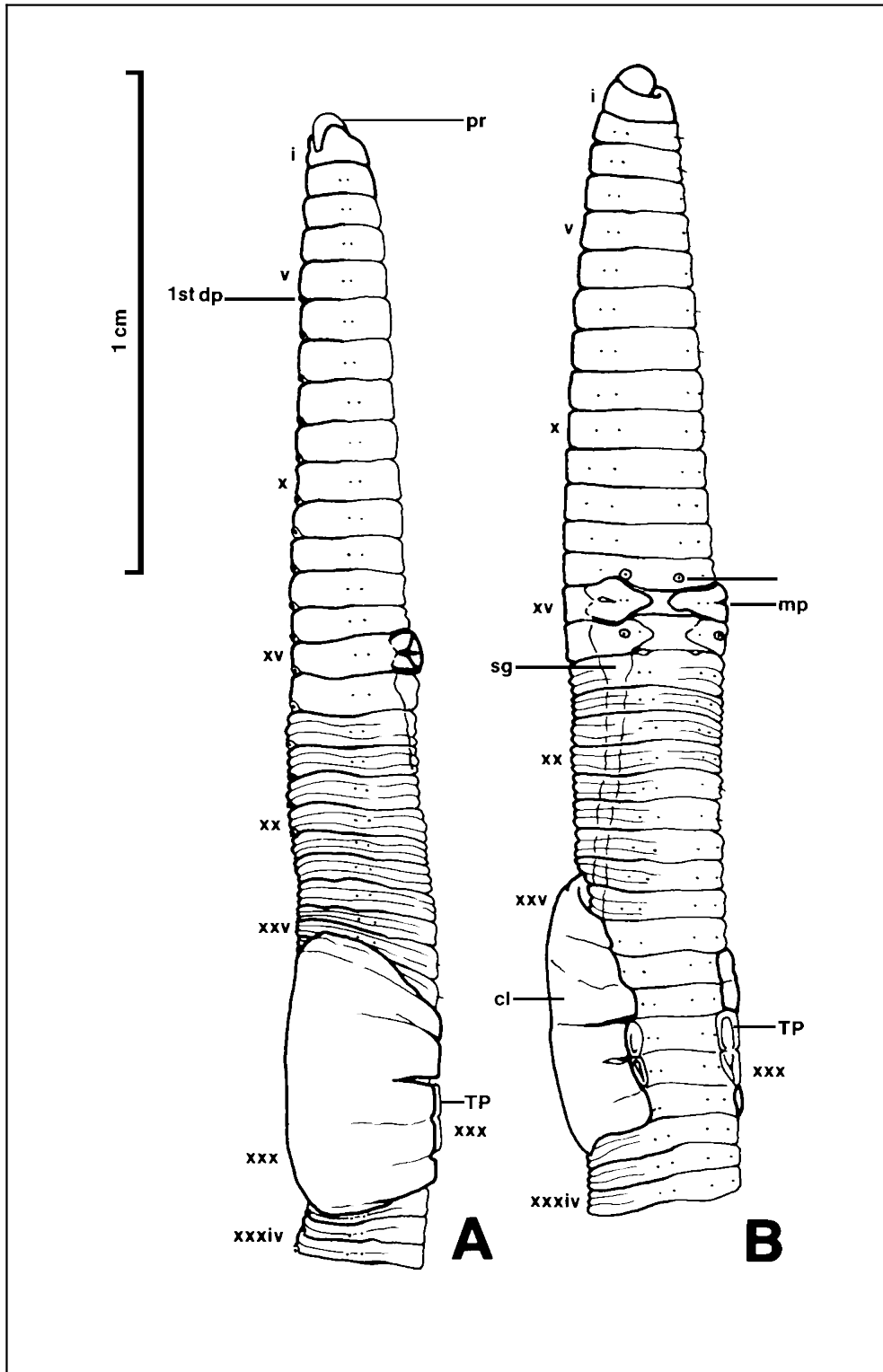


Fig. 19. External longitudinal views of *Dendrodrilus rubidus* showing taxonomic characters. A. Lateral View. B. Ventral view (from Reynolds, 1977a).

Genus *Eisenia* Malm, 1877

- 1877 *Eisenia* Malm, Öfv. Salsk. Hortik. Förh. Göteborg 1: 45.
1900 *Eisenia* (part.)-Michaelsen, Das Tierreich, Oligochaeta 10: 474.
1969 *Eisenia*-Gates, J. Nat. Hist. London 9: 305.
1977 *Eisenia*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 74.
1978 *Eisenia*-Gates, Megadrilologica 3(8): 131.

Type species

Enterion foetidum Savigny, 1826 by Gates (1969).

Diagnosis (after Gates, 1972a; 1975a; Reynolds, 1977a)

Calciferous gland, without sacs, opening into gut behind insertion of 10/11 through a circumferential circle of small pores. Calciferous sacs, lacking. Gizzard, mostly in xvii. Hearts, in vii–xi. Nephridial bladders, sausage-shaped or digitiform, transversely placed. Nephropores, inconspicuous, in two ranks on each side, alternating irregularly and with asymmetry between *a* level just above *B* and one above *D*. Setae, closely paired. Prostomium epolobic. Longitudinal musculature, pinnate. Pigment, red.

Discussion

Eisenia was erected for three species, *Enterion foetidum* Savigny, 1826, and *Allolobophora norvegica* and *A. subrubicunda* Eisen, 1873 by Malm (1877) without the designation of a type species.

By 1837, *Enterion roseum* already was in *Lumbricus*, the only megadrile genus then recognized. In 1874, it was placed as *mucosa*, in Eisen's heterogeneous *Allolobophora*. Not until 1893 was Savigny's species name recognized as valid.

The two *Allolobophora* species are now synonyms of *Dendrodrilus rubidus*. Gates (1969a) redefined *Eisenia* with *Eisenia foetida* as type species, but another of Savigny's species, *Enterion roseum*, has been congeneric with *Eisenia foetida* since Michaelsen (1900a) solely because of spermathecal pore location. If future revisions are based on the more conservative somatic anatomy these two species will not remain congeneric. Most European workers have followed Pop (1941) and Omodeo (1956) and have transferred *Eisenia rosea* to *Allolobophora*. However, on the basis of somatic anatomy it was not reasonable to place *Eisenia rosea* in any genus of which *Enterion chloroticum* Savigny is the type species. Gates (1976) transferred *Eisenia rosea* to the genus *Aporrectodea*.

***Eisenia fetida* (Savigny, 1826)**

Manure worm — Ver du fumier

(Fig. 20)

- 1826 *Enterion fetidum* (corr. *foetidum*) Savigny, Mém, Acad. Sci. Inst. France 5: 182. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1835 *Lumbricus semifasciatus* Burmeister, Zool. Hand. Atl. 33: 3.
- 1836 *Lumbricus annularis* R. Templeton, Ann. Mag. Nat. Hist. 9: 234.
- 1837 *Lumbricus foetidus*-Dugès, Ann. Sci. Nat., (2), 8: 17, 21.
- 1842 *Lumbricus olidus* Hoffmeister, Verm. Lumbric., p. 25.
- 1849 ? *Lumbricus luteus* Blanchard, Hist. Chile 3: 42.
- 1873 ? *Lumbricus rubro-fasciatus* Baird, Proc. Linn. Soc. London 11: 96.
- 1873 *Allobophora foetida*-Eisen, Öfv. Vet.-Akad. Förh. Stockholm 30(8): 50.
- 1877 *Lumbricus annulatus* Hutton, Trans. N.Z. Inst. 9: 352.
- 1877 *Eisenia foetida*-Malm, Öfv. Salsk. Hortik. Förh. Göteborg 1: 45.
- 1887 *Endrilus annulatus* W.W. Smith, Trans. N.Z. Inst. 19: 136.
- 1889 *Lumbricus* (*Allobophora*) *annulatus* + *L. (A.) foetidus*-L. Vaillant, Hist. Nat. Annel. 3(1): 147, 149.
- 1913 *Helodrilus* (*Eisenia*) *foetidus*-Michaelsen, Zool. Jb. Syst. 34: 551.
- 1963 *Eisenia foetida* var. *unicolor* André, Bull. Biol. France Belgique 81: 1.
- 1972 *Eisenia fetida fetida* + *E. f. andrei* Bouché, Inst. Natn. Rech. Agron., p. 380, 381.
- 1976 *Eisenia foetida*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 74.
- 1978 *Eisenia foetida*-Gates, Megadrilogica 3(8): 131.

Diagnosis (after Reynolds *et al.*, 1974: 34; Reynolds, 1977a: 76)

Small to medium sized earthworm, length 35–130 mm (generally < 70 mm), diameter 3–5 mm, segment number 80–110, prostomium epilobic ½ open, first dorsal pore 4/5 (sometimes 3/4 or 5/6). Clitellum saddle on xxiv, xxv, xxvi–xxxii. Tubercula pubertatis on xxviii–xxx. Setae closely paired, $AB = CD$, $BC < AA$, anteriorly $DD = \frac{1}{2} C$ but posteriorly $DD < \frac{1}{2} C$. Genital tumescences may be present around any of the setae on ix–xii, usually around setae *a* and *b* of xxiv–xxxii. Male pores with large glandular papillae on segment xv. Seminal vesicles, four pairs in 9–12. Spermathecae, two pairs with ducts opening near mD line in 9/10 and 10/11. Colour variable, purple, red, dark red, brownish red, sometimes alternating bands of red-brown on dorsum with pigmentless yellow intersegmental areas. Body cylindrical.

Biology

Olson (1928) found this species in manure and decaying vegetation where moisture concentrations were high. Černosvitov and Evans (1947) and Gerard (1964) recorded its habitats as manure, compost heaps, and soil high in organic matter, as well as forests, gardens, and under stones and leaves. Murchie (1956) reported *E. fetida* from manure and bait castaways but never from what he considered "natural" habitats. In Tennessee, Reynolds *et al.* (1974) recorded scattered distribution of this species with it occurring most commonly under logs and debris and at roadside dumps. According to Gates (1972a), the available records give a pH range of 6.8–7.6, and while in Scandinavia it has been considered a species dependent on human culture. *E. fetida* is known from caves in Europe and North America, and Russian records report it from taiga, forests, and steppes (Turbanov *et al.*, 2016 in Georgia and Russia). In Ontario, *E. fetida* was found most frequently under logs and usually not far from human habitation. There are few data available concerning its natural habitat in North America.

Eisenia fetida is a species only found in temperate and boreal countries. In nature, this epigeic species lives near the soil surface, within the decomposing organic matter or in dead woods. Due to its high affinity with composting material, it has become the main species used in vermiculture. It is also a central species as model in toxicological studies and scientific research on earthworm molecular biology.

Reproduction

Eisenia fetida is generally amphimictic with some parthenogenetic morphs (Reynolds, 1974a; Moment, 1979; Jaenike, 1982). There is little information on rest periods in the life-cycle (Gates, 1972a). One assumes that under favourable conditions activity can occur throughout the year. Feeding is selective in that there is minimal ingestion of earth. Copulation is subterranean and although the species has been thought to be obligatorily amphimictic, uniparental reproduction is possible, though very rare (Gates, 1972a). Experimental self-fertilizing was demonstrated by André (1963). *E. fetida* has a maximum life expectancy of 4–5 years, although between 1 and 2 years is more usual. *Eisenia fetida* has been reared on earthworm farms and sold in every Canadian province and American state for fish bait. Harman (1955) reported on the commercial aspects of this species.

Climatic zone: Boreal, temperate, mediterranean, sub-tropical.

Ecological type

Eisenia fetida is an epigeic, epi-endogeic, or corticole species depending on the habitat (Reynolds, 2018).

Origin, range

Eisenia fetida is a native of Palaearctis. It is a peregrine species and now is known from many European, North American, South American, Asian, African, and Australasian countries (Gates, 1972a). It is also known from Bermuda (Reynolds and Fragoso, 2004), Greenland (Støp-Bowitz, 1969), Iceland (Backlund, 1949), Turkey (Reynolds and Mısırlıoğlu, 2018), Bangladesh (Makin *et al.*, 2014), which is a surprise because in my four working trips to that country and two papers I never encountered any lumbricids, only Oriental species (Reynolds, 1994c; Reynolds *et al.*, 1995).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: all provinces and territories due to vermicomposting.

United States: all states due to vermicomposting.

Mexico: Chiapas, Distrito Federal, Guanajuato, México, Puebla, Tlaxacala, Veracruz (Fragoso and Reynolds, 1997; Fragoso, 2001).

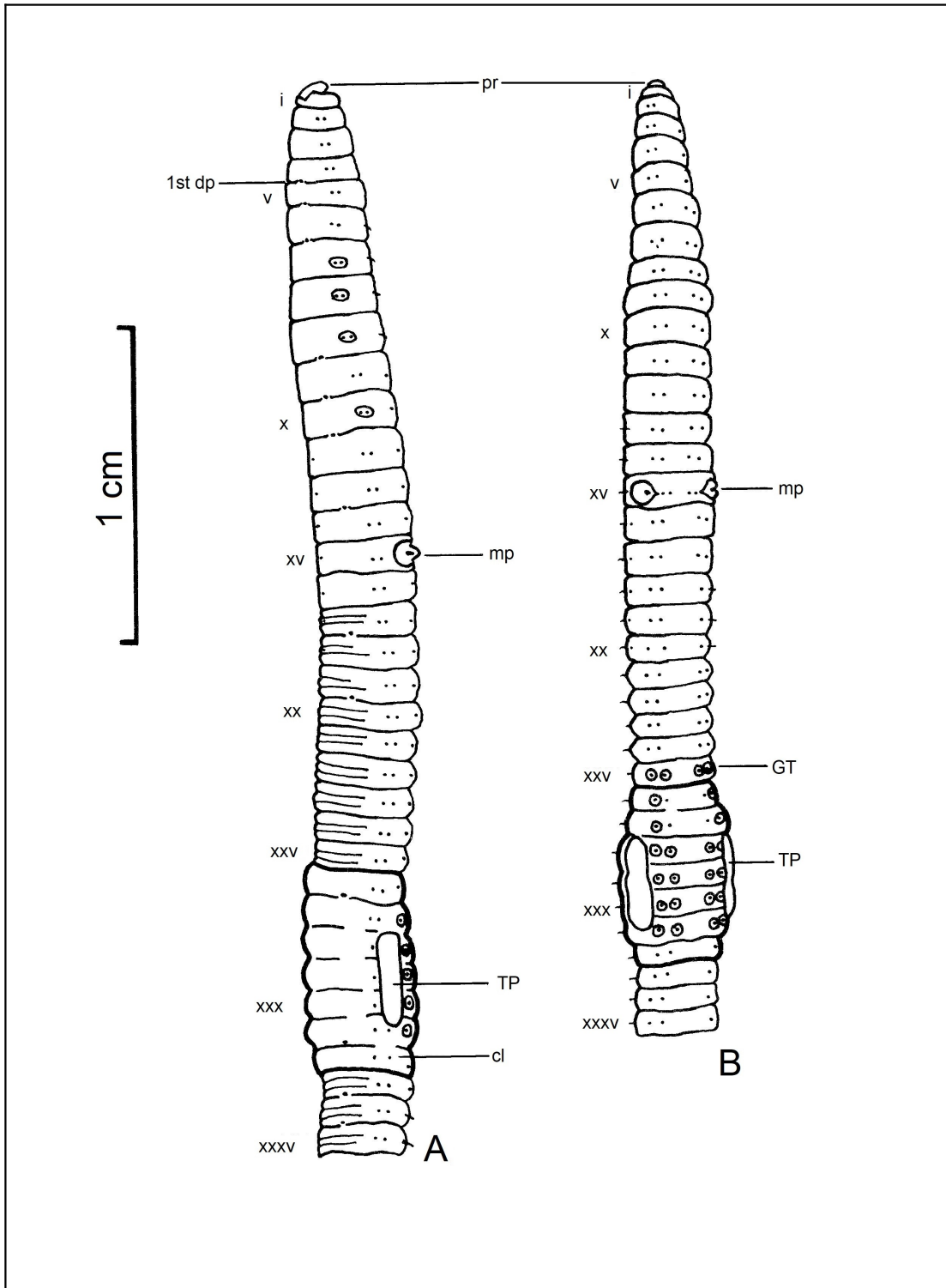


Fig. 20. External longitudinal views of *Eisenia fetida* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Eisenia hortensis* (Michaelsen, 1890)**
European nightcrawler — Ver nocturne rampant européen
(Fig. 21)

- 1890 *Allolobophora subrubicunda* var. *hortensis* Michaelsen, Mitt. Mus. Hamburg 7: 15. Type species are in the Zoologisches Museum Hamburg, Universität Hamburg, cat. no. 50! and Museo ed Istituto di Zoologia Sistemática dell Università di Torino, cat. no. 618 (Reynolds and Cook, 1967).
- 1956 *Dendrobaena hortensis*-Omodeo, Arch. Zool. Italiano 41: 173.
- 1966 *Eisenia veneta* var. *hibernica* Mihailova, Bulgarian Acad. Sci. 3: 187.
- 1972 *Dendrobaena (Dendrobaena) veneta hortensis*-Bouché, Inst. Natn. Rech. Agron., p. 398.
- 1991 *Dendrobaena hortensis* +*D. slovenica* Mršič, Slovenska Akad. 31: 622, 640.
- 1995 *Eisenia hortensis*-Reynolds, Earthworm ecology and biogeography, p. 11.
- 2018 *Eisenia hortensis*-Reynolds, Megadrilogica 23(1): 3, 8, 9, 14, 18, 24, 26, 27, 34, 35.

Diagnosis (after Michaelsen, 1900: 477, translated from German by JWR; Bouché, 1972: 398–399, translated from French by JWR)

Small earthworm, length 17–42 mm, diameter 2–3 mm, number of segments 50–114. Prostomium epilobic open ½ to tanylobic. Dorsal pores beginning in 5/6. Clitellum saddle on xxiv, xxv, xxvi, xxvii–xxxi, xxxii, xxxiii. Tuberculata pubertatus, 2 pairs in xxx–xxxi above setae *b*. Genital tumescences in xi around setae *a* and *b*. Setae widely paired, $aa = 1/5 cd$, $ab = cd$, $dd = 6cd$. Male pore ½ xv. Females pores inconspicuous in xiv. Seminal vesicles, 3 pairs in ix, xi, xii and definite banding of the colour. Calciferous glands in 10–11, 11–12 or 11–13. Calciferous sacs, lacking. Spermathecae simple in 9 and 10. spermathecal pores in 9/10 and 10/11, near mD. Nephropores alternating irregularly, and lack of pale "epaulets" on ix–xi. Colour, reddish-violet/purple.

Biology

European distribution is by way of compost transport (Bouché, 1972). *Eisenia hortensis* lives in aerobic waste material, and as soon as it becomes anaerobic they move out of the waste (Edwards and Bohlen, 1996). In Quebec, *E. hortensis* was found at one site under a pile of leaves (Reynolds and Reynolds, 1992). *Eisenia hortensis* has been reported as a troglophile in Abkhazian caves by Turbanov *et al.* (2016).

Reproduction

Eisenia hortensis is an amphimictic species (Reynolds, 1974a).

Climatic zone: Boreal, temperate.

Ecological type

Eisenia hortensis is an epigeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis, *Eisenia hortensis* is known from Europe and Argentina (Mischiš, 2007), the Canary Islands (Talavera, 2007), Chile (Zicsi and Csuzdi, 2007), Iceland (Blakemore, 2007b), India (Paliwal and Julka, 2005), Iran (Ezzatpanah, 2010), Madeira (Talavera, 1996) and Turkey (Reynolds and Mısırlıoğlu, 2018).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This is a rare species in North America.

Canada: Alberta, Quebec.

United States: Arkansas, California, Illinois, Maine, New York, Ohio, Oregon, Virginia, Washington.

Mexico: none.

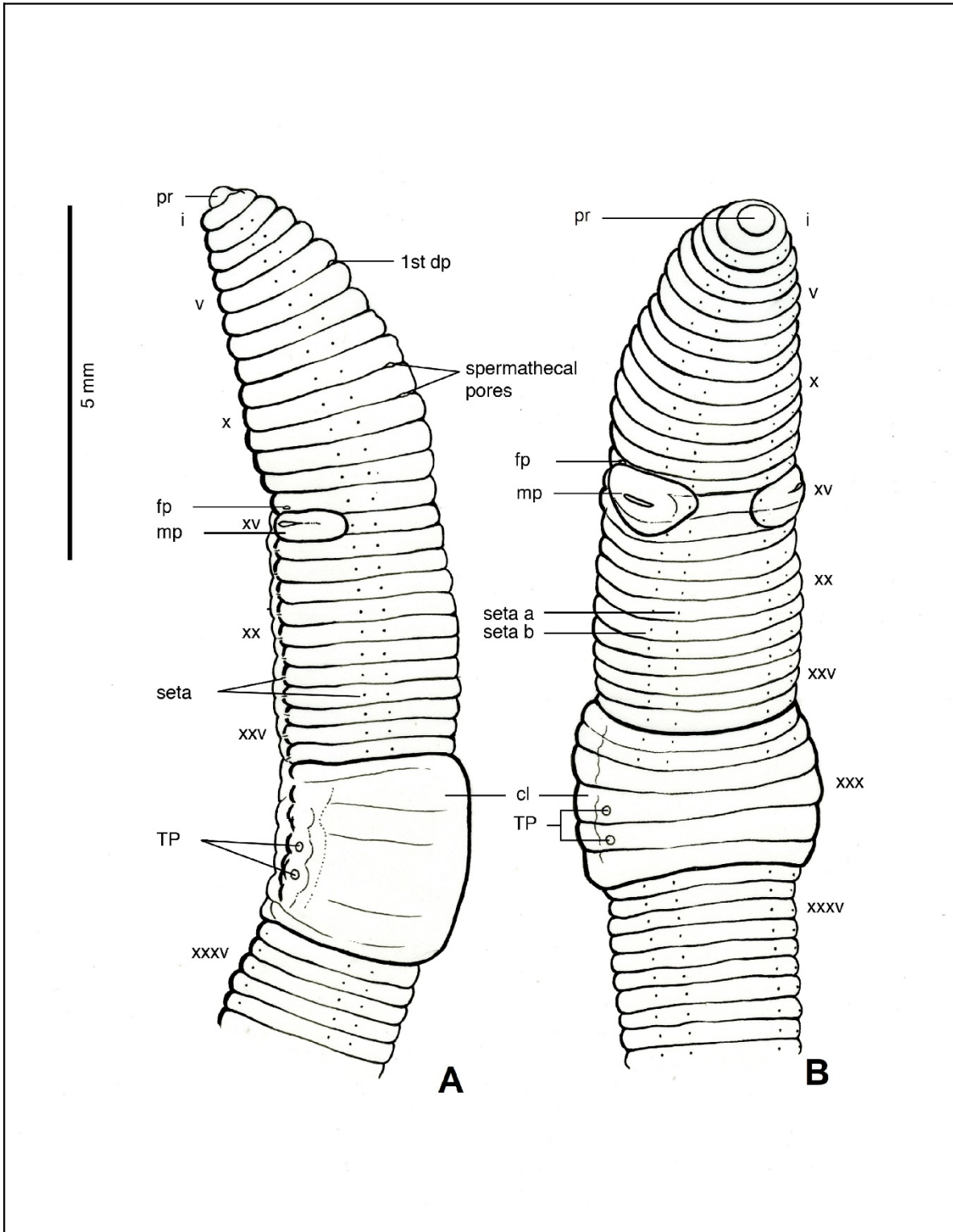


Fig. 21. External longitudinal views of *Eisenia hortensis* showing taxonomic characters. A. Lateral view, B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

Genus *Eiseniella* Michaelsen, 1900

- 1826 *Enterion* (part.) Savigny, Mém, Acad. Sci. Inst. France 5: 184.
1828 *Lumbricus* (part.)-Dugès, Ann. Sci. Nat. 15: 289.
1900 *Eiseniella* Michaelsen, Das Tierreich, Oligochaeta 10: 471.
1972 *Eiseniella*-Bouché, Inst. Natn. Rech. Agron., p. 214.
1977 *Eiseniella*-Gates, Megadrilogica 3(5): 71.
1977 *Eiseniella*-Reynolds, Roy. Ontario Mus., Misc. Publ., p. 83.

Type species

Enterion tetraedrum Savigny, 1826.

Diagnosis (after Gates, 1972a: 108)

Calciferous sacs, in x, digitiform, opening posteriorly into the gut ventrally in region of insertion of 10/11. Esophagus of nearly uniform width through xi–xiv, calciferous channels narrow, lamellae low and continued along the lateral walls of the sacs. Intestinal origin, in xv. Gizzard, in xvii, weak, 17/18 not fenestrated. Typhlosole, simply lamelliform. Extrasophageal trunks, joining dorsal vessel in xii. Hearts, in vii–xi. Nephridial bladder, short, sausage-shaped. Nephropores, inconspicuous, behind xv alternating irregularly and with asymmetry between a level just above *B* and one above *D*. Setae, not closely paired behind the clitellum. Prostomium epilobic. Longitudinal musculature, pinnate.

Discussion

Prior to 1850 species now in the genus were placed in *Enterion* and *Lumbricus* by various authors particularly Savigny (1826) and Dugès (1828). Michaelsen (1900a) proposed the new name *Eiseniella* for a genus erected by Eisen in 1873. Although designated only as a new name for *Allurus* Eisen, 1873, Michaelsen included a second genus of Eisen's (*Tetragonurus* Eisen, 1874) in his *Eiseniella*. Both of Eisen's generic names were preoccupied (*i.e.*, already in use as generic names in other groups); *Allurus* Foerster, 1862 had been used as a genus of hymenopterous insects, while *Tetragonurus* Risso, 1810 had been employed as a genus of fish. The type species for both of Eisen's genera are synonyms of *Enterion tetraedrum* Savigny, 1826. Insufficient data are available concerning the somatic anatomy of species included at various times in the classical *Eiseniella* to determine if they can be congeneric with *Eiseniella tetraedra*.

***Eiseniella tetraedra* (Savigny, 1826)**
 Square-tail worm — Ver à queue carrée
 (Fig. 22)

- 1826 *Enterion tetraedrum* Savigny, Mém. Acad. Sci. Inst. France 5: 184. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1826 ? *Lumbricus quadrangularis* Risso, Hist. Nat. Eur. Mérid. 4: 426.
- 1828 ? *Lumbricus amphisbaena* Dugès, Ann. Sci. Nat. 15: 289.
- 1837 *Lumbricus tetraedrus*-Dugès, Ann. Sci. Nat. (2), 8: 17, 23.
- 1843 *Lumbricus agilis* Hoffmeister, Arch. Naturg. 9(1): 191.
- 1871 *Lumbricus tetraedrus*-Eisen + *L. t. luteus* + *L. t. obscurus* Eisen, Öfv, Vet.-Akad. Förh. Stockholm 27(10): 966, 967, 968.
- 1873 *Allurus tetraedrus*-Eisen, Öfv, Vet.-Akad. Förh. Stockholm 30(8): 54.
- 1874 *Tetragonurus pupa* Eisen, Öfv, Vet.-Akad. Förh. Stockholm 31(2): 47.
- 1885 *Allurus neapolitanus* Örley, Ertek. Term. Magyar Akad. 15(18): 12.
- 1886 *Allurus ninnii* Rosa, Atti Ist. Veneto, (6), 4: 680.
- 1889 *Lumbricus (Allolobophora) neapolitanus* + *L. (Allurus) tetraedrus* + *L. (Eisenia) pupa*-L. Vaillant, Hist. Nat. Annel. 3(1): 113, 151, 154.
- 1889 *Allurus hercynius*-Michaelsen + *A. dubius* Michaelsen + *A. ninnii*-Michaelsen, Mitt. Mus. Hamburg 7(3): 7, 10.
- 1890 *Eisenia pupa*-Benham, Quart. J. Micros. Soc. (n.s.), 31(2): 266.
- 1892 *Allolobophora tetragonurus*-Friend, Sci. Gossip 28: 194.
- 1892 *Allurus tetraedrus* + *A. amphisbaena* + *A. flavus* + *A. tetragonurus*-Friend, Proc. Roy. Irish Acad. (3), 2: 402.
- 1896 *Allurus tetraedrus*-Ribaucourt + *A. bernensis* + *A. novis* + *A. infinitesimalis* Ribaucourt, Rev. Suisse Zool. 4: 69, 73, 74.
- 1900 *Eiseniella tetraedra*-Michaelsen, Das Tierreich, Oligochaeta 10: 471.
- 1931 *Eiseniella intermedia* Jackson, J. Roy. Soc. West. Australia 17: 123.
- 1937 *Eiseniella tetraedra* f. *typica*-Černosvitov, Rec. Indian Mus. 39: 107.
- 1974 *Eisenia tetraedra* (laps.)-Vail, Bull. Tall Timbers Res. Stn., No. 11: 2.

Diagnosis (after Reynolds *et al.*, 1974: 38; Reynolds, 1977a: 84.)

Small earthworm, length 30–60 mm, diameter 2–4 mm, segment number 60–90, prostomium epilobic ½ open, first dorsal pore 4/5–5/6. Clitellum saddle on xxii, xxiii–xxvi, xxvii. Tubercula pubertatis uniformly broad on xxiii–xxv, xxvi. Setae closely paired, AA:AB:BC:CD:DD = 3:1:3:1:6–8 posteriorly. Ventral setae on x, or ix and x modified into genital setae. Male pores on xiii with slightly elevated glandular papillae in Černosvitov's "typical form". This is a misnomer because the normal or "typical" position for other members of the family is on xv. A second form of the same species, not recorded from Canada, has male pores on xv. Female pores in xiv. Seminal vesicles, four pairs on 9–12. Spermathecae, two pairs opening between *d* and mD line in 9/10 and 10/11. Body cylindrical in front of clitellum and quadrangular behind. Colour variable, from dark brown, greenish, ruddy to bright golden yellow.

Biology

Eiseniella tetraedra is a limicolous species and shows a marked preference for damp habitats. It is known from wells, springs, subterranean waters, rivers, ponds, lakes, and canals, and may be one of the dominant animals in the dense moss of swift streams (Gates, 1972a). In Ohio it has been recorded from soils with a pH range of 6.8 to 8.5, a moisture content of 25–35%, and an organic matter content of 4–5% (Olson, 1928). It is the most common megadrile in British caves and is known from caves in the rest of Europe and in South Africa. Olson (1928, 1936) and Eaton (1942) reported this species from water-soaked banks of streams, lakes, and ponds. Murchie (1956) reported it from the bottom deposits of streams, lakes, or ponds, from wet to very moist stream banks and lake shores, from bottom lands subject to flooding, or with a high water table, and from seepage areas around springs at upland sites. The soil type for these sites varied from peaty organic material to sandy gravel. The sources of specimens for the present study were

all moist to wet habitats. Species reported from caves in Slovenia by Novak (2005) and Russia by Turbanov *et al.* (2016). Under favourable conditions activity can be year round, but in Canada there are probably summer and winter rest periods. Aestivation involves immobility and tight coiling in a small mucus-lined cavity; whether hibernation involves quiescence or diapause is not known.

Reproduction

Eiseniella tetraedra is obligatorily parthenogenetic (Muldal, 1952; Omodeo, 1955b; Reynolds, 1974a). The first reports of uniparental reproduction for megadriles involved experiments with *Eiseniella tetraedra* (Gavrilov, 1935, 1939).

Climatic zone: Boreal, temperate, mediterranean, sub-tropical.

Ecological type

Eiseniella tetraedra is a limicolous species but may be considered epigeic in some cases. Others have called it an aquatic species.

Origin, range

Eiseniella tetraedra is a native of Palaearctis, and a peregrine species now known from Europe, North America, South America, Asia, Africa, and Australasia (Gates, 1972a). It also occurs in the Falkland Islands (Reynolds and Jones, 2006), Iceland (Backlund, 1949), the Isle of Man (Reynolds, 1996b), Morocco (Reynolds and Reeves, 2019), the Tristão da Cunha Islands (Blakemore, 2008) and Turkey (Reynolds and Mısırlıoğlu, 2018). It is another cosmopolitan species that has been carried around the world. It was recently reported from the Yukon for the first time in a creek bottom under rocks and in shrub heath tundra in a seep under a rock (Reynolds *et al.*, 2019b).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Northwest Territory, Nova Scotia, Nunavut, Ontario, Prince Edward Island, Quebec, Yukon.

United States: Alaska, Arkansas, Arizona, California, Colorado, Connecticut, District of Columbia, Georgia, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Dakota, Tennessee, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Mexico: México, Puebla, Veracruz states (Fragoso, 2001).

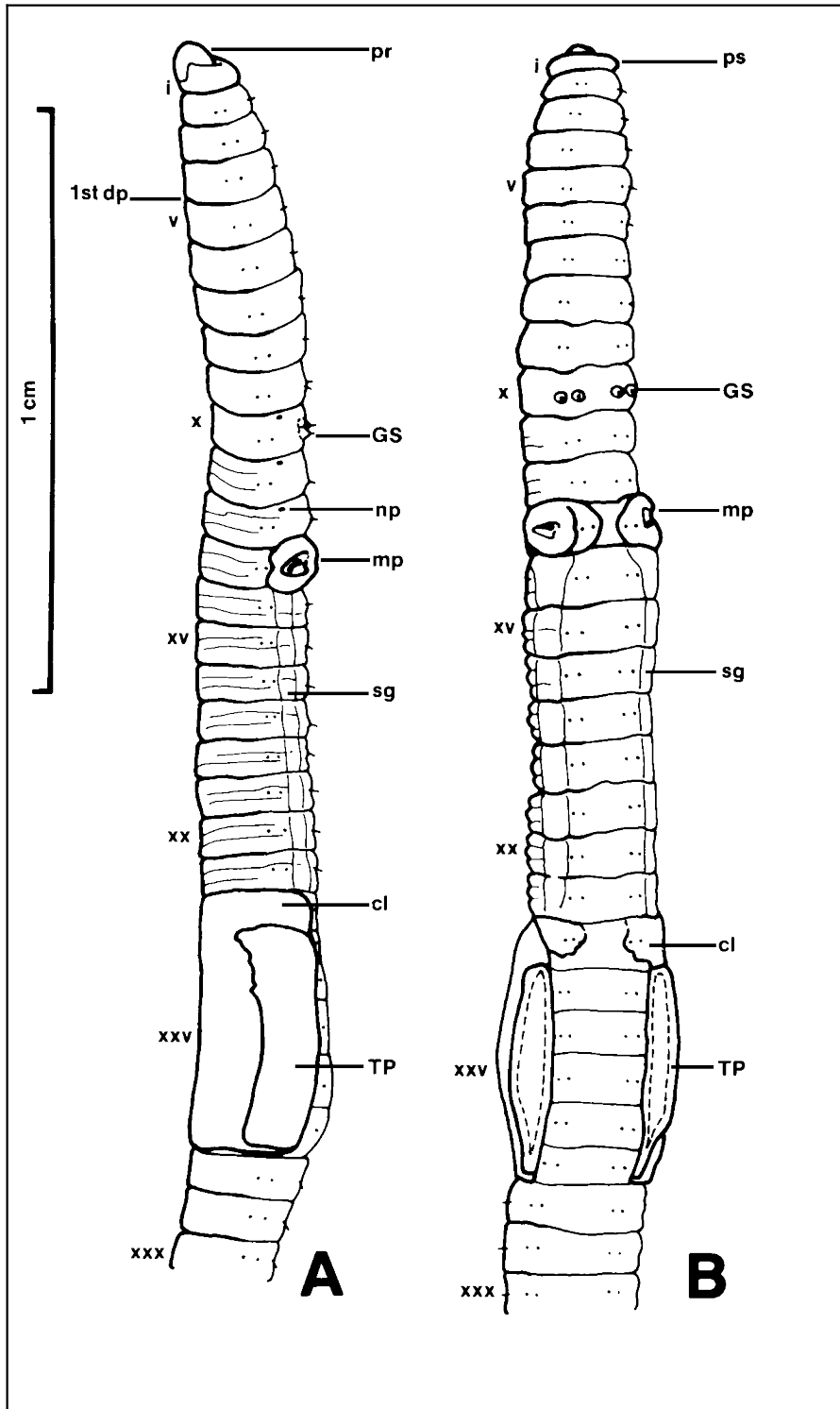


Fig. 22. External longitudinal views of *Eiseniella tetraedra* showing taxonomic characters. A, Lateral View, B, Ventral view (from Reynolds, 1977a).

Genus *Lumbricus* Linnaeus, 1758

- 1758 *Lumbricus* (part.) Linnaeus, Syst. Nat. (ed. 10), p. 647.
1774 *Lumbricus* (part.)-Müller, Verm. Terr. Fluv. 1(2): 24.
1780 *Lumbricus* (part.)-Fabricius, Fauna Grønlandica, p. 277.
1826 *Enterion* (part.) Savigny, Mém. Acad. Sci. Inst. France 5: 179.
1836 *Lumbricus* (part.)-Templeton + *Omilurus* Templeton, Ann. Mag. Nat. Hist. 9: 235.
1845 *Lumbricus* (part.)-Hoffmeister, Regenwürmer, p. 4.
1873 *Lumbricus*-Eisen, Öfv, Vet.-Akad. Förh. Stockholm 30(8): 45.
1876 *Lumbricus* (part.)-Claus, Grundzüge der Zool. (ed. 3) 1: 416.
1880 *Lumbricus* (part.)-Claus, Grundzüge der Zool. (ed. 4) 1: 478.
1881 *Lumbricus* (part.) + *Enterion*-Örley, Math. Term. Kozlem. Magyar Akad. 16: 580, 587.
1894 *Allolobophora* (part.)-W.W. Smith, Trans. New Zealand Inst. 26: 117.
1900 *Lumbricus*-Michaelsen, Das Tierreich, Oligochaeta 10: 508.
1930 *Lumbricus*-Stephenson, Oligochaeta, p. 914.
1975 *Lumbricus*-Gates, Megadrilogica 2(1): 3.
1977 *Lumbricus*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 88.

Type species

Lumbricus terrestris Linnaeus, 1758, by Sims (1973).

Diagnosis (after Gates, 1972a: 113, 1975a: 3)

Calciferous sacs, in x, digitiform to pyriform, opening into gut posteriorly and ventrally in region of insertion of 10/11, lamellae continued along lateral walls. Esophagus, widened and markedly moniliform in xi–xii, in those segments with a vertically slitlike lumen which widens as lamellae gradually narrow behind 12/13. Intestinal origin, in xv. Gizzard, mainly in xvii. Typhlosole, high, rather thick and nearly oblong vertically, grooves not continuous across ventral face. Extraesophageal trunks, joining dorsal trunk in region of ix–x. Hearts, in vii–xi. Nephridial bladder, J-shaped, closed end laterally, duct passing into parietes near *B*. Nephropores, obvious, behind xv irregularly alternating, with asymmetry, between levels just above *B* and well above *D*. Setae, closely paired. First dorsal pore, anterior to 10/11. Prostomium, tanylobic. Body compressed dorsoventrally behind clitellum and with a more or less trapezoidal transverse section. Longitudinal musculature, pinnate. Pigment, lacking immediately underneath intersegmental furrows, in circular muscle layer.

Discussion

The genus *Lumbricus* (Linnaeus, 1758, p. 647) originally contained only two species, *L. terrestris* and *L. marinus*. Since the latter was not a member of the Oligochaeta, the type species was declared to be *Lumbricus terrestris* (J.C.Z.N., Opinion 75). Discussions of what was really meant by *L. terrestris* Linnaeus, 1758 (and his lengthened definition of Syst. Nat., 12th ed., 1767, pp. 1076–1077) have raged ever since but were officially settled by Sims (1973), Gates (1973b) and Bouché (1973). The result of this action was the neotypification of *Lumbricus terrestris* Linnaeus by Sims (1973) with an expanded definition, and the deposition of type material from Sweden in the British Museum (Natural History). For more than 200 years there was a question as to whether *L. herculeus* Savigny, 1826 was a synonym of *L. terrestris* L. 1758. This was not a result of careless research, but honest errors, because until recently DNA techniques were not available. The characters separating these two distinct species was presented by James *et al.* (2020).

***Lumbricus castaneus* (Savigny, 1826)**

Chestnut worm — Ver alezan

(Fig. 23)

- 1826 *Enterion castaneus* + *E. pumilum* Savigny, Mém. Acad. Sci. Inst. France 5: 180, 181. Type species missing (Reynolds and Cook, 1976).
- 1837 *Lumbricus castaneus*-Dugès, Ann. Sci. Nat., (2), 8: 17, 22.
- 1851 *Lumbricus triannularis* Grube, In: Middendorff, Reise Sibirien 2(1): 18.
- 1865 *Lumbricus minor* Johnston, Cat. British Non-paras. worms, p. 59.
- 1867 *Lumbricus josephinae* Kinberg, Öfv. Vet.-Akad. Förh, Stockholm 23: 98.
- 1871 *Lumbricus purpureus* Eisen, Öfv. Vet.-Akad. Förh. Stockholm 27(10): 956.
- 1881 *Enterion pupureum* + *Lumbricus purpureus*-Örley, Math. Term. Kozlem. Magyar Akad. 16: 588, 590.
- 1889 *Lumbricus* (L.) *castaneus* + L. (L.) *purpureus* + L. (L.) *triannularis*-L. Vaillant, Hist. Nat. Annel. 3(1): 124, 127, 129.
- 1894 *Allolobophora purpureus*-W.W. Smith, Trans. New Zealand Inst. 26: 117.
- 1895 *Lumbricus pumilosum* (laps.)-Beddard, Monogr. Oligo. (Oxford), p. 722.
- 1896 *Lumbricus castaneus*-Ribaucourt + *L. morelli* Ribaucourt + *L. perrieri* Ribaucourt, Rev. Suisse Zool. 4: 10, 13, 14.
- 1900 *Lumbricus castaneus*-Michaelsen, Das Tierreich, Oligochaeta 10: 510.
- 1936 *Lumbricus castaneus* var. *disjonctus* Téry, Bull. Soc. Sci. Nancy (n.s.), 1936: 196.
- 1949 *Lumbricus castaneus* f. *typica* Pop Anal. Acad. Repub. Pop. Române Sect. Științe Geol. Geogr. Biol. 1(9): 476.
- 1957 *Lumbricus castaneus* var. *pictus* Chandebois, Bull. Soc. Zool. France 82: 417.
- 1972 *Lumbricus castaneus*-Bouché, Inst. Natn. Rech. Agron., p. 362.
- 1976 *Lumbricus castaneus*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 89.

Diagnosis (after Reynolds, 1977a: 89)

Small earthworm, length, 30–50 mm (generally <35mm), diameter 3–5 mm, segment number 70–100, prostomium tanylobic, first dorsal pore 5/6-8/9. Clitellum saddle on xxviii–xxxiii. Tubercula pubertatis xxix–xxxii. Setae closely paired, $AA \approx BC$, $AB > CD$, $DD \approx \frac{1}{2}C$ anteriorly and $DD < \frac{1}{2}C$ posteriorly. Setae *a* and *b* on ix and/or x on pale genital tumescences fused ventrally. Male pores inconspicuous on xv. Female pores inconspicuous on xiv. Seminal vesicles, three pairs in 9, 11, and 12+ 13. Spermathecae, two pairs with short ducts in 9/10 and 10/11. Colour, deeply pigmented, dark red, chestnut, violet brown and strongly iridescent. Body cylindrical and dorsoventrally flattened posteriorly.

Biology

Lumbricus castaneus has been recorded from soils with a pH range of 4.6–8.0, from gardens, cultivated fields, pastures, forests, taiga, steppes, among organic matter such as manure and compost or leaf litter, and in banks by water (Gates, 1972a). It has been found in caves in Europe. Gerard (1964) reported it as terrestrial, mostly in soil rich in organic matter, in gardens, parks, pastures, forests, on river and marsh banks, and under stones, leaves and dung. Apart from this author's records all previous North American records failed to give habitat information, but my findings are similar to those of Gerard in England. In Ontario, *L. castaneus* was collected from a stream. Recently in the Yukon, it was collected from under log in wet leaves (Reynolds *et al.*, 2019). Found in caves in Slovenia by Novak (2005).

Reproduction: *Lumbricus castaneus* is an obligatorily amphimictic species (Reynolds, 1974a).

Climatic zone: Boreal, temperate, mediterranean.

Ecological type: *Lumbricus castaneus* is an epigeic species (Reynolds, 2018).

Origin, range

Lumbricus castaneus is a native of Palaearctis, and a peregrine species now known from Europe and North America. It has been reported also from Bangladesh (Makin *et al.*, 2014), which is a surprise because in my four working trips to that country and two papers I never encountered any lumbricids, only Oriental species (Reynolds, 1994c; Reynolds *et al.*, 1995).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia, New Brunswick, Newfoundland and Labrador, Ontario, Prince Edward Island, Quebec, Yukon.

United States: Alaska, Connecticut, Delaware, Idaho, Kentucky, Maine, Maryland, Massachusetts, Michigan, New Hampshire, New Jersey, New York, Oregon, Pennsylvania, Vermont, Virginia, Washington, West Virginia.

Mexico: Distrito Federal, México (Fragoso, 2001).

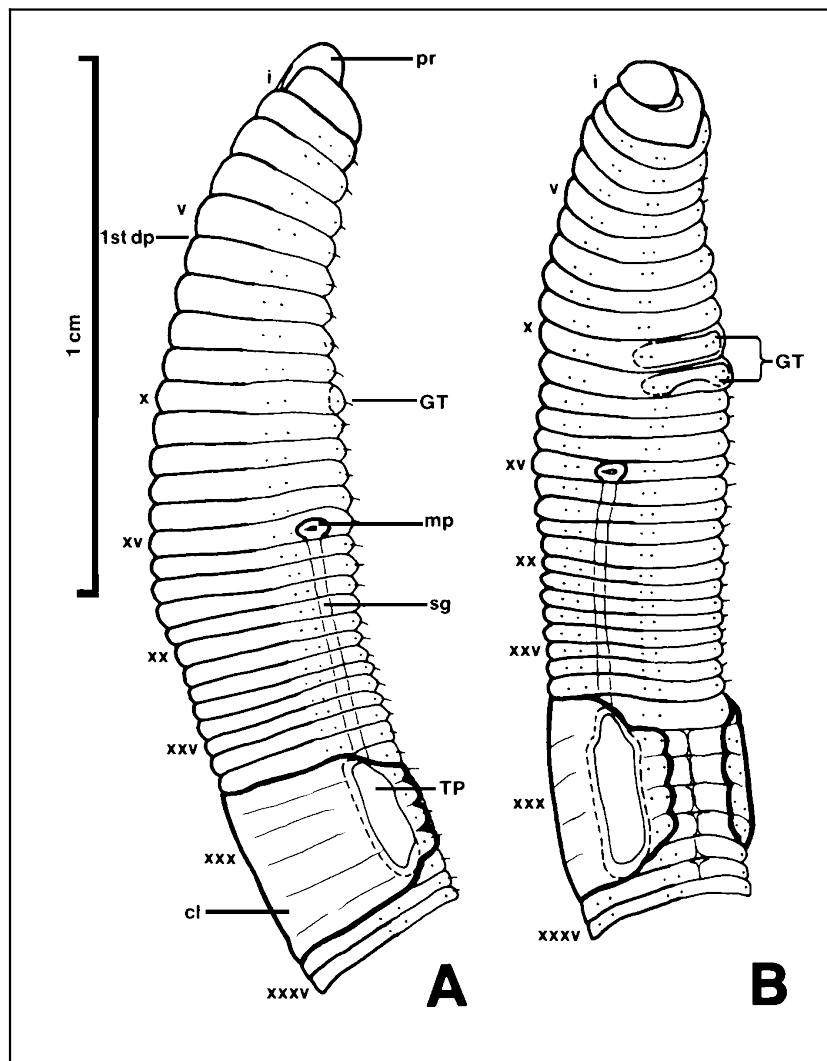


Fig. 23. External longitudinal views of *Lumbricus castaneus* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Lumbricus festivus* (Savigny, 1826)**

Quebec worm — Ver québécois

(Fig. 24)

- 1826 *Enterion festivum* Savigny, Mém, Acad. Sci. Inst. France 5: 180. Type species unknown (Reynolds and Cook, 1976).
- 1836 *Lumbricus omilurus* R. Templeton, Ann. Mag. Nat. Hist. 9: 235.
- 1837 *Lumbricus festivus*-Dugès, Ann. Sci. Nat. (2), 8: 17, 21.
- 1891 *Lumbricus rubescens* Friend, Nature 44: 273.
- 1900 *Lumbricus festivus*-Michaelsen, Das Tierreich, Oligochaeta 10: 512.
- 1976 *Lumbricus festivus*-Reynolds, Roy. Ontario Mus., Life Sci., Misc. Publ., p. 92.
- 1977 *Lumbricus festivus*-Reynolds, Canadian Field-Nat. 91(4): 395.
- 2008 *Lumbricus festivus*-Reynolds, Megadrilogica 12(2): 24.

Diagnosis (after Reynolds, 1977a: 92)

Medium to large earthworm, length 48–105 mm, diameter 4–5 mm, segment number 100–143, prostomium tanylobic, first dorsal pore 5/6. Clitellum saddle on xxxiv–xxxix. Tubercula pubertatis xxxv–xxxvii, xxxviii. Genital tumescences in Setae closely paired, $AA:AB:BC:CD = 34:12:25:8$ anteriorly, and $35:10:25:8$ posteriorly. Setae on segments v–x are notably enlarged and more widely paired. Some of the ventral setae on viii–xiv, xviii, xxv–xxxix are on genital tumescences. Male pores on xv with glandular papillae extending onto xiv and xvi. Female pores on xiv. Seminal vesicles, three pairs in 9, 11 and 12 + 13 + 14. Spermathecae, two pairs with short ducts opening on level C in 9/10 and 10/11. Colour, ruddy brown, iridescent dorsally and lightly coloured ventrally. Body cylindrical and slightly dorsoventrally flattened posteriorly.

Biology

Lumbricus festivus is rare and little is known about its habits. Gerard (1964) recorded the habitats of this species as pastures, on river banks, in soil beneath dung, leaves, and under stones. I found the species at ten sites in Ontario, six times under logs, three times under debris, and once under a leaf pile. The British Columbia records were from a single cultivated field. First report from the USA was from a ditch in northern Vermont (Reynolds, 1977b).

Reproduction

Lumbricus festivus is assumed to be obligatorily amphimictic (Reynolds, 1974a) and copulation occurs beneath the soil surface. In surveys by Reynolds (1975b, 1975c, 1977b) specimens with spermatophores were found in Quebec, but not in British Columbia (Reynolds, 1977b).

Climatic zone: Temperate.

Ecological type

Lumbricus festivus is an epigeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis, *Lumbricus festivus* is a peregrine species now known from Europe: Austria, Denmark, England, Finland, France, Germany, Norway, Scotland, Spain and Sweden. In Canada, known from Quebec and the adjacent provinces plus one field in British Columbia (Reynolds, 1977b). Stafford (1902) listed it from Nova Scotia, but extensive collecting in the province since has failed to uncover the species (Reynolds, 1976a, 2010b). The Vermont record was a single adult from under a log a few hundred metres south of the Quebec border (Reynolds, 2008a).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia, New Brunswick, Ontario, Quebec.

United States: Vermont.

Mexico: none.

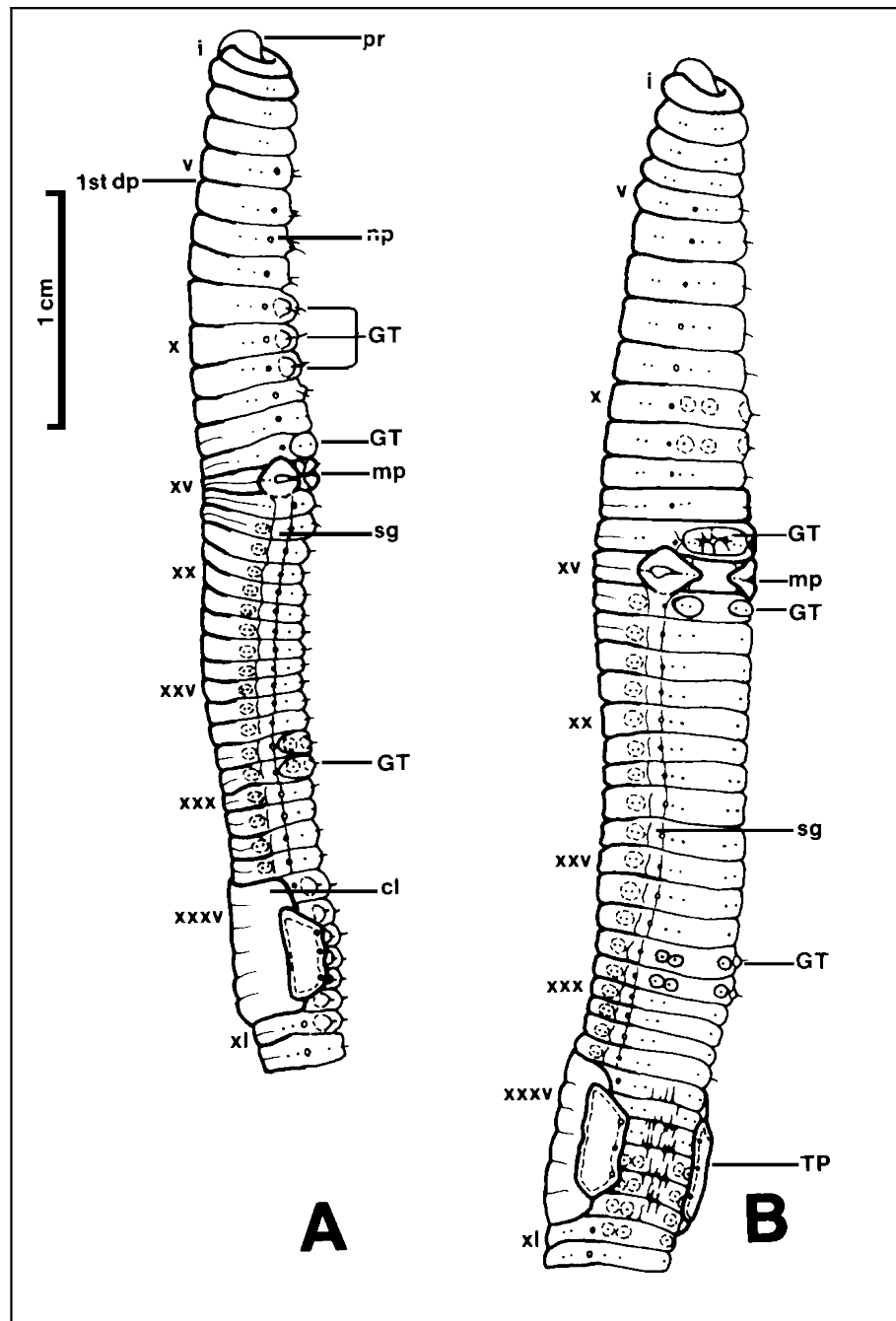


Fig. 24. External longitudinal views of *Lumbricus festivus* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a).

***Lumbricus rubellus* Hoffmeister, 1843**
Red marsh worm — Ver rouge du marécage
(Fig. 25)

- 1843 *Lumbricus rubellus* Hoffmeister, Arch. Naturg. 9(1): 187. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1877 *Lumbricus campestris* Hutton, Trans. New Zealand Inst. 9: 351.
- 1881 *Enterion rubellum* var. *parvum* + *E. r.* var. *magnum* Örley, Math. Term. Kozlem, Magyar Akad. 16: 588, 589.
- 1883 *Digaster campestris* (part.)-Hutton, New Zealand J. Sci. 1: 586.
- 1887 *Endrilus campestris* (part.)-W.W. Smith, Trans. New Zealand Inst. 19: 137.
- 1892 *Lumbricus rubellus* var. *curticaudatus* Friend, J. Linn. Soc. London 24: 312.
- 1894 *Allolobophora rubellus*-W.W. Smith, Trans. New Zealand Inst. 26: 117.
- 1899 *Allolobophora herculeana* Bretscher, Rev. Suisse Zool. 6: 419.
- 1900 *Lumbricus rubellus*-Michaelsen, Das Tierreich, Oligochaeta 10: 509.
- 1901 *Allolobophora ribaucourti* Bretscher, Rev. Suisse Zool. 9: 220.
- 1909 *Allolobophora relictata* Southern, Proc. Roy. Irish Acad. 27B(8): 119.
- 1923 *Lumbricus rubellus*-Stephenson, Fauna British India, Oligochaeta, p. 508.
- 1972 *Lumbricus rubellus rubellus*- Bouché + *L. r. castaneoides* + *L. r. friendoides* Bouché, Inst. Natn. Rech. Agron., p. 368, 371, 372.
- 1976 *Lumbricus rubellus*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 94.

Diagnosis (after Reynolds *et al.*, 1974: 42; Reynolds, 1977a: 95)

Medium to large earthworm, length 50–150 mm (usually > 60 mm), diameter 4–6 mm, segment number 70–120, prostomium tanylobic, first dorsal pore 5/6–8/9. Clitellum saddle on xxvi, xxvii–xxxii, xxxiii. Tubercula pubertatis on xxviii–xxxi, xxxii. Setae closely paired, $AA > BC$, $AB > CD$, $DD = \frac{1}{2}C$ posteriorly. Setae *a* and *b* in genital tumescences, occasionally on 10. Genital tumescences in viii–xii, xx–xxiii, xxvi–xxxvi. Male pores, inconspicuous, without glandular papillae on xv. Female pores, inconspicuous on xiv. Ovisacs present. Calciferous glands in 10–14 with bilobed diverticula in 10, 11, 12. Non moniliforme hearts in 7–11. Seminal vesicles, three pairs in 9, 11 (smaller), and 12 + 13. Spermathecae simple, two pairs with short ducts opening in 9/10 and 10/11. Colour, ruddy brown or red-violet and iridescent dorsally, pale yellow ventrally. Body cylindrical and sometimes dorsoventrally flattened posteriorly. Ventral surface with transverse ridges forming a honeycomb pattern.

Biology

Lumbricus rubellus has been recorded from natural soils of pH 3.8–8.0 and shows a wide tolerance of habitat factors. Olson (1928, 1936) reported it from under debris. Eaton (1942) found it in stream banks, under logs, and in woody peat and stated that it seemed to require a great deal of moisture and organic matter. Černosvitov and Evans (1947) recorded the habitats of this species as places rich in humus, abundant in parks, gardens, pastures, on river banks, under stones, moss, or old leaves. Gerard (1964) also found this species frequently aggregated beneath dung in pastures as well as the sites mentioned above. In Ontario, *L. rubellus* was obtained from a wide variety of habitats. This species inhabits soils rich in organic matter, and mainly found in the litter and within the first centimetres below the soil surface. It can be found in croplands, natural or planted forests, pastures and gardens. common in coniferous forests (Reynolds *et al.*, 1974). As well as in pastures, where it is commonly associated with dungs. It is also important in the decomposition of litter. Often found in caves (Reeves and Reynolds, 1999; Holler *et al.* (2020); Novak, 2005).

Species often found in plant roots, suggesting that this species actively feeds in the rhizosphere (Hale *et al.*, 2008). It burrows and produces casts in the upper mineral soil layer (Hale *et al.*, 2008). Relatively frost (Tiunov *et al.*, 2006) and low pH tolerant (pH 3.0 to 7.7) (Wironen and Moore, 2006). As invasive species, its first impacts tend to be physical disruption of the stratified humus layers, thus preparing later settlement of alien endogeic species (James and Hendrix, 2004). In the Tristão da Cunha Islands, I reported it from open bush with grass and ferns and drainage areas with ponds (Reynolds and Hänel, 2005).

This species has been cultured by the fish bait industry (Gates, 1972a). It is also known for its capacity to break down organic wastes. However, further research into its potential in vermicomposting is needed due to its relatively slow reproduction rate (Edwards and Arancon, 2004). It is also important in the decomposition of litter. Numerous sporezoans can parasitize *L. rubellus*, such as species belonging to the genus *Monocystis* (Sporozoa, Gregarinida) (Purrini and Pižl, 1982).

The statistically significant smaller size of *L. rubellus* from the Rainy River District may be an example, in earthworms, of a size shift as a result of character displacement (see Reynolds and Mayville, 1994).

During the 2000s, *L. rubellus* became a major research model earthworm in ecotoxicology and molecular biology (Stürzenbaum *et al.*, 1998; Morgan *et al.*, 2004; Owen *et al.*, 2008; Guo *et al.*, 2009).

Reproduction

Under suitable conditions activity, including breeding, is year round. *L. rubellus* is obligatorily amphimictic (Reynolds, 1974c) and copulation, like defecation, occurs below the soil surface, or in the litter layer, at any time of day. It seems that copulation does not involve a mucous tube (Gates, 1972a).

Climatic zone: Boreal, temperate, mediterranean.

Ecological type

Lumbricus rubellus epigeic and an epi-endogeic species (Reynolds, 2018).

Origin, range

A native of Palaearctis, *Lumbricus rubellus* is today widely distributed in Europe and Russia, except in the arctic area. It has been introduced into North America where it is found in 42 of the 48 U.S. states (see below). In the southern hemisphere, it has been introduced in many temperate areas, such as Eastern Australia, New Zealand, Bolivia, Chile, South Africa, southern Patagonia and Uruguay. It has also been reported from the following: the Canary Islands (Talavera, 1987), the Isle of Man (Reynolds, 1996b), the Falkland Islands (Reynolds and Jones, 2006), the Faroe Islands (Enckell *et al.*, 1986), Greenland (Blakemore, 2007b), Madeira (Talavera, 1996), Tristão da Cunha Islands (Reynolds and Hänel, 2005) and Turkey (Reynolds and Mısırlıoğlu, 2018).

It has been reported from Bangladesh (Makin *et al.*, 2014), which is a surprise because in my four working trips to that country and two papers I never encountered any lumbricids, only Oriental species (Reynolds, 1994c; Reynolds *et al.*, 1995).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Northwest Territory, Nova Scotia, Ontario, Prince Edward Island, Quebec, Yukon.

United States: Alaska, Arkansas, Arizona, California, Colorado, Connecticut, District of Columbia, Delaware, Georgia, Florida, Idaho, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin.

Mexico: Distrito Federal, México, Michoacán, Morelos, Puebla, Veracruz states (Fragoso and Reynolds, 1997; Fragoso, 2001).

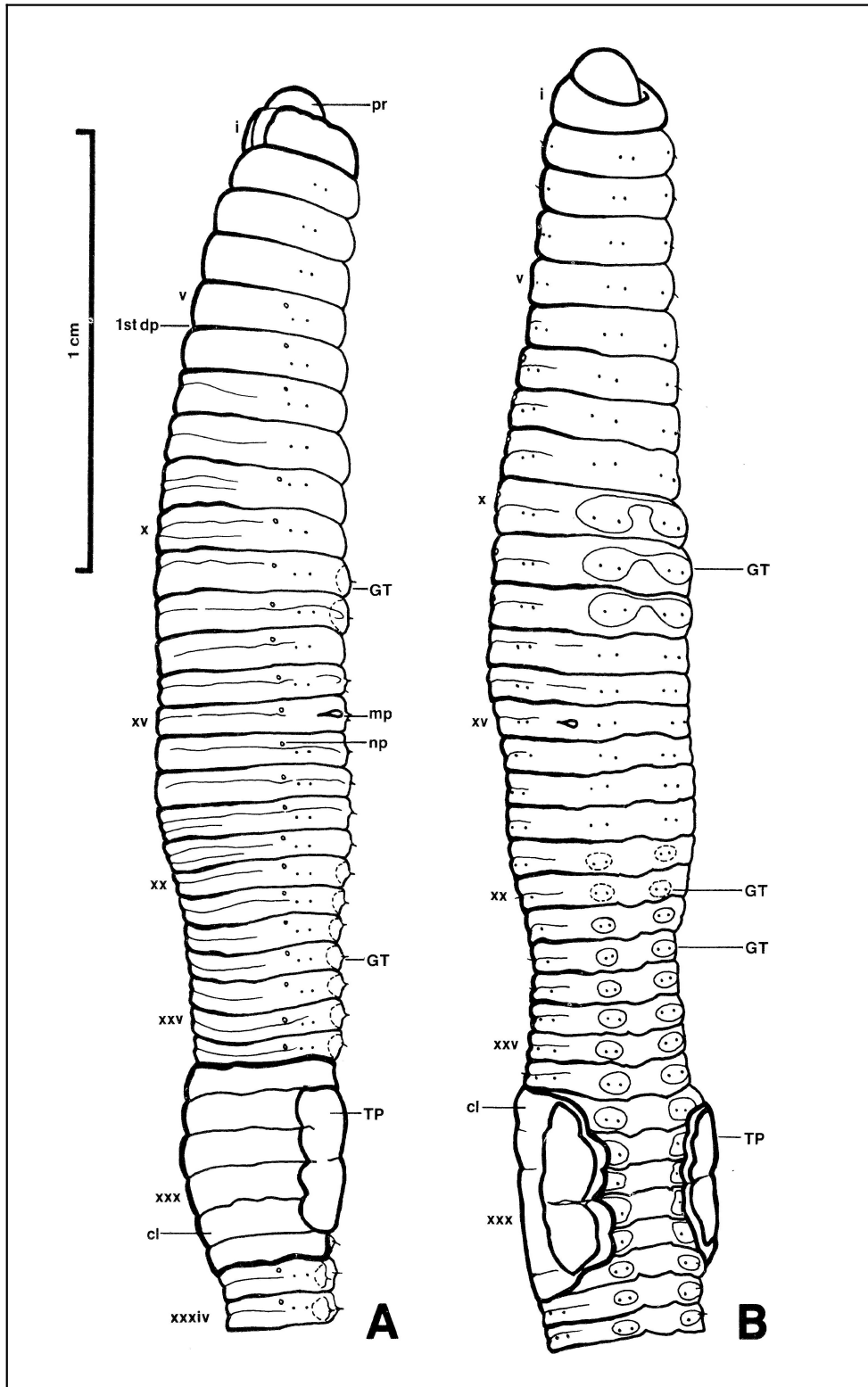


Fig. 25. External longitudinal views of *Lumbricus rubellus* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a).

***Lumbricus terrestris* Linnaeus, 1758**
 Nightcrawler, Dew-worm — Ver nocture rampant, Ver de rosée
 (Fig. 26)

- 1758 *Lumbricus terrestris* Linnaeus, Syst. Nat., ed. 10, p. 647. Type species is in the British Museum Natural History, London cat. no. 1973:1:1—neotype, see Sims, R.W. (1973); (Reynolds and Cook, 1976).
- 1774 *Lumbricus terrestris* (part.)—Müller, Verm. Terr. Fluv. 1(2): 74.
- 1780 *Lumbricus terrestris* (part.) + *L. norvegicus* (part.)—Fabricius, Fauna Grønlandica, p. 277.
- 1825 *Lumbricus terrester* (part.)—Blumenbach, Hand. Naturg. (ed. 11), p. 365.
- 1826 *Enterion herculeum* Savigny, Mém, Acad. Sci. Inst. France 5: 180.
- 1837 *Lumbricus herculeus*-Dugès, Ann. Sci. Nat., (2), 8: 17, 21.
- 1842 *Lumbricus agricola* Hoffmeister, Verm. Lumbric., p. 24.
- 1867 *Lumbricus infelix* Kinberg, Öfv, Vet.-Akad. Förh. Stockholm 23: 98.
- 1872 ? *Lumbricus americanus* E. Perrier, Nouv. Arch. Mus. Paris 8: 44.
- 1884 *Lumbricus herculeus*-Rosa, Lumbric. Piemonte, p. 22.
- 1896 *Lumbricus studeri* Ribaucourt, Rev. Suisse Zool. 4: 5.
- 1900 *Lumbricus terrestris*-Michaelsen, Das Tierreich, Oligochaeta 10: 511.
- 1937 *Lumbricus herculeus*-Tétay, Bull. Mus. Hist. Nat. 9: 151.
- 1953 *Lumbricus terrestris*-Graff, Zool. Anz. 161(11/12): 324.
- 1958 *Lumbricus terrestris*-Gates, Breviora, Mus. Comp. Zool. 91: 8.
- 1969 *Lumbricus herculeus*-Bouché, Inst. Natn. Rech. Agron., p. 89.
- 1970 *Lumbricus herculeus*-Bouché, Rev. Écol. Biol. Sol 7(4): 541.
- 1972 *Lumbricus herculeus*-Bouché and Beugnot, Rev. Écol. Biol. Sol 9(4): 697.
- 1972 *Nicodrilus terrestris voconcus* Bouché, Inst. Natn. Rech. Agron., p. 321.
- 1972 *Lumbricus herculeus*-Bouché, Inst. Natn. Rech. Agron., p. 352.
- 1973 *Lumbricus terrestris*-Sims, Bull. Zool. Nomencl. 30(1): 27.
- 1976 *Lumbricus terrestris*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 99.
- 1998 *Lumbricus terrestris terrestris* (part.)—Qiu and Bouché, 1998q: 192.
- 2010 *Lumbricus terrestris*-James, Porco, Decaëns, Richard, Rougerie and Erséus, PLoS One 12: 1.
- 2013 *Allolobophora terrestris*-Paoletti, Sommaggio and Fusaro, Biol. Ambientale 27(2): 31.

Note: These are the major synonyms and references for *Lumbricus terrestris* Linnaeus. Unfortunately, *Lumbricus terrestris* has become almost synonymous with "earthworm" in many parts of the world. This has led to many published studies and reports about the species which in fact were undertaken on different, and frequently distantly related, species (Örley, 1881a,b; Vaillant, 1889; Stephenson, 1930: xi; Causey, 1952; Stebbings, 1962: 905; Cameron and Fogal, 1963; Gates, 1972a: 114–115 and 120–123).

Diagnosis (after Reynolds *et al.*, 1974: 43–44; Reynolds, 1977a: 99)

Large earthworm, length 90–300 mm, diameter 6–10 mm, segment number 120–160, prostomium tanylobic, first dorsal pore 7/8. Citellum saddle, on xxxi, xxxii–xxxvii. Tubercula pubertatis xxxiii–xxxvi. Setae enlarged and widely paired in the caudal and cephalic regions (*i.e.*, *AB* and *CD* are greater) but closely paired and smaller in the central region, $AA > BC$, $AB > CD$, and $DD = \frac{1}{2} C$ anteriorly, $DD < \frac{1}{2} C$ posteriorly. The ventral setae of x, xxvi, and sometimes xxv are on broad genital tumescences modified into genital setae. Genital tumescences, occasionally in viii–xiv and xxiv–xxxix. Male pores prominent with large elevated glandular papillae extending over xiv–xvi. Seminal vesicles, three pairs in 9, 11, and 12+ 13. Spermathecae, two pairs with short ducts opening at 9/10 and 10/11. Body cylindrical and strongly compressed dorsoventrally posteriorly.

Biology

Lumbricus terrestris has been found in soils of pH 4.0–8.08 and can adapt to a wide variety of habitats. According to Gerard (1964), it is almost purely terrestrial and is found in gardens, arable and pasture lands, forests, and river banks.

Gates (1972a) records additional habitats such as streams, mud flats, woody peat, under logs in a stream bed, under cow pats, and in compost. It has been found in greenhouses and botanical gardens in Europe and North America and in European caves (Gates, 1972a). The species does not normally occur in forests in North America (Reynolds, 1976b). After intensive collecting by the author in eastern North America, it now appears that a statement such as "*Lumbricus terrestris* is becoming increasingly important in the United States, following its importation and gradual replacement of endemic populations" (Edwards *et al.*, 1969) is not true. Many erroneous statements such as this have been made about *L. terrestris* without data to support their claims. Data for naturally occurring populations of *L. terrestris* in North American areas south of the limits of Quaternary glaciations are lacking (Reynolds, 1994b, 2011a). A few limited collections of this species were obtained in Tennessee, Maryland, and Delaware, three states south of the southern limits of Pleistocene glaciation, by Reynolds *et al.* (1974), Reynolds (1974b), and Reynolds (1973a), respectively. In Ontario, *L. terrestris* was collected from a variety of habitats, but primarily from under logs.

Lumbricus terrestris can stand cold temperatures and tolerate soils with pH values from 3.5 to 8. However, it is not frost-tolerant indicating that it probably hibernates in deep soil layers during the winter (Tiunov *et al.*, 2006; Wironen and Moore, 2006). This species comes to the surface to feed where it pulls leaves into the mouth of its burrow where they partially decay before being eaten. It is considered invasive in the north-central United States where it thrives in fence rows and woodlots and can lead to reductions in native herb and tree regrowth.

Lumbricus terrestris is also collected annually at night by the millions as the major species of worm for fish bait in the northern portion of North America. For decades worm pickers used golf courses as their source, but in recent years they have switched to pastures (Steckley, 2020). The relatively long life cycle makes it unprofitable to rear this species commercially for fish bait (cf. *Aporrectodea tuberculata* and *Eisenia fetida*). It is also gathered annually in large numbers for biological supply institutions which distribute this species for use in laboratory studies at high schools and universities, for *L. terrestris* is nearly always the textbook example of the oligochaetes. For example, 20,000 specimens per year are shipped to South Africa for biological studies because it cannot be found locally (Reinecke, *in litt.* 5 March, 1975).

Feeding may be both selective and indiscriminate and certainly during burrowing much soil is swallowed. Casting is usually beneath the soil surface. Unusual activities of this species are the lining of burrows with pebbles, or fecal earth, and the drawing into the burrows of leaves. The entrances to burrows may be blocked with seeds, sticks, straws, and feathers. *Lumbricus terrestris* is an important species in litter decomposition. Laboratory studies illustrated that *L. terrestris* can distinguish between leaf species and will select in a predictable order which I termed the leaf palatability scale: *Robinia* >> *Populus* > *Ulmus* = *Acer* ~ *Liriodendron* > *Fraxinus* = *Tilia* = *Betula* > *Quercus* = *Fagus* << *Abies* = *Larix* = *Picea* = *Pinus* = *Thuja* = *Tsuga* (Reynolds, 1972a, 1972b). In essence, these studies showed that the more rapidly a leaf species decomposes the more palatable and available it becomes for earthworm utilization and nutrition.

Reproduction

Lumbricus terrestris is obligatorily amphimictic (Reynolds, 1974a) and copulation is nocturnal and takes place on the surface of the soil. Under favourable conditions activity, including copulation, is year round but a summer and winter rest period may be climatically imposed in certain areas.

Climatic zone: Boreal, temperate.

Ecological type

Lumbricus terrestris is an anecic species (Reynolds, 2018).

Origin, range

Lumbricus terrestris is a native of Palaearctis and is known from Europe, Iceland, North America, South America, Siberia, and Australasia (Reynolds, 1976). It also occurs in the following locations: Egypt (Mahmoud, 2007), the Falkland Islands (Blakemore, 2008c), the Faroe Islands (Enckell and Rundgren, 1988), Greenland (Blakemore,

2007b), Iceland (Backlund, 1949), India (Paliwal and Julka, 2005), Madeira (Talavera, 1996) and Sudan (Babiker, 2012). It has been reported from Bangladesh (Makin *et al.*, 2014), which is a surprise because in my four working trips to that country and two papers I never encountered any lumbricids, only Oriental species (Reynolds, 1994; Reynolds *et al.*, 1995).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan, Yukon.

United States: Alaska, Arkansas, California, Colorado, Connecticut, District of Columbia, Delaware, Florida, Georgia, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, Montana, Nevada, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin.

Mexico: Distrito Federal (Fragoso, 2001).

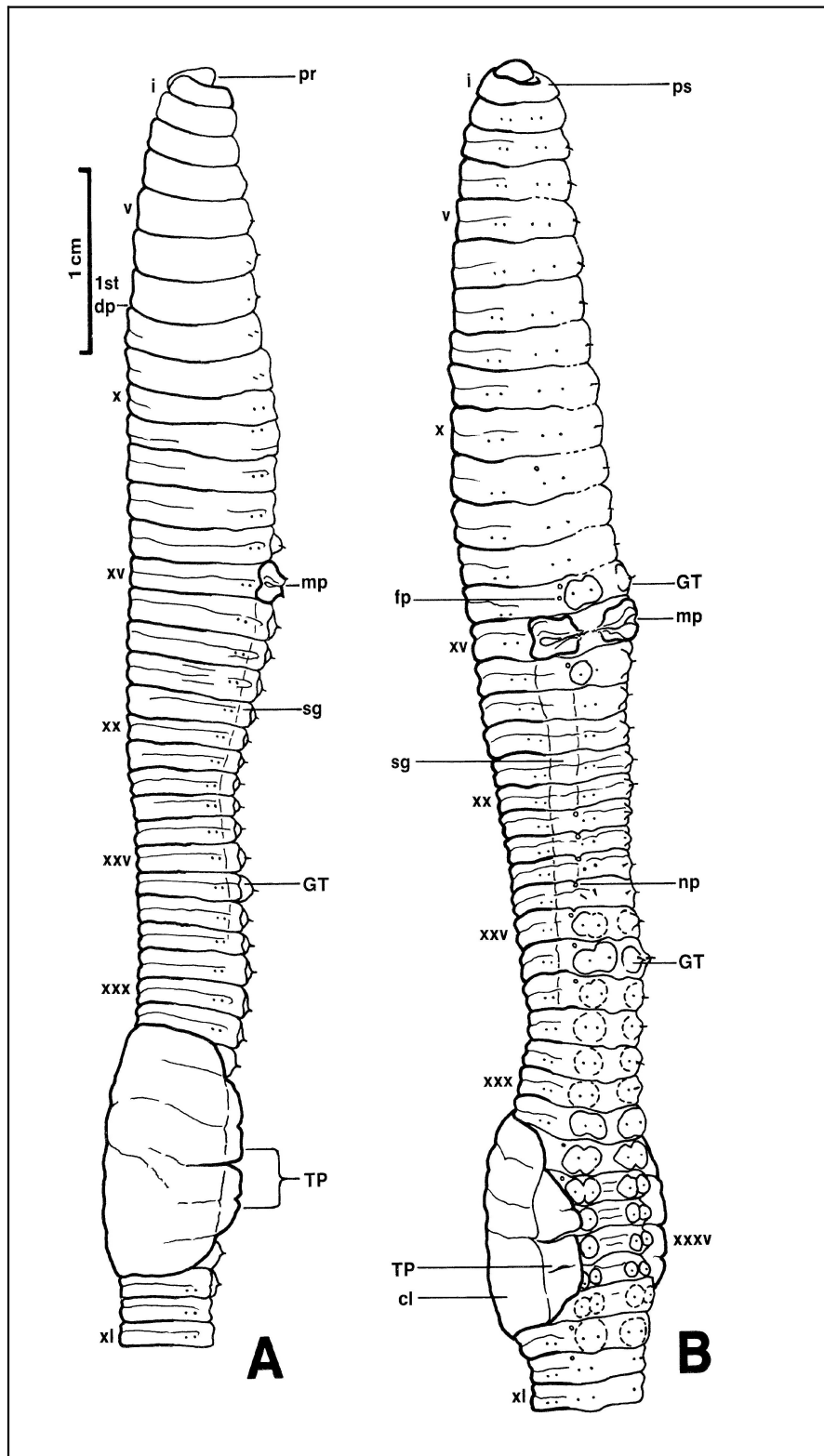


Fig. 26. External longitudinal views of *Lumbricus terrestris* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a).

Genus *Octolasion* Örley, 1885

- 1885 *Octolasion* (part.) Örley, Ertek. Term. Magyar Akad. 15(18): 13.
1889 *Lumbricus* (*Octolasion*) (part.) + *L. (Allobophora)* (part.) + *Dendrobaena* (part.) + *L. (L.)* (part.) + *Titanus?* (part.)-L. Vaillant, Hist. Nat. Annel. 3(1): 113, 130, 116, 121, 93.
1896 *Octolasion* + *Allolobophora* (*Octolasion*)-Ribaucourt, Rev. Suisse Zool. 4: 95.
1900 *Octolasium* (part.)-Michaelsen, Das Tierreich, Oligochaeta 10: 504.
1930 *Octolasium* (part.)-Stephenson, Oligochaeta (Oxford), p. 914.
1972 *Octolasium*-Bouché, Inst. Natn. Rech. Agron., p. 253.
1975 *Octolasion*-Gates, Megadrilogica 2(1): 4.
1976 *Octolasion*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 104.
1982 *Octolasium*-Zicsi, Acta Zool. Acad. Sci. Hungaricae 28(3-4): 431.

Type species

Enterion tyrtaeum Savigny, 1826 (= *Octolasion lacteum* Örley, 1885).

Diagnosis (after Gates, 1972c: 123, 1975a: 4)

Calciferous sacs, in x, large, lateral, communicating vertically and widely with gut lumen though reaching beyond esophagus both dorsally and ventrally. Calciferous lamellae continued onto posterior walls of sacs. Intestinal origin, in xv. Gizzard, mostly in xvii. Extraesophageals, passing up to dorsal trunk posteriorly in xii. Hearts, vi–xi. Nephridial bladders, ocarina-shaped, Nephropores, obvious, behind xv in one regular rank on each side, just above *B*. Setae, behind the clitellum not closely paired. Prostomium epilobic. Longitudinal musculature, pinnate.

Discussion

There has been considerable confusion concerning the spelling of this genus name since the early 1900s. Michaelsen (1900b) changed many of the Greek generic endings to Latin endings, *i.e.*, *Octolasion* to *Octolasium* and *Bimastos* to *Bimastus*. According to the International Code of Zoological Nomenclature (Article 32), the original spelling is the correct spelling. Therefore, *Octolasion* Örley, 1885 and *Bimastos* Moore, 1893 are the correct spellings and most current oligochaetologists are now employing them. The genus *Octolasion* Örley, 1885 contains only five species, *O. cyaneum*, *O. lacteovicinum*, *O. lacteum*, *O. montanum* and *O. tyrtaeum*. Species in Europe and elsewhere often placed in *Octolasion* are now considered to belong in the genus *Octodrilus* Omodeo, 1956 with *Lumbricus complanatus* Dugès, 1828 as the type (*cf.* Bouché, 1972, Gates, 1975a) or *Octodriloides* Zicsi, 1986 with *Octolasium* (*Octodrilus*) *kovacevici* Zicsi, 1970 as type (*cf.* Mršić, 1991).

***Octolasion cyaneum* (Savigny, 1826)**
Woodland blue worm — Ver bleu des bois
(Fig. 27)

- 1826 *Enterion cyaneum* Savigny, Mém. Acad. Sci. Inst. France 5: 181. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1774 *Lumbricus terrestris* (part.)-Müller, Verm. Terr. Fluv. 1(2): 24.
- 1837 *Lumbricus cyaneus*-Dugès, Ann. Sci. Nat., (2), 8: 17, 21.
- 1845 *Lumbricus stagnalis* (part.) Hoffmeister, Regenwürmer, p. 35.
- 1867 *Lumbricus alyattes* Kinberg, Öfv. Vet.-Akad. Förh. Stockholm 23: 99.
- 1884 *Allolobophora profuga* Rosa, Lumbricidi del Piemonte, 1884: 47.
- 1889 *Lumbricus alyattes* + *Lumbricus (Dendrobaena) stagnalis* + *Lumbricus cyaneus*-L. Vaillant, Hist. Nat. Annel, 3(1): 96, 118, 124.
- 1890 *Allolobophora studiosa* Michaelsen, Arch. Ver. Mecklenburg 44: 50.
- 1893 *Allolobophora (Octolasion) cyanea* (part.)-Rosa, Mem. Acc. Torino, (2), 43: 424, 455, 456.
- 1895 *Allolobophora cyanea profuga* Protz, Schr. Ges. Danzig 9: 255.
- 1896 *Allolobophora (Octolasion) cyanea studiosa*-Ribaucourt, Rev. Suisse Zool. 4: 95.
- 1900 *Octolasion cyaneum*-Michaelsen, Das Tierreich, Oligochaeta 10: 506.
- 1948 *Dendrobaena jeanneli* Pop, Ann. Acad. Repub. Române, Sect. Științ. Geol. Geogr. Biol., (A), 1(9): 244.
- 1972 *Octolasion cyaneum*-Bouché + *O. c.* var. *armoricum* Bouché + *Dendrobaena (D.) jeanneli* Bouché, Inst. Natn. Rech. Agron., p. 258, 260, 404.
- 1972 *Octolasion cyaneum*-Edwards and Lofty, Biol. Earthworms, p. 214.
- 1972 *Octolasion cyaneum*-Gates, Bull. Tall Timbers Res. Stn. 14: 31.
- 1976 *Octolasion cyaneum*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 105.

Diagnosis (after Reynolds *et al.*, 1974: 45; Reynolds, 1977a: 105)

Medium sized earthworm, length 65–180 mm, diameter 7–8 mm, segment number 140–158, prostomium epilobic $\frac{1}{3}$ – $\frac{1}{2}$ closed, first dorsal pore 9/10, 11/12 or 12/13. Clitellum saddle on xxix–xxxiv. Tubercula pubertatis xxx–xxxiii. Setae closely paired anteriorly, $CD < AB < BC < AA < DD$, and widely paired posteriorly, $AB > BC > CD$. Setae of x, xviii, xix, xx, xxi frequently on white genital tumescences. Male pores on xv with well-defined narrow papillae in area *B*. Female pores on xiv. Calciferous gland on 10–14. Nephropores, well developed in area *B* and above setae *b*. Seminal vesicles, four pairs in 9–12, with the pairs in 11 and 12 larger than the pairs in 9 and 10. Spermathecae, simple as two pairs opening between *c* and *d* in 9/10 and 10/11. Body cylindrical but octagonal posteriorly. Colour, blue-grey or whitish.

Biology

This species is known from soils of pH 5.2–8.0 and may well be ubiquitous with respect to this factor. Gates (1973b) records it from under stones in water, in moss, stream banks, and other limnic habitats. It is known also from ploughed fields, wet sand, forest soils, and from caves in Europe. Černosvitov and Evans (1947) reported it mostly from under stones and occasionally under moss. Gates (1973b) found the species under logs and under rocks near stream beds. Under logs and rocks was the most common site for *O. cyaneum* in Ontario. This was also true for Quebec (Reynolds and Reynolds, 1992).

Activity may be year round but in central Maine summer drought and winter freezing impose two periods of inactivity (Gates, 1961), and this is probably the case in Ontario. In experimental studies casting was below ground but occasional surface casting has been reported (Gates, 1973b). This species is relatively rare in North America and is of little or no economic importance.

Reproduction

Octolasion cyaneum is obligatorily parthenogenetic (Reynolds, 1974a); copulation has not been recorded; and may never have been observed (Gates, 1973b).

Climatic zone: Boreal, temperate.

Ecological type

Octolasion cyaneum is an endogeic species (Reynolds, 2018).

Origin, range

Octolasion cyaneum is a native of Palaearctis and now known from Europe, North America, South America,, and Australasia (Gates, 1972a). It has also been reported from Iceland (Backlund, 1949), India (Paliwal and Julka, 2005), Madeira (Talavera, 2011), Tierra del Fuego (Mischis, 2007) and Turkey (Reynolds and Mısırlıoğlu, 2018). It has been reported from Bangladesh (Makin *et al.*, 2014), which is a surprise because in my four working trips to that country and two papers I never encountered any lumbricids, only Oriental species (Reynolds, 1994c; Reynolds *et al.*, 1995). A large collection was reported from Anticosti Island, Quebec (Reynolds *et al.*, 2014).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This species is not frequently encountered in North America.

Canada: British Columbia, New Brunswick, Nova Scotia, Ontario, Quebec.

United States: Alaska, California, Colorado, Georgia, Iowa, Indiana, Kansas, Maine, Maryland, Massachusetts, Michigan, Mississippi, New York, North Carolina, Oregon, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia, Washington, Wisconsin.

Mexico: Distrito Federal, México, Veracruz states (Fragoso, 2001).

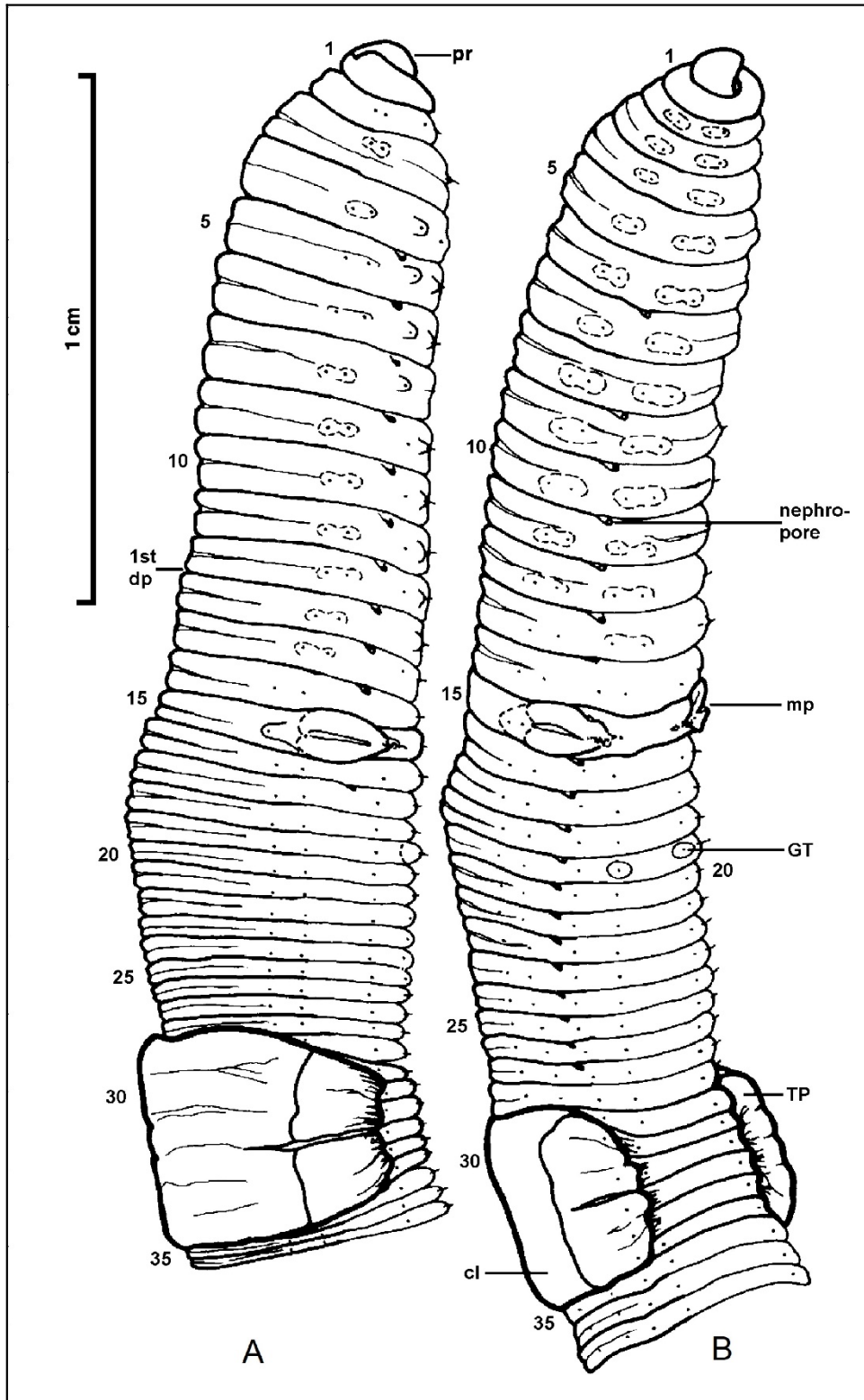


Fig. 27. External longitudinal views of *Octolasion cyaneum* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

***Octolasion tyrtaeum* (Savigny, 1826)**
Woodland white worm — Ver blanc des bois
(Fig. 28)

- 1826 *Enterion tyrtaeum* Savigny, Mém. Acad. Sci. Inst. France 5: 180. Type species are in the Museum National d'Histoire, Naturelle Laboratoire de Zoologie (Vers), Paris, cat. no. unknown (Reynolds and Cook, 1976).
- 1837 *Lumbricus tyrtaeus*-Dugès, Ann. Sci. Nat. (2), 8: 17, 22.
- 1845 *Lumbricus communis cyaneus* + *L. stagnalis* (part.) Hoffmeister, Regenwürmer, p. 24, 35.
- 1881 *Lumbricus terrestris* var. *lacteus* Örley+ *L. t.* var. *rubidus* Örley, Math. Term. Kozlern. Magyar Akad. 16: 584.
- 1884 *Allolobophora profuga* Rosa, Lumbric. Piemonte, p. 47.
- 1885 *Octolasion rubidum*-Örley + *O. profugum*-Örley + *O. gracile*-Örley + *O. lacteum*-Örley, Ertek. Term. Magyar Akad. 15(18): 16, 17, 18, 21.
- 1889 *Lumbricus (Allolobophora) profugus* + *L. (O.) gracilis* L. Vaillant, Hist. Nat. Annel. 3(1): 113.
- 1896 *Allolobophora (Octolasion) rubida*-Ribaucourt + *A. (O.) gracilis*-Ribaucourt + *A. sylvestris* Ribaucourt, Rev. Suisse Zool. 4: 63, 65, 67, 95.
- 1900 *Octolasion lacteum*-Michaelsen, Das Tierreich, Oligochaeta 10: 506.
- 1900 *Allolobophora (Octolasion) profuga*-Michaelsen, Abh. Nat. Verh. Hamburg 16(1): 16.
- 1900 *Allolobophora profuga*-Smith, Bull. Illinois St. Lab. Nat. Hist. 5: 441.
- 1917 *Octolasion lacteum*-Smith, Proc. United States Natn. Mus. 52(2174): 178.
- 1952 *Octolasion lacteum* (laps.)-Goff, American Midl. Nat. 47(2): 484.
- 1971 *Octolasion lacteum*-Crossley, Reichle and Edwards, Pedobiologia 11: 71.
- 1972 *Octolasion lacteum*-Edwards and Lofty, Biol. earthworms. p. 216.
- 1972 *Octolasion lacteum lacteum* + *O. l. gracile*-Bouché, Inst. Natn. Rech. Agron., p. 253, 257.
- 1972 *Octolasion tyrtaeum*-Gates, Bull. Tall Timbers Res. Stn. 14: 35.
- 1976 *Octolasion tyrtaeum*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 105.

Diagnosis (after Reynolds *et al.*, 1974: 46; Reynolds, 1977a: 108)

Small to medium sized earthworm, length 25–130 mm, diameter 3–6 mm, segment number 75–165, prostomium epilobitic $\frac{1}{3}$ – $\frac{2}{3}$ closed, first dorsal pore 9/10–13/14, usually 11/12. Clitellum, saddle on xxx–xxxv. Tubercula pubertatis xxxi–xxxiv. Setal pairings, widely paired, *AA:AB:BC:CD:DD* = 10:5:4:3:22. Frequently setae *a* and/or *b* on xxii and occasionally on ix–xii, xiv, xvii, xix–xxiii, xxvii, xxxvii, or xxxviii are on genital tumescences and modified into genital setae. Male pores on xv and on large glandular papillae extending over xiv and xvi, occasionally limited to xv in area *B*. Female pores on xiv, in area *B*. Calciferous glands $\frac{1}{2}$ 10–14. Seminal vesicles, four pairs in 9–12, with pairs in 11 and 12 larger than pairs in 9 and 10. Spermathecae, simple, two pairs opening on level *C* or between *c* and *d* in 9/10 and 10/11. Body cylindrical but slightly octagonal posteriorly. Colour variable, milky white, grey, blue, or pink.

Biology

Reported from soils of pH 5.5–8.08, *O. tyrtaeum* has been found under stones and logs, in peat, leaf mould, compost, forest litter, gardens, cultivated fields and pastures, bogs, stream banks, in springs, and around the roots of submerged vegetation (Gates, 1972a). The species is also known from caves in Europe and North America. Smith (1917) reported this species as commonly found under logs, leaf mould, and debris of various kinds, in compost heaps, and to some extent in the soil. Some workers believed this species preferred rich, moist organic material (Causey, 1952), while others presented data to the contrary (Eaton, 1942). *Octolasion tyrtaeum* was the most abundant species in Tennessee (Reynolds *et al.*, 1974) and was obtained under logs, debris, and rocks, and by digging. In Ontario and Quebec, it was most frequently found under logs and in woods (Reynolds and Reynolds, 1992). In New Brunswick, *O. tyrtaeum* was found along stream banks (Reynolds *et al.*, 2015).

It has been reported in caves in the United States by Reeves and Reynolds (1999), Holler *et al.* (2020) and in Slovenia by Novak (2005).

Octolasion tyrtaeum is of little economic importance although one dealer in Michigan is reported to have sold it for fish bait (Gates, 1972a).

Reproduction

Activity may be year round although summer drought and winter cold may impose two rest periods. *Octolasion tyrtaeum* is an obligatorily parthenogenetic species (Reynolds, 1974c) and copulation occurs below the surface of the soil.

Climatic zone: Boreal, temperate.

Ecological type

Octolasion tyrtaeum is an endogeic species (Reynolds, 2018).

Origin, range

Octolasion tyrtaeum is a native of Palaearctis and is a peregrine species known from Europe, North America, South America, and Asia (Reynolds, 1977a). The following are the specific countries where it has been reported: Argentina (Mischis, 2007), Burma (Myanmar)(Reynolds, 2009), Chile (Gates, 1969b), Czech Republic (Pižl, 2001b), Finland (Terhivuo, 1988b), Germany (Jansch *et al.*, 2013), India (Deepshikha *et al.*, 2011), Ireland (Carpenter *et al.*, 2012), Scotland (Carpenter *et al.*, 2012), Slovenia (Novak, 2005), Spain (Díaz Cosín *et al.*, 1992), Switzerland (Le Bayon *et al.*, 2013), The Netherlands (van Gestel *et al.*, 2009), United Kingdom (Sims and Gerard, 1999) and Turkey (Reynolds and Mısırlıoğlu, 2018).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Quebec.

United States: Alabama, Arkansas, California, Colorado, Connecticut, Florida, Georgia, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Mexico: Chiapas, Distrito Federal, Hidalgo, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Veracruz states (Fragoso and Reynolds, 1997; Fragoso, 2001).

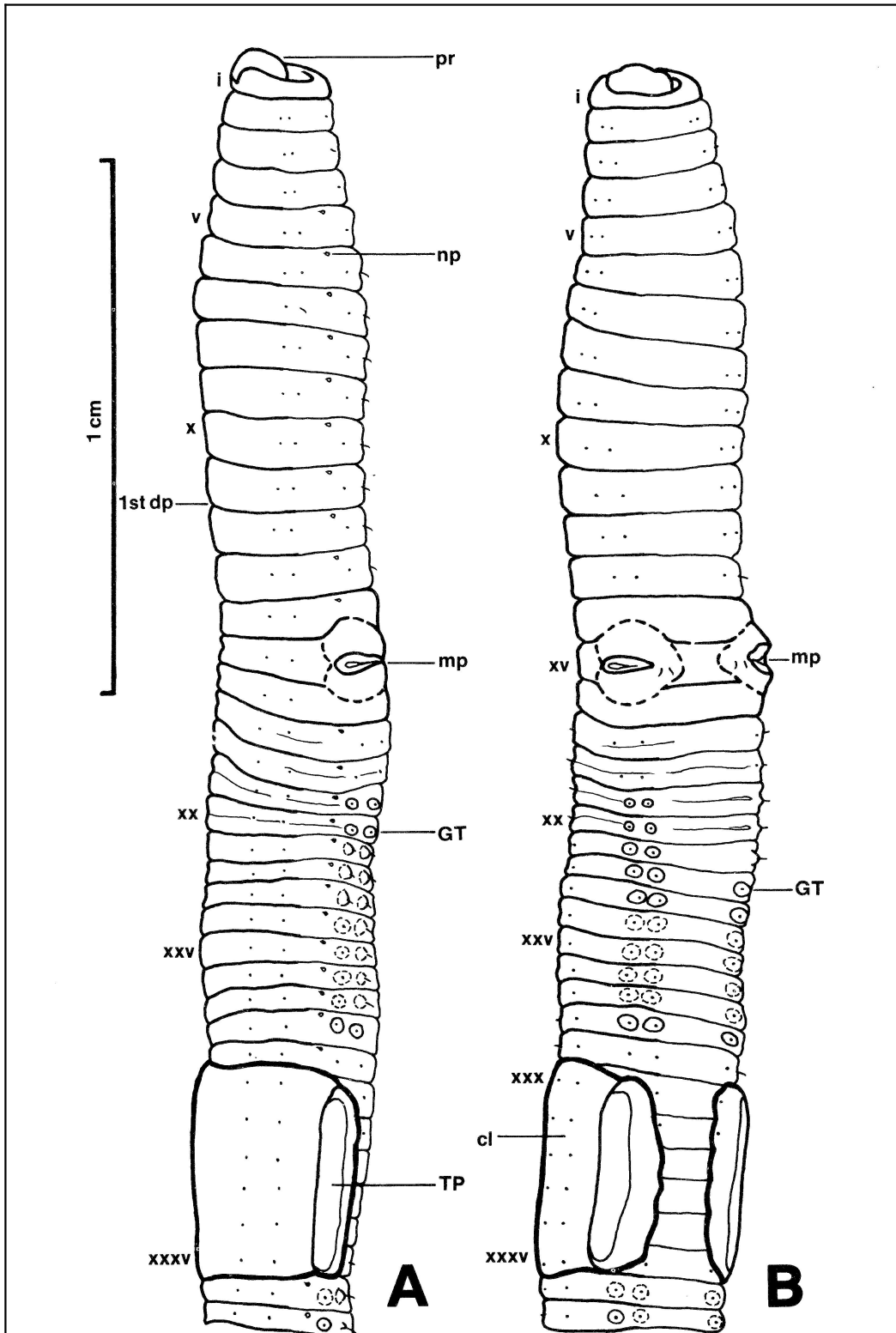


Fig. 28. External longitudinal views of *Octolasion tyrtaeum* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a).

Genus *Satchellius* Gates, 1975

- 1826 *Enterion* (part.) Savigny, Mém. Acad. Sci. Inst. France 5: 179.
1873 *Dendrobaena* (part.) Eisen, Öfv, Vet.-Akad. Förh. Stockholm 30(8): 53.
1893 *Allolobophora* (*Dendrobaena*) (part.)-Rosa, Mem. Acc. Torino, (2), 43: 424.
1900 *Helodrilus* (*Dendrobaena*) (part.)-Michaelsen, Das Tierreich. 10, Oligochaeta, p. 488.
1941 *Dendrobaena* (part.)-Pop, Zool. Jb. Syst. 74: 518.
1975 *Satchellius* Gates, Megadrilogica 2(1): 4.
1982 *Dendrobaena* (part.)-Zicsi, Acta Zool. Hungaricae 28(3-4): 432.
1983 *Satchellius*-Easton, Earthworm Ecol., p. 484.
1991 *Satchellius*-Mršić, Monograph on earthworms (Lumbricidae) of the Balkans, p. 667.
2016 *Satchellius*-Szederjesi and Csuzdi, Biologia 71(2): 169.

Type species

Enterion mammale Savigny, 1826 by Gates (1975a).

Diagnosis (after Gates, 1975: 4)

Calciferous sacs opening posteriorly and ventrally into esophagus of x just in front of insertion of 10/11. Calciferous glands in 10–12. Calciferous lamellae continued along lateral walls of the sacs. Prostomium epilobous. First dorsal pore 3/4 – 6/7. Male pores on xv on porophores. Nephridial vesicles, sausage-shaped. Nephropores, obvious, alternating irregularly and with asymmetry on each side of the body between a level above *B* and one in *DD*. Spermathecae, 2 pairs on line *C* or *D*. Seminal vesicles 4 pairs in 9–12. Prostomium, epilobous. Setae are widely paired. Pigment, red violet, at least on dorsum in the anterior part of the body.

Discussion

The finding in 1954 of Davies' specimens in New Jersey, raised another problem for Gates because of important somatic differences from the type species of the genus in which Davies' worms were then thought to belong. Through co- operation of the zoologists (Pickford, Roots and Satchell), a few specimens of the species became available to him (Gates, 1975a).

Megadrile somatic anatomy, as the author has been showing for some years, rather generally is more conservative than much of the genitalia. With much further knowledge of somatic structures, polyphyletic congeries masquerading as genera and families probably can be replaced by monophyletic groups with more invariable common anatomy than in many classical and neoclassical taxa. With this reasoning Gates removed *mammalis* from *Dendrobaena* where it was generally placed at the time, and erected the new genus *Satchellius* in honour of John Satchell who provided him with the greatest number of specimens for examination. He also recognized Satchell's long time contribution to earthworm ecology.

Satchellius differed from the genus *Dendrobaena* Eisen, 1873 where *Enterion mammale* resided for a long time, mainly by the structure of the calciferous glands. The species in the genus *Dendrobaena* possess calciferous glands in segment 11 and 12 or in either of them and the glands open directly into the esophagus. However, the calciferous glands in *Satchellius mammalis* open into the esophagus through a pair of large calciferous sacs joining the esophagus in segment 10 (Szederjesi and Csuzdi, 2016).

***Satchellius mammalis* (Savigny, 1826)**

Little tree worm — Petit ver d'arbre

(Fig. 29)

- 1826 *Enterion mammale* Savigny, Mém. Acad. Sci. Inst. France 5: 181. Types species unknown (Reynolds and Cook, 1976).
- 1886 *Allolobophora celtica* Rosa, Atti Reale Ist. Veneto Sci. 4: 673.
- 1892 *Dendrobaena celtica* var. *rosea* Friend, British Annelida. Essex Nat. 6: 187.
- 1893 *Allolobophora (Dendrobaena) mammalis*-Rosa, 1893: 424.
- 1900 *Helodrilus (Dendrobaena) mammalis*-Michaelsen, Das Tierreich, Oligochaeta 10: 493.
- 1954 *Dendrobaena mammalis*-Davies, Breviora, Mus. Comp. Zool., no. 26, 13 pp.
- 1972 *Dendrobaena (Dendrobaena) mammalis*-Bouché, Inst. Natn. Rech. Agron., p. 402.
- 1975 *Satchellius mammalis*-Gates, Megadrilogica 2(1): 4.
- 1982 *Dendrobaena mammalis*-Zicsi, Acta Zool. Hungaricae 28(3-4): 433.
- 1998 *Satchellius mammalis hispanicus* Qiu and Bouché, Doc. pédozool. intégral. 4: 160.
- 2014 *Satchellius mammalis*-Reynolds, Megadrilogica 17(6): 73, 80.
- 2016 *Satchellius mammalis*-Reynolds, Megadrilogica 21(2): 14.
- 2017 *Satchellisu mammalis* (laps.)-Reynolds, Megadrilogica 22(8): 153.

Diagnosis (after Michaelsen, 1900: 493, translated from German by JWR; Bouché, 1972: 402–403, translated from French by JWR.)

Small earthworm, length 24–40 mm, diameter 2.5–3 mm, number of segments 86–100. Prostomium, epilobous, tongue short and ½ opened. Clitellum, saddle in xxxi–xxxvi, but occasionally not quite reaching xxx/xxxi or xxxvi/xxxvii. Tubercula, longitudinal, uninterrupted, fairly wide bands of greyish translucence just lateral to *B*, the median margins often slightly concave, in xxxiii–xxxiv. Setae, widely paired, usually all present from ii where *c* is about at mL but *d* is much further from mD than in *D. octaedra*, intervals widening posteriorly, the most obvious increase being that of *BC* in xi. Setal arrangement behind clitellum: *AA:AB:BC:CD:DD* = 1.5:1:1.4:1.5:3.25. First dorsal pore at the intersegmental furrow 6/7. However, rather pore-like markings usually were also recognizable at 4/5–6/7. Male pores, minute on segment xv, surrounded by a large glandular crescents, protruding into the neighbouring segments as well, much nearer *C* than *B*. Female pores, inconspicuous on xiv. Genital tumescences, obvious to quite inconspicuous or even unrecognizable, including anyone, two or three of *a*, *b*, *c* setae but never *d*, in ix–xi, xiv, xxiv–xxvi, xxxi–xxxii, xxxv–xxxvi. Presence in xxxi–xxxii may be constant as the ventral setae of those segments are genital in macerated specimens with unrecognizable tumescences. Nephropores, obvious, from iii–vii, viii, ix or x at or close to *D*, then at *D* or just above *B* but often with asymmetry to xiii, always at lower level in xiv–xvi, behind xvi more often at the lower than the upper level. Spermathecae, 2 pairs, with pores, at 9/10–10/11, at or somewhat above *C*. Colour, red, circumferential in first 8–9 segments, then lacking ventrally in *BB*, only flecks recognizable under binocular in male tumescences especially laterally, posteriorly unrecognizable below *C* until near hind end where last few segments may have scattered flecks in the ventrum. Body, subcircular to nearly octagonal in cross section, the difference possibly due to diversity in preservation technique.

Biology

In Quebec, a single specimen was collected in a university garden in Montreal (Reynolds, 2014b). Davies (1954) collected it in New Jersey from moist soil at the edge of a stream. In England, it has been recorded from damp fields, sheep pasture and on peaty alluvial silt (Gates, 1975a). Bouché (1972) found it to be acid tolerant in France.

Reproduction

Satchellius mammalis is a presumably amphimictic species (Reynolds, 1974a). Iridescence has been recorded on male funnels and in spermathecae and spermatophores are present, usually with spermatozoal iridescence.

Climatic zone: Temperate, mediterranean.

Ecological type

Satchellius mammalis is an epigeic species (Reynolds, 2018).

Origin, range

Satchellius mammalis is a native of Palaearctis and is a species known from a few countries: Belgium (Muys, 2013), Denmark (Blakemore, 2007), England (Reynolds, 2016), France (Bouché, 1972), Germany (Lehmitz *et al.*, 2014), Ireland (Blakemore, 2008), Italy (Bouché, 1972), Norway (Blakemore, 2007), Scotland (Carpenter, 2011), Spain (Diaz *et al.*, 1992) and Switzerland (Amone III and Zaller, 2014).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This species is very rare in North America.

Canada: Quebec.

United States: New Jersey.

Mexico: none.

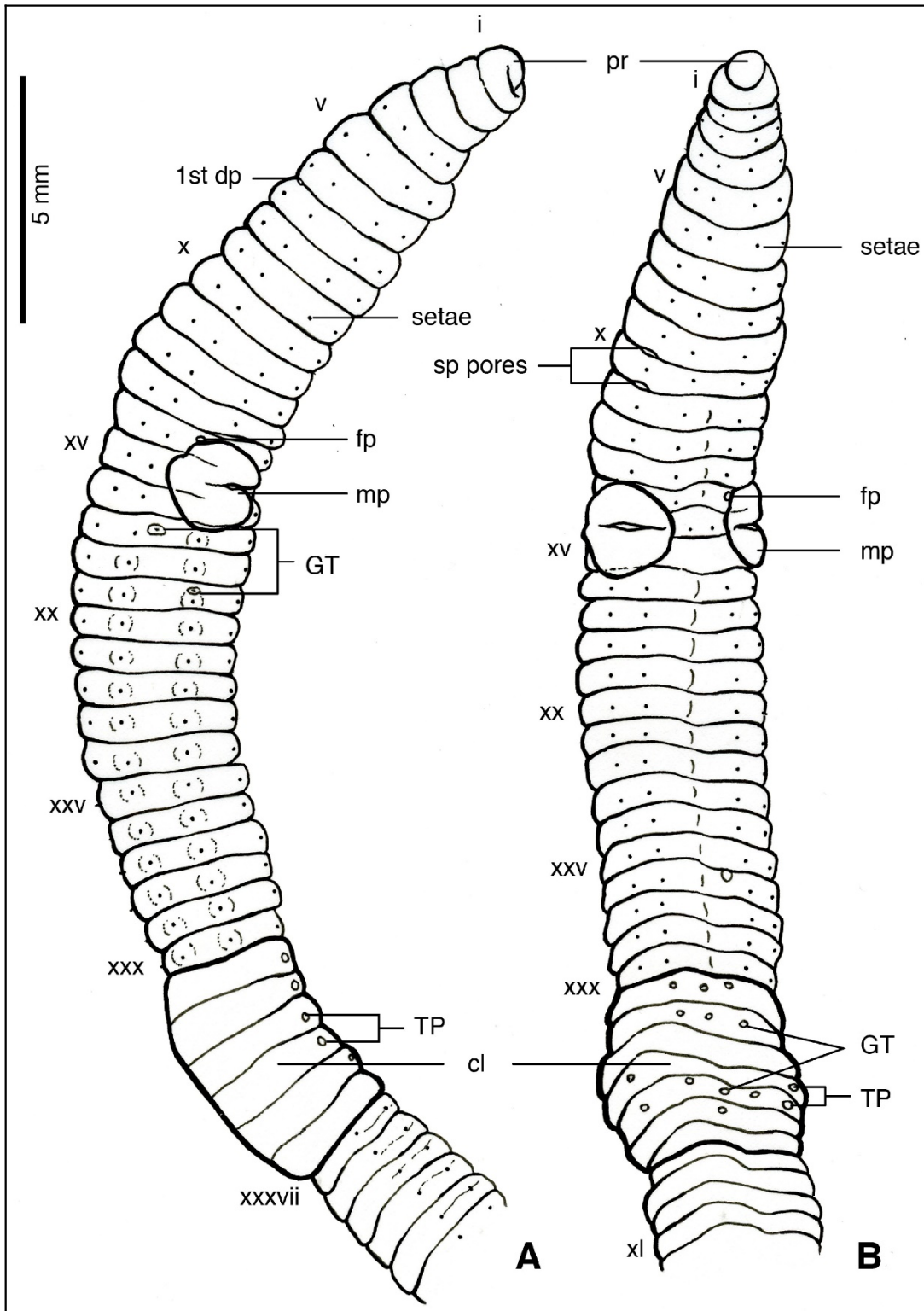


Fig. 29. External longitudinal views of *Satchellius mammalis* showing taxonomic characters. A. Lateral view, B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

Family MEGASCOLECIDAE Rosa, 1891

- 1891 Megascolecidae (part.) Rosa, Ann. Naturhist. Hofmus. Wien 8: 379.
1930 Megascolecinae (Megascolecidae) (part.)-Stephenson, The Oligochaeta, p. 828.
1959 Megascolecidae-Gates, Bull. Mus Comp. Zool. Harvard College 112: 255.

Note: (part.) indicates excluding all species without truly racemose prostates.

Distribution

The Megascolecidae is the largest family of earthworms (>2,000 species) and includes some 92 genera. The available molecular studies all support its monophyly and show just slight differentiation inside the family. Therefore, contrary to the proposed (but contradictory) taxonomic divisions (*e.g.*, Jamieson *et al.*, 2002; Blakemore, 2013), here I do not distinguish subordinate family rank taxa.

The ancient taxa of Megascolecidae show a predominantly southeastern distribution with most species in Australia (*ca.* 45+ genera and 400+ species), New Zealand (8 genera and 50 species), Southeastern Asia (<30 genera and <200 species)

(Jamieson, 2000; Sims, 1980; Reynolds and Wetzel, 2004, 2008, 2012, 2021). Interestingly, the North American pluteoid megascolecids seem to be basal to several modern megascolecid groups such as the Asian *Amyntas* and Australian *Perionychella*, *Megascolides*, and *Diporochaeta* (Buckley *et al.*, 2011).

At least 25 species in the genera *Amyntas*, *Metaphire*, *Perionyx* (*Pe. excavatus*), *Pithemera* (*Pi. bicincta*), *Polypheretima* (*Po. elongata*, *Po. taprobanae*) and *Pontodrilus* (*Pn. litoralis*) are probably some of the most widely distributed earthworms in the world. In fact, many of these species were described from specimens originating outside their native ranges in Asia, *e.g.*, *Metaphire californica* from San Francisco (Kinberg, 1867), *Amyntas gracilis* from Rio de Janeiro (Kinberg, 1867), *Amyntas corticis* from Hawaii (Kinberg, 1867), and *Polypheretima elongata* from Peru (Perrier, 1872). Therefore, they had been already extensively transported by humans from Asia to other continents even before they were recorded from their native habitats. The presence of parthenogenetic morphs, and wide plasticity in terms of soil and habitat preferences in several of these species means that they are excellent invaders, particularly in subtropical, tropical and even temperate regions (Chang *et al.*, 2017; Brown *et al.*, 2006). Some species, such as *Pithemera bicincta* and *Pontodrilus litoralis* may have been extensively transported with Polynesians that sailed throughout the Pacific Ocean, as well as in flotsam or sailing ship ballast (James, 2011; Blakemore, 2007). Several *Amyntas* and *Metaphire* species invaded cold-temperate regions, including the continental USA, causing extreme alterations in the native ecosystems (Chang *et al.*, 2016).

Diagnosis (after Gates, 1972a: 131)

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. Male pores, behind female pores. Spermathecae, in front of gonadal segment, with seminal chambers. Clitellum, multilayered, female pore always included. Ovaries, in xiii, fan-shaped and with numerous egg strings. Ova, not yolky. Seminal vesicles, trabeculate. Prostates, racemose and of mesoblastic origin.

Type genus: *Megascolex* Templeton, 1844.

Origin, range

The origin is probably in the Oriental or Australian Regions; the proper range has been expanded, in large part through transportation by man, to include many parts of the world. In North America when I started studying earthworms over 50 years ago, they were limited to the southeastern United States. Now several species have extended up the Atlantic Coast to New England and crossing the border into southwestern Ontario (Moore *et al.*, 2018; Reynolds, 2014a).

Genus *Amyntas* Kinberg, 1867

- 1867 *Amyntas* + *Amyntas* + *Pheretima* (part.) + *Nitocris* Kinberg, Öfv. Vet.-Abd. Förh. Stockholm 23: 97, 101, 102, 112.
1895 *Perichaeta* (part.)-Beddard, Monogr. Oligo., p 388.
1972 *Amyntas*-Sims and Easton, Biol. J. Linn. Soc. 4(3): 211.
1978 *Amyntas*-Reynolds, Megadrilogica 3(7): 118.

Type species

Amyntas aeruginosus Kinberg, 1867 by monotypy.

Diagnosis (after Sims and Easton, 1972: 211.)

Megascolecidae with cylindrical bodies of varying length. Setae numerous, regularly arranged around each segment. Clitellum annular, xiv–xvi, rarely beginning on xiii. Male pores paired, discharging directly onto the surface of xviii (rarely xix). Female pore single, rarely paired, xiv. Spermathecal pores small or large, usually paired (bithecal) but occasionally numerous (polythecal) or single (monothecal) between 4/5 and 8/9. Gizzard between septa 7/8 and 9/10. Esophageal pouches absent. Intestinal caeca present originating in xxvii. Testes holandric or metandric. Prostatic glands racemose. Copulatory pouches absent. Ovaries paired in xiii. Spermathecae usually paired, rarely multiple or single. Meronephridial, nephridial layer rarely present on spermathecal ducts.

Discussion

Considerable confusion has existed in the nomenclatural history of many oligochete groups and the genus *Pheretima* (*auct.*) is no exception. *Pheretima* was originally erected by Kinberg (1867: 102) for his species *californica* and *montana* (now type for *Pheretima* s.s.). In the same article, he described the monotypic genera *Amyntas* (p. 97 and a variant spelling *Amyntas* on p. 101) and *Nitocris* (p. 112). The nomenclatural history and taxonomic situation *re Megascolex*, *Perichaeta* and *Pheretima* are discussed by Sims *et* Easton (1972: 175–6). The alternate spelling *Amyntas* was not employed by the first revisor (Vaillant, 1889: 62) although it had been pre-occupied by Wollaston (1865) for a group of beetles (Insecta: Coleoptera). *Nitocris* too was unavailable. Rafinesque-Schmaltz (1815: 123) had employed the name for a group of insects (Insecta: Hymenoptera), Adams and Adams (1854: 308) for a genus of mollusks (Mollusca: Gastropoda) and Thomson (1858: 198) for a second group of insects (Insecta: Coleoptera). The members of *Amyntas* differ from *Metaphire* and *Pheretima* by the absence of copulatory pouches. In a paper by Reynolds and Reinecke (1976), the authors explained their reasons for adopting the Sims *et* Easton Classification (1972) for the pheretimoid earthworms.

Amyntas agrestis (Goto and Hatai, 1899)

Crazy snake worm — Ver de serpent fou

(Fig. 31)

- 1899 *Perichaeta agrestis* Goto and Hatai, Annot. Zool. Japonenses 3(1): 17, 24. Type species unknown (Reynolds and Cook, 1976).
1939 *Pheretima agrestis*-Howell, J. Exp. Zool. 81(2): 231.
1953 *Pheretima agrestis*-Gates, Breviora, Mus. Comp. Zool., Harvard 15: 5.
1972 *Amyntas agrestis*-Sims and Easton, Biol. J. Linn. Soc. 4 (3): 235.
1978 *Amyntas agrestis*-Reynolds, Megadrilogica 3(7): 122.
2003 *Metaphire agrestis*-Blakemore, Organisms Diversity and Evolution, Electronic Suppl. 11: 7, 28.
2008 *Amyntas agrestis*-Reynolds and Wetzels, Megadrilogica 12(12): 179.
2010 *Amyntas agrestis*-Blakemore, VermEcology, p. 429.
2014 *Amyntas agrestis*-Reynolds, Megadrilogica 16(10): 116.

Note: additional detail in diagnosis is presented as this species is rare in Canada (one site Essex Co., Ontario). The identification of this species may require dissection.

Diagnosis (after Tandy, 1969; Reynolds, 1978)

Medium to large earthworm, length 70–200 mm, diameter 5–8 mm, number of segments 70–110. Prostomium epilobic with open tongue. First dorsal pore usually 12/13. Clitellum annular xiii/xiv–xvi/xvii. Genital markings usually lacking. Male pores usually absent; when present minute and located on an eversible papilla, inside a transverse slit-like parietal invagination on an elevated porophore, in the setal circle of xviii *ea* $\frac{1}{3}$ C apart. Female pore single, mV on xiv. Intestinal caeca manicate, arising in xxvii and extending forward to *ca.* xxiv, with 6–9 secondary caeca. Typhlosole low and lamelliform, arising in xxvii and terminating in region of lxiv–lxxvii. Hearts of x lacking, those of xi–xiii latero- esophageal. Testis sacs unpaired and ventral in x and xi. Seminal vesicles in xi and xii, filling coelomic cavities of those segments. Sixthelcal, spermathecal pores, 3 pairs or fewer, minute and superficial in 5/6–7/8, *ea.* $\frac{1}{3}$ C apart. Spermathecae present or absent; when fully present, three pairs in vi–viii, duct shorter than ampulla; diverticulum longer than duct and ampulla combined. Spermathecal duct with thick wall, shorter than ampulla. Genital marking glands low and confined to or extending only slightly above parietes. Pre-clitellar genital markings present or absent; when present, ventral, areas of slight epidermal modification on vii and/or viii, occasionally on vi and ix, unpaired and median or symmetrically paired, forming setal gaps, epidermis finely wrinkled or crosshatched, sometimes darker in colour in live specimens. Post-clitellar genital markings usually absent; when present, single, large circular pad, pre-setal on xviii, just median to male pores, with a concave centre surrounded by a narrow but distinct, raised rim, reaching posteriorly slightly behind the setal line on xviii and anteriorly to the setal line on xvii. Prostate glands usually absent; when present, extending through some or all of xvi–xxiii, ducts in xviii. Intestinal caeca paired in xxvii, manicate. Colour, in live specimens, reddish on preclitellar portion, becoming light brownish in the postclitellar region.

Biology

Amyntas agrestis was first reported from Tennessee by Reynolds (1978). In Tennessee, I found *Amyntas agrestis* at 17 sites, but only three were associated with streams, etc. Eight of the sites could be considered in the general category of *dumps* and the remainder were found in fields under logs. In Louisiana (Tandy, 1969) reported that the species was frequently brought into an area for the purpose of establishing a bait population. Half of his sites were around the margins of lakes, etc. with the others almost equally divided between dumps and flower beds. In Ontario, there has only been one site, I found a large number in a wood chip pile on the Ojibway Prairie during a Bioblitz (Reynolds, 2014a).

Amyntas agrestis has been frequently reported in the continental USA. The first record of this species in the continental US was in 1939 from the Homewood campus of the Johns Hopkins University, Baltimore, Maryland (Howell, 1939; Gates, 1954; 1982). That record was the second of *A. agrestis* outside Japan, where the species is native. It has recently been confirmed to be abundant in Baltimore and has been observed to co-occur frequently with *A. hilgendorfi* and/or *A. tokioensis* in Maryland, Connecticut, Vermont, New Hampshire, and Wisconsin, two species morphologically similar to *A. agrestis*. This latter observation suggests the high possibility of misidentification. It has been known to compete with native millipedes in southeastern US for food resources, particularly the fragmented, partially decomposed leaf litter (Snyder *et al.*, 2011, 2013). Current practice of using commercial mulch for horticulture and landscaping may help spreading of this invasive species (Bellitürk *et al.*, 2015).

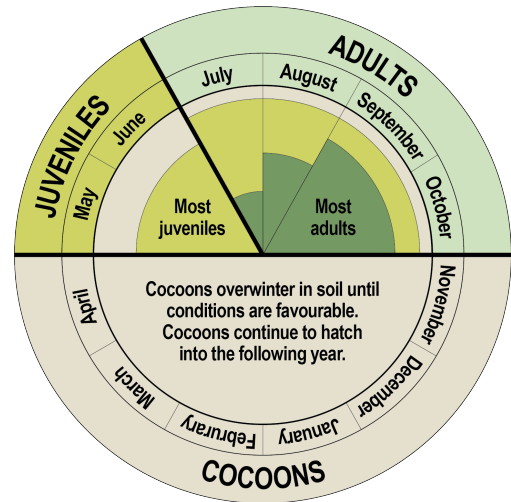
Reproduction

Reproduction of *A. agrestis* in North America is obligatorily parthenogenetic (Reynolds, 1974a). In field conditions, *A. agrestis*, an annual species, overwinters only as cocoons and the adults reproduce in summer and die by the end of fall (Callaham *et al.*, 2003; Richardson *et al.*, 2009; Görres *et al.*, 2014). However, in the laboratory, its adults can survive through November–February (Snyder *et al.*, 2013; Ikeda *et al.*, 2015).

All earthworms are hermaphrodites and many, including *A. agrestis*, have developed parthenogenesis (Gates, 1958; Chang *et al.*, 2016). Thus, most individuals encountered in the native or introduced range lack male pores and/or other parts of the male sexual system. Unlike many earthworms, *A. agrestis* has an annual life cycle (Tandy, 1969; Reynolds, 1978; Callaham *et al.*, 2003; Chang *et al.*, 2016). It took several years of research before the life history was fully understood. They overwinter as cocoons, hatch in spring, reach adulthood in summer, lay cocoons and all adults die

by winter. *A. agrestis* lays spherical or subspherical cocoons of slightly under 2 mm diameter (Snyder *et al.*, 2013). Cocoon colour is variable, from yellow to brown to red. Most cocoons contain one individual, but ~2% contain two individuals (Ikeda *et al.*, 2015). Cocoon viability after 4 months has been shown to be between 60 and 70% (Ikeda *et al.*, 2015). External sexual structures do not develop until near sexual maturity.

Fig. 30. The life cycle of *Amyntas agrestis* and *A. hilgendorfi*. These two species share an annual life cycle, along with several other pheretimoid earthworms, in which they overwinter in the soil as cocoons, hatch in the spring (or when conditions are favourable), and mature from juveniles to clitellate adults over the summer months. Months of diagram are based on populations of these worms in the USA Midwest (Wisconsin, Illinois); (modified from McCay *et al.*, 2020; Marie R. Johnston, University of Wisconsin Arboretum, made that figure and permission to use it is provided by the Creative Commons "BY-NC-ND 4.0" (<https://creativecommons.org/licenses/by-nc-nd/4.0/>).



Climate zone: Temperate.

Ecological type

Amyntas agrestis is epi-endogeic species (Reynolds, 2018) and its successful invasion in US forests has been attributed to dietary flexibility (Zhang *et al.*, 2010).

Origin, range

Amyntas agrestis is a native of the Orient (Japan). Currently it is known only from Canada (Reynolds (2014a), Japan (Blakemore, 2003b), Korea (Blakemore, 2008c), and the United States (Reynolds, 2018).

The native range of *A. agrestis* includes the four main islands of Japan and the Korean Peninsula. Following introduction, it has become widespread in eastern North America, from Alabama and Georgia to New Hampshire and Vermont. Additional locations include northern Louisiana, eastern Texas, southeastern Oklahoma (Tandy, 1969; Gates, 1982; Damoff and Reynolds, 2009), one location in Wisconsin (Qiu and Turner, 2017), one in Ontario (Reynolds, 2014a) and a greenhouse in Maine (Gates, 1966). While many of these localities consist of natural or managed habitats, such as arboreta (e.g., Gates, 1953), *A. agrestis* has been recorded in many human-created environments (e.g., culture beds, nurseries, compost heaps; Gates, 1954; 1958; 1963; Reynolds, 1977).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: Ontario.

United States: Alabama, Connecticut, Florida, Georgia, Louisiana, Maine, Maryland, Massachusetts, Missouri, New Hampshire, New Jersey, New York, North Carolina, Oklahoma, Pennsylvania, Rhode Island, South Carolina, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin.

Mexico: none.

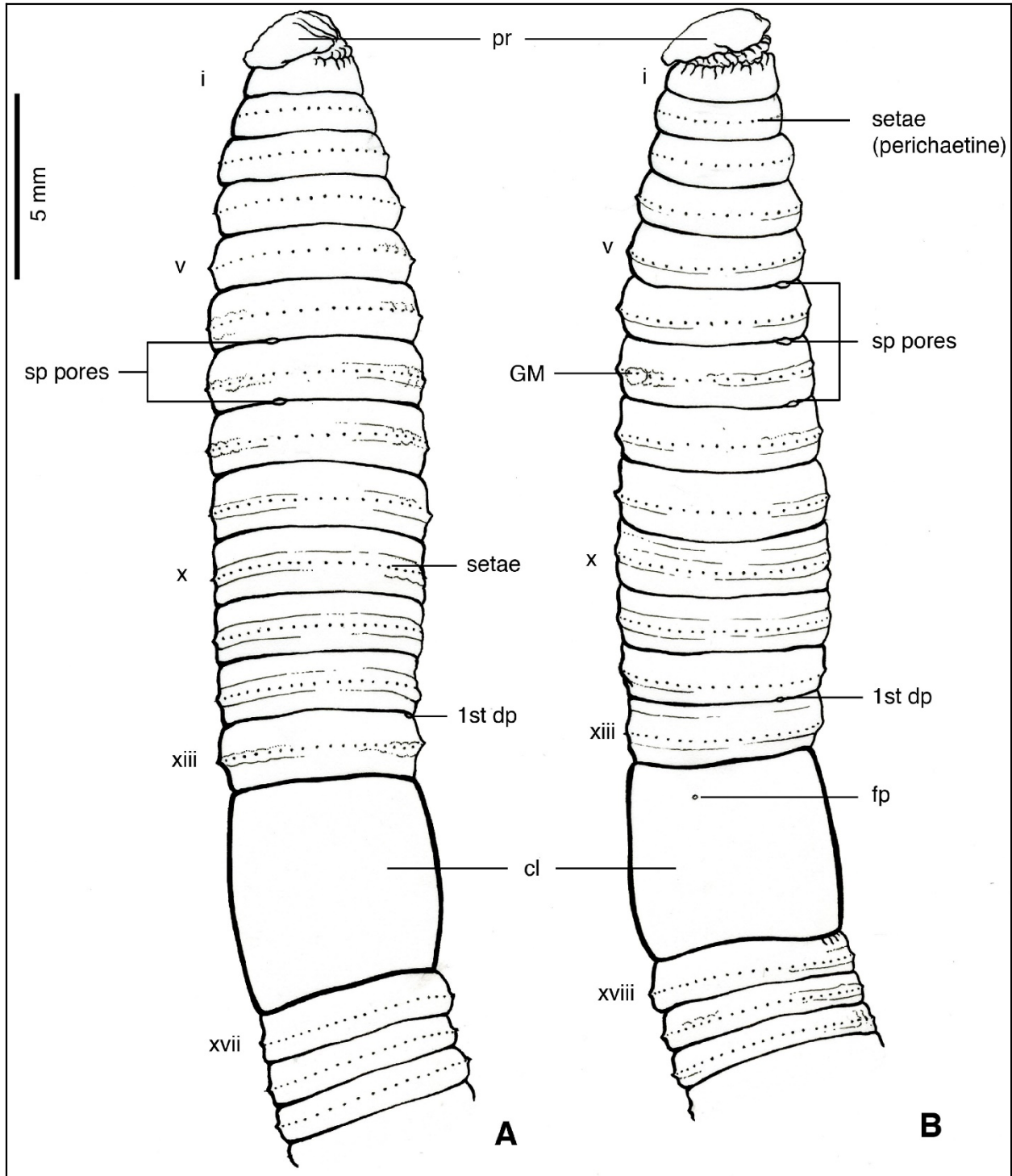


Fig. 31. External longitudinal views of *Amynthus agrestis* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

***Amyntas hilgendorfi* (Michaelsen, 1892)**
Asian jumping worm — Ver de saut asiatique
(Fig. 32)

- 1892 *Perichaeta hilgendorfi* Michaelsen, 1892: 235. Type species are in the MNHU cat. nos. 2114, 2123, 2149. (Reynolds and Cook, 1976).
- 1954 *Pheretima hilgendorfi*-Gates, Bull. Mus. Comp. Zool. 111(6): 230.
- 1958 *Pheretima hilgendorfi*-Gates, 1954: 230; 1958: 11, 31; 1982: 49.
- 1972 *Amyntas hilgendorfi*-Sims and Easton, 1972: 235, 237.
- 1978 *Amyntas hilgendorfi*-Reynolds, Megadrilogica 3(7): 122, 127.
- 2008 *Amyntas hilgendorfi*-Reynolds, Megadrilogica 12(12): 179.
- 2010 *Metaphire hilgendorfi*-Blakemore, VermEcology, p. 416.
- 2011 *Amyntas hilgendorfi*-Reynolds, Megadrilogica 16(10): 116.
- 2015 *Amyntas hilgendorfi*-Reynolds, Görres and Knowles, Megadrilogica 17(9): 132.

Note: additional detail in diagnosis is presented as this species is rare in Canada (one site Essex Co., Ontario). The identification of this species may require dissection.

Amyntas hilgendorfi was recently transferred from *Amyntas* to *Metaphire* by Blakemore (2010; 2013), but this change has not been totally reflected in North American literature.

Diagnosis (after Tandy, 1969; Reynolds, 1978)

Medium to large earthworm, length 110–170 mm, diameter 6–8 mm, number of segments 90–118, prostomium epilobic open, first dorsal pore usually 11/12. Clitellum annular xiii/xiv–xvi/xvii. Genital markings, usually present, small, circular, pre-setal, unpaired, median patches on some or all of xiii–xi, xvii, xviii. Male pores, usually absent, when present in a transversely slit-like copulatory pouch on xviii. Female pore single, mV on xiv. Other post-clitellar genital markings present or absent; when present, unpaired, mid-ventral, pre-setal clusters of numerous small tubercles on xvii–xviii, occasionally on xix–xxii. Pre-clitellar genital markings unpaired, mid-ventral, pre-setal clusters of numerous small tubercles on viii–ix, occasionally on vii, x, xi, similar to those in the post-clitellar region. Intestinal caeca manicate, arising in xxvii and extending forward to ca. xxiv–xxii, with 7–9 secondary caeca. Typhlosole low and lamelliform, arising in xxvii and terminating in region of lxx. Hearts of x lacking, those of xi–xiii latero-esophageal. Testis sacs unpaired and ventral in x and xi. Seminal vesicles, frequently small, in xi and xii. Spermathecae large, 2 pairs in vii and viii. Spermathecal duct, with thick wall, shorter than ampulla. Quadrithecal, spermathecal pores minute and superficial in 6/7–7/8, ea. $\frac{1}{2}$ C apart. Genital marking glands, stalked and coelomic. Colour, in dorsum, reddish, brownish.

Biology

Reynolds (1978) was the first to report *Amyntas hilgendorfi* from Tennessee. This species was collected at only one site in the state under leaf litter in the Cherokee National Forest. Tandy (1969: 14) found *A. hilgendorfi* at only eight sites in Louisiana: digging in flower beds (3), stream banks (2) and dump, cemetery and sawmill, once each. In Ontario, there has only been one site: I found a few under a board in the middle of a field on the Ojibway Prairie (Essex Co.) during a Bioblitz (Reynolds, 2014a).

Frequently reported in the continental US and one of the two pheretimoid species recorded in Canada, it was first recorded in 1948 in Kingston, New York (Gates, 1954). Co-occurrence of *A. agrestis* and *A. hilgendorfi* may be quite common (Chang *et al.*, 2018). At high abundance it transforms the top several centimetres of soil into granular casts. It is common in urban and suburban areas and is also invading deciduous forests in eastern USA (Chang *et al.*, 2016). Its spread is probably facilitated by commercial mulches, as is the case for *A. agrestis* (Bellitürk *et al.*, 2015). It has been shown to be the superior competitor when interacting with *Lumbricus rubellus*, an epi-endogeic European earthworm common in Canada and the USA, within the leaf litter.

Reproduction

Amyntas hilgendorfi is an obligatorily parthenogenetic species (Reynolds, 1974a). In field conditions, *A. hilgendorfi*, an annual species, overwinters only as cocoons and the adults reproduce in summer and die by the end of fall (Chang *et al.*, 2018; see diagram in *Amyntas agrestis* section).

Climatic zone: Temperate.

Ecological type

Amyntas hilgendorfi is an epi-endogeic species (Reynolds, 1974a).

Origin, range

Amyntas hilgendorfi is a native of the Orient (Japan). Currently it is only known from Canada (Reynolds (2014a), Japan (Blakemore, 2003), Korea (Blakemore, 2003), Russia (Blakemore, 2006), United States (Reynolds, 2018) and Vietnam (Blakemore, 2006).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: New Brunswick, Ontario.

United States: Arkansas, California, Connecticut, Louisiana, Maryland, Michigan, New York, Oklahoma, South Carolina, Tennessee, Texas, Virginia.

Mexico: none.

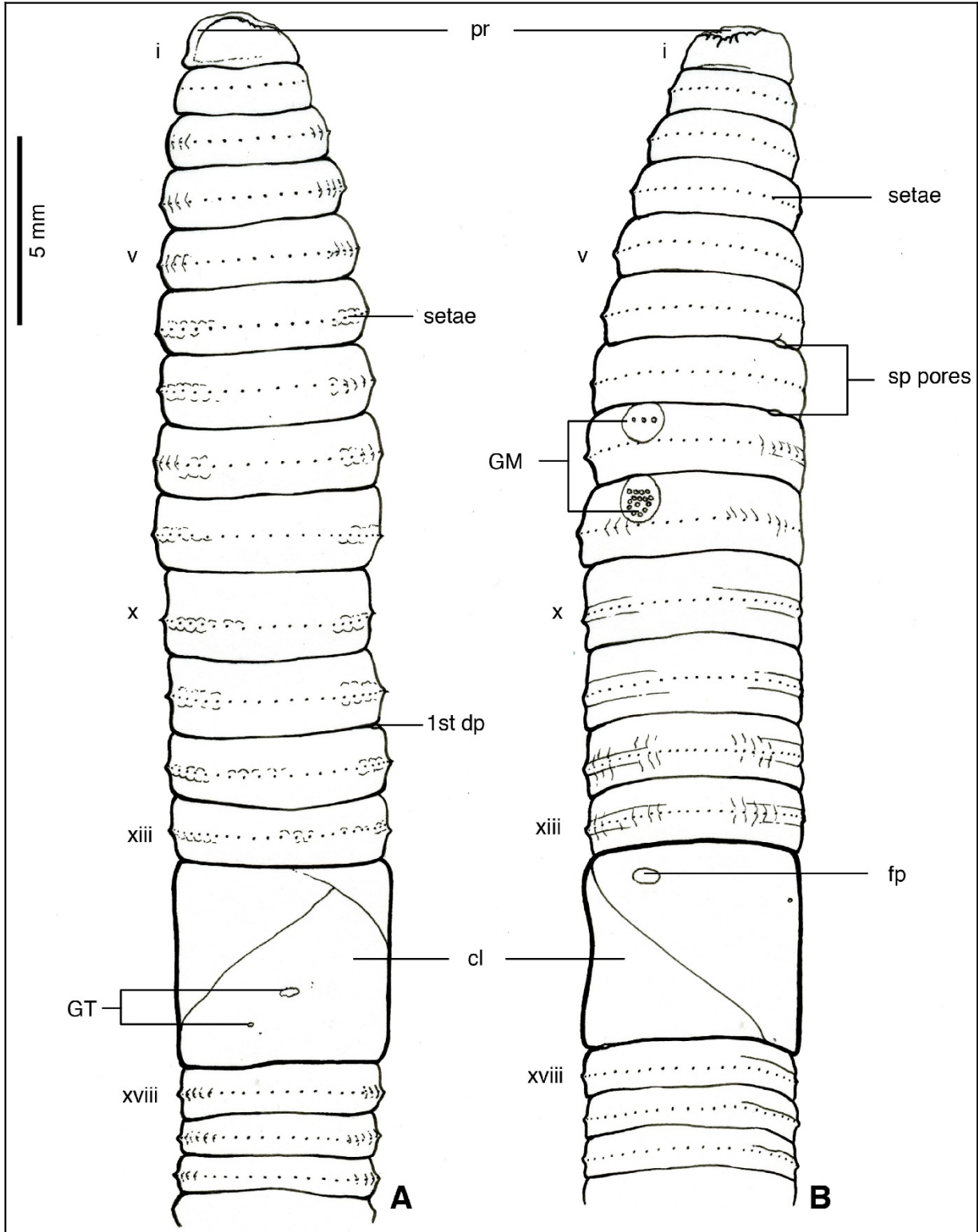


Fig. 32. External longitudinal views of *Amynthus hilgendorfi* showing taxonomic characters. A. Lateral view. B. Ventrolateral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

Genus *Arctiostrotus* McKey-Fender, 1982

- 1873 *Plutellus* (part.) Perrier, Arch. Zool. Exp. Gén. 2: 250.
1893 *Argilophilus* (part.) Eisen, Zoe 4(3): 252.
1982 *Arctiostrotus* McKey-Fender, Megadrilogica 4(3): 81.
1990 *Arctiostrotus*-Fender and McKey-Fender, Soil Biology, p. 358.
1994 *Arctiostrotus*-McKey-Fender, Fender and Marshall, Canadian J. Zool. 72: 1326.

Type species

Plutellus perrieri Benham, 1892.

The Megascolecidae (*sensu lato*) of western North America were traditionally placed in *Plutellus* Perrier 1873, and were removed to *Argilophilus* Eisen 1893 by Jamieson (1972) and Gates (1977a). McKey-Fender and Fender (1982) erected *Arctiostrotus*.

Diagnosis (after McKey-Fender, 1982; Fender and McKey-Fender, 1990: 372–373)

Clitellum annular in xiii–xviii. Prostomium tanylobic. Dorsal pores lacking except a few in caudal bulb. Nephropores alternating at two levels (pattern varying specifically), first pores at or near ends of prostomial grooves. Holonephric exonephridia, vesiculate, vesicles may be inconspicuous, terminal ducts may be confluent bilaterally in one or more anterior segments. Genital markings segmental, intersegmental, or a combination, or absent. Spermathecae 3–5 pairs, most posterior pair in ix. Prostates with slender ducts, confined to xviii. Penial setae small, weak, but present. Moderate gizzard in v, v and vi, or vi. Esophagus simple, calciferous lamellae low, longitudinal, or partly transverse (specific variation). Intestinal origin xvii, without caeca or ventral ciliated groove. Typhlosole present, a simple lamella to nearly obsolete (reduced to a dorsal longitudinal vein). Most posterior hearts in xiii. Musculature of body wall thick ventrally, ventral setae large, those of spermathecal segments (vi–ix) very large. Pigmented or unpigmented.

Range

The genus is found among the islands of western British Columbia south along the coast and in the Puget Trough of Washington. In Oregon, its range continues west of the summits of the Cascade Range south to Coos Bay and in the mountains of central Idaho. In the western Yukon, it has been found in Tombstone Territorial Park (Reynolds *et al.*, 2019a) and in Kluane National Park (Reynolds *et al.*, 2019b).

Remarks

Whereas the morphology of the gizzard in this genus is specifically distinctive, the segmental position of the gizzard is difficult to ascertain and sufficiently labile (individually, specifically, and between populations) that its exact position is of little help in identification. However, form, thickness of the wall, internal creases, degree of compressibility, etc. may be useful. Within this genus, as well as some other Argilophilini, the gizzard appears to be shifting posteriorly, though in only one species (*A. pluvialis*) have we found gizzard tissue behind 6/7. There may be major thickening in v, v and vi, or vi, the position of the thin septum 5/6 being a variable factor.

While in earthworms as a group, the typhlosole is clearly an apomorphy with at least two nonhomologous origins (*e.g.*, lumbricid and megascolecid typhlosoles involve different layers of the gut wall), in the western North American Megascolecidae in general and in *Arctiostrotus* in particular, a prominent typhlosole is associated with the most plesiomorphic taxa, and a very small typhlosole with otherwise derived taxa. For this reason Fender and McKey-Fender (1990) feel justified in considering the very low, almost nonexistent typhlosole in some *Arctiostrotus* species to be reduced.

***Arctiostrotus fontinalis* McKey-Fender, 1994**
Fountain moss worm — Ver de mousse de fontaine
(Fig. 33)

- 1994 *fontinalis*, *Arctiostrotus* McKey-Fender, Canadian J. Zool. 72: 72. Types species in the Canadian Museum of Nature (Aylmer, Quebec) cat. no. 1994-0006 (Reynolds and Wetzel, 2021).
2019 *fontinalis*, *Arctiostrotus*-Reynolds, Godin and Horwood, Megadrilogica 24(2): 18.
2019 *fontinalis*, *Arctiostrotus*-Reynolds, Cameron, Sweeney, Bennett and Godin, Megadrilogica 25(1): 2.

Note: additional detail in diagnosis is presented as this species is very rare in Canada (3 specimens in Yukon). The identification of this species may require dissection.

Diagnosis (after McKey-Fender *et al.*, 1994: 72)

Small earthworm, length 34–104 mm, diameter 1–2 mm, number of segments 67–105. Prostomium tanylobic, broad. Two or three dorsal pores (usually 3) in caudal bulb. Sexthecal, spermathecal porophores small, whitened points in grooves 6/7, 7/8, and 8/9 in line *B*. Clitellum xiii–xviii, annular. Tuberculata pubertatis, absent. Genital markings mV in 12/13, paired 17/18, 18/19 in *A*, or (often) absent. Male porophores flat, round, 1.5–2 times *AB* in xviii. Female pore in xiv. Setae separate, *DD* interval nearly 50%, *AA:AB:BC:CD:DD* = 2.2:1.0:1.6:1.6:9.8, *DD:U* about 0.48, posteriorly, and 2.2:1.0:2.0:1.7:9.2, *DD:U* about 0.44, on x. Nephropores (behind x) irregularly alternating, with no discernible pattern in *C* and a variable distance dorsal to *D*. Penial setae 300 × 5 µm, sculptured over distal sixth with large triangular shaggy scales.

Gizzard strong but compressible, mostly in v, 5/6 adherent to posterior third, short, fat, barrel-shaped. Internally with several irregular circumferential wrinkles. Esophagus slightly moniliform, lined with short, low, anteroposteriorly oriented vascular folds in viii–xv; posterior calciferous region (especially xii–xiv) with brown circumferential vascular striae externally. Gut narrow in xvi and about 9 low, continuous nonvascular folds (pre-intestinal constriction). Intestinal origin in xvii. Typhlosole a low lamella up to ¼ height of intestinal lumen, from 20 to about 50. Spermathecae 3 pairs in vii, viii, and ix, ampulla elongate-oval, duct extremely short, scarcely distinguishable, bearing an elongate basal diverticulum. Holandric. Prostates short (length 6–10 times width) with slender ducts. Nephridia without confluence of terminal ducts. Nephridial vesicles slender, firm. Musculature completely longitudinally divided into 8 bands. Unpigmented.

Biology

Arctiostrotus fontinalis is the smallest and the most hygrophilous of the known *Arctiostrotus* species. Few of the collections of this species were from terrestrial sites, almost all having been found in seepage areas, at margins of springs or spring-fed rivulets, or near springs, at the contact of saturated humus and mineral soil. In the Yukon, it was collected in a wet black organic soil (Organic Cryosol) at the base of a slope under birch and willow (Reynolds *et al.*, 2019a) and in wet moss in soil, alpine tundra meadow in depression amongst diamond-leaf willow (*Salix pulchra* Cham.), glandular birch (*Betula glandulosa* Michx.) (Reynolds *et al.*, 2019b).

The following is a summary of the few collections (from the American west coast): recently cleared right of way for power line through spruce-hemlock forest (seepage on slope), Little Nestucca River Gorge, just downstream from mouth of Austin Creek, elev. 31 m, spruce-hemlock forest on bluff, source of springs flowing down over bluff, under roots of large clumps of sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and spreading wood fern (*Dryopteris austriaca* (Jacq. Woynar)) in saturated soil, including one anterior fragment; same locality, west end of bridge in gorge upstream from confluence of Austin Creek, alders, young western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), oxalis (*Oxalis oregona* Nutt.), sword fern, deep duff layer, mostly hemlock needles and mycelial threads, over fluffy dry soil, pH 4 (H₂O); elev. 91 m, mature spruce-hemlock forest, vine maple (*Acer circinatum* Pursh.) and red alder (*Alnus rubra* Bong.), skunk cabbage (*Lysichiton americanus*) Hultén and H. St. John) along stream, moss and humus, in very wet yellow clay, along small creek at contact of water and bank, estuary of the Naselle River, in clay and humus below spring, elev. 23 m, alder-fir woods, grass, brown to yellow silty soil, pH 4.5 (H₂O).

Reproduction

Unknown at this time, presumably amphimictic until evidence to the contrary.

Climatic zone: Temperate.

Ecological type

Arctiostrotus fontinalis is a limicolous-epigeic species (Reynolds, 2018).

Origin, range

Arctiostrotus fontinalis is a native North American species and limited to the northwestern USA and the Yukon.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This species is very rare in North America.

Canada: Yukon.

United States: Oregon, Washington.

Mexico: none.

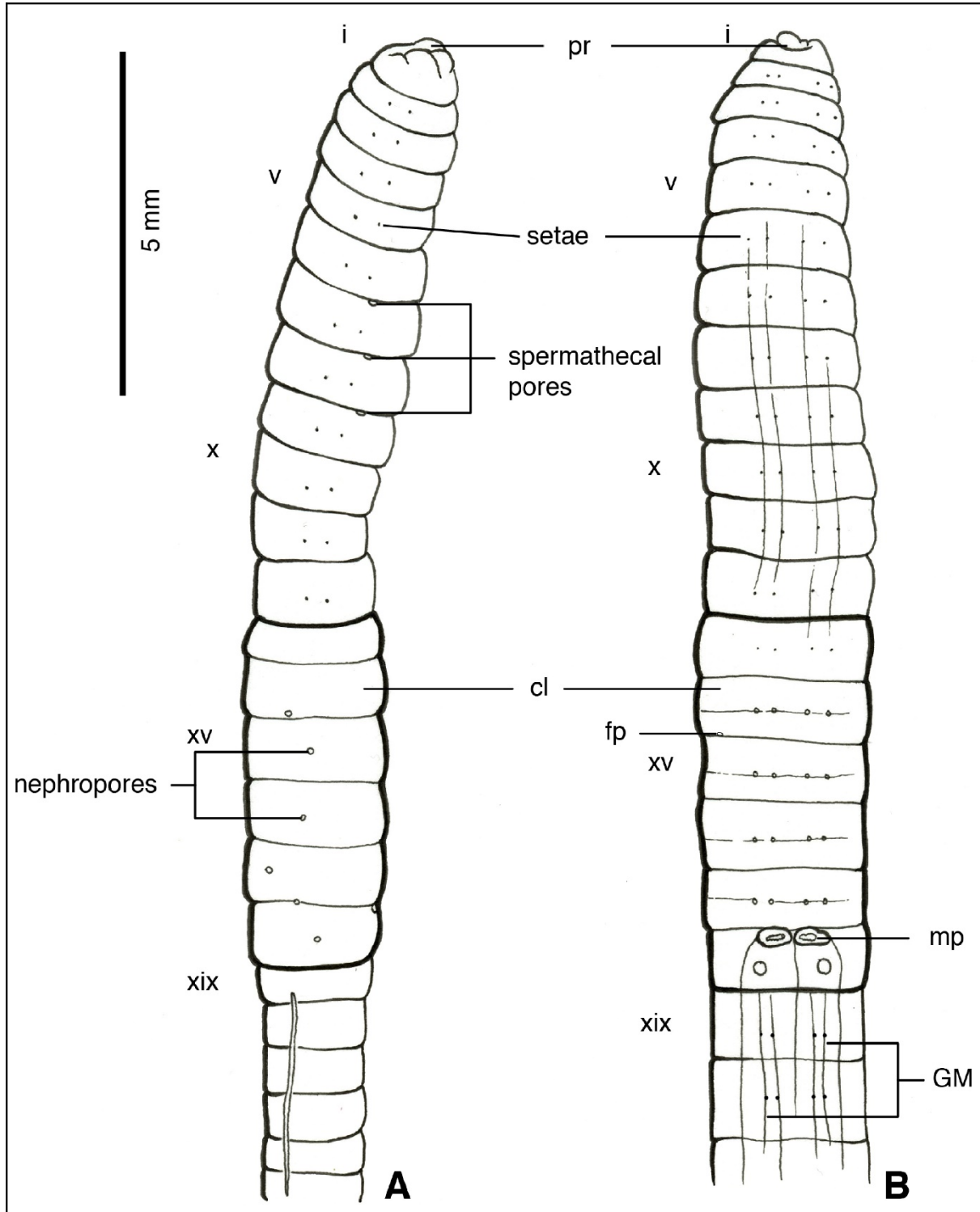


Fig. 33. External longitudinal views of *Arctiostrotus fontinalis* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

***Arctiostrotus perrieri* (Benham, 1892)**
Perrier's worm — Ver de Perrier
(Fig. 34)

- 1892 *perrieri*, *Plutellus* Benham, Proc. Zool. Soc. London, 1892, p. 138. Type species are missing (Reynolds and Wetzel, 2021).
- 1942 *perrieri*, *Megascolides*-Gates, American Midl. Nat. 27(1): 90.
- 1995 *perrieri*, *Arctiostrotus*-Fender, Earthworm Ecology Biogeography, p. 57.
- 2018 *perrieri*, *Arctiostrotus*-Reynolds, Megadrilogica 23(1): 6.

Note: additional detail in diagnosis is presented as this species very rare in Canada (Queen Charlotte Islands/Haida Gwai'i and Vancouver Island, British Columbia). The identification of this species may require dissection.

Diagnosis (after McKey-Fender *et al.*, 1994: 1331)

Small to moderately large earthworm. Length 50–204 mm, diameter 2.25–4 mm, number of segments 135–170. Prostomium tanylobic, prostomial lobe firm, markedly broader than tongue, sides of tongue parallel. Clitellum annular in xiii–xviii. Tubercula pubertatis, absent. Dorsal pores lacking. Genital markings paired or median or absent (always presetal and intrasegmental), midventral, round to broadly oval (often with 2 centres) or paired in *A* or *AB* or lateral to *B*, on (vi), (vii), viii, and ix (x), most often on viii and ix. Male field a quadrangular pale area bounded anteriorly 17/18 and posteriorly 18/19 by straight glandular bars. Male pores on very small conical papillae in *AB* in xviii. Female pore in xiv. Complete series of nephropores present. Nephropores quite regularly alternating, anteriorly in *C* and dorsal to *D*, changing posteriorly to between *B* and *D*. Setal intervals *AA:AB:BC:CD:DD* = 1.7:1.0:1.8:2.5:9.3 on x and 1.7:1.0:1.9:2.0:8.1 on xxx. Dorsal interval moderately large though less than half the circumference, *DD:U* < 0.5, posteriorly 0.40–0.43. Penial setae very slender, *e.g.*, 640 × 3 µm, curved, especially at both ends, shaft nearly straight, sculptured, with transverse rings of fine spines or unsculptured except for irregular, discontinuous transverse streaks distally on shaft, possibly due to wear. Ventral setae v–ix (spermathecal setae) very large, *e.g.*, 535 × 70 µm. Pregicerate segment iv and anterior v (proventriculus) thick but soft.

Gizzard in v, soft, weak, at most moderately strengthened, posterior half with several circumferential grooves not affecting thickness of wall. Esophagus narrow in vii, widened posteriorly (viii *et seq.*), with circumferential vascular striae ix–xiv or xv, brown. Epithelium in viii and ix with short and not very deep irregular folds, more regular and anteroposteriorly oriented x–xv, short, but some ends coinciding with intersegmental boundaries, length of folds $\frac{3}{4}$ their height. Pre-intestinal constriction with 8 or 9 continuous nonvascular folds. Typhlosole very low, height one-tenth intestinal lumen at most. Spermathecae four pairs, in vi, vii, viii, and ix. Octothecal, pores in 5/6, 6/7, 7/8, and 8/9, in or very slightly anterior to furrow, extremely small, marked by whitened spots in line *B* (pores smaller than nephropores of same segment). Ampulla elongate-oval, nearly sessile. Spermathecal duct so short as to be nearly nonexistent. Spermathecal diverticulum a small basal bulge. Proandric. Seminal vesicles one pair in xi, septa 9/10 and 10/11 usually contiguous dorsally. Prostates small and slender, duct weak, bent in a C-shape, length less than 10 times width. Nephridia vesiculate, vesicles broad, clear. Terminal ducts simple, none confluent, nephropore series complete. Muscles divided into 8 separate bands. Pigmented purple-brown to quite pale or even unpigmented (possibly bleached specimens).

Biology

In the Coos Bay area (Oregon, USA), the southern limit of this genus, *A. perrieri* has been found in cool canyons, in a cold-water spring, and on an exposed ocean headland, all niches suited to cryophilic organisms. On the open coast it has also been collected from soil still wet from the night's storm tide. It was found in forest soils, leaf mould, rotting stump, stream bed and moss, in wet soils in British Columbia (McKey-Fender *et al.*, 1994).

Reproduction

Arctiostrotus perrieri is a parthenogenetic species (Fender and McKey-Fender, 1990).

Climate zone: Temperate.

Ecological type

Arctiostrotus perrieri is an epigeic species (Reynolds, 2018).

Origin, range

A North American native species described originally from the Queen Charlotte Islands/Haida Gwaii, this species has also been found from Vancouver Island and adjacent islets, south of the Puget Sound in the Puget Trough of Washington, and in Oregon west of the Cascade Range summits, south to Coos Bay. However, it seems to be absent in the centre of its range, the north Washington coastal region, replaced there by the decathecal species *A. altmani*, *A. johnsoni*, and *A. adunatus*. Numerous attempts to collect native earthworms have been made in the Queen Charlotte Islands over the years by many collectors, but in 1991 was the first time anyone has found *A. perrieri* there since 1892. Gates (1972a, 1977a) suggested that the collection record was an error and used this presumption of error to bolster his rebuttal of the theory that the western North American earthworms migrated overland from Asia (Gates 1972a, p. 39). Comparison with the type specimens enabled McKey-Fender and Fender (1982) to confirm *A. perrieri*'s identity as a North American resident, yet it is gratifying, after all these years, to be able to confirm the presence of this interesting species in the Queen Charlotte Islands. Further, like the original specimens, this one was collected along with an unusually large enchytraeid (Benham, 1892) that seems to be the common oligochaete of those soils.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia.

United States: Oregon, Washington.

Mexico: none.

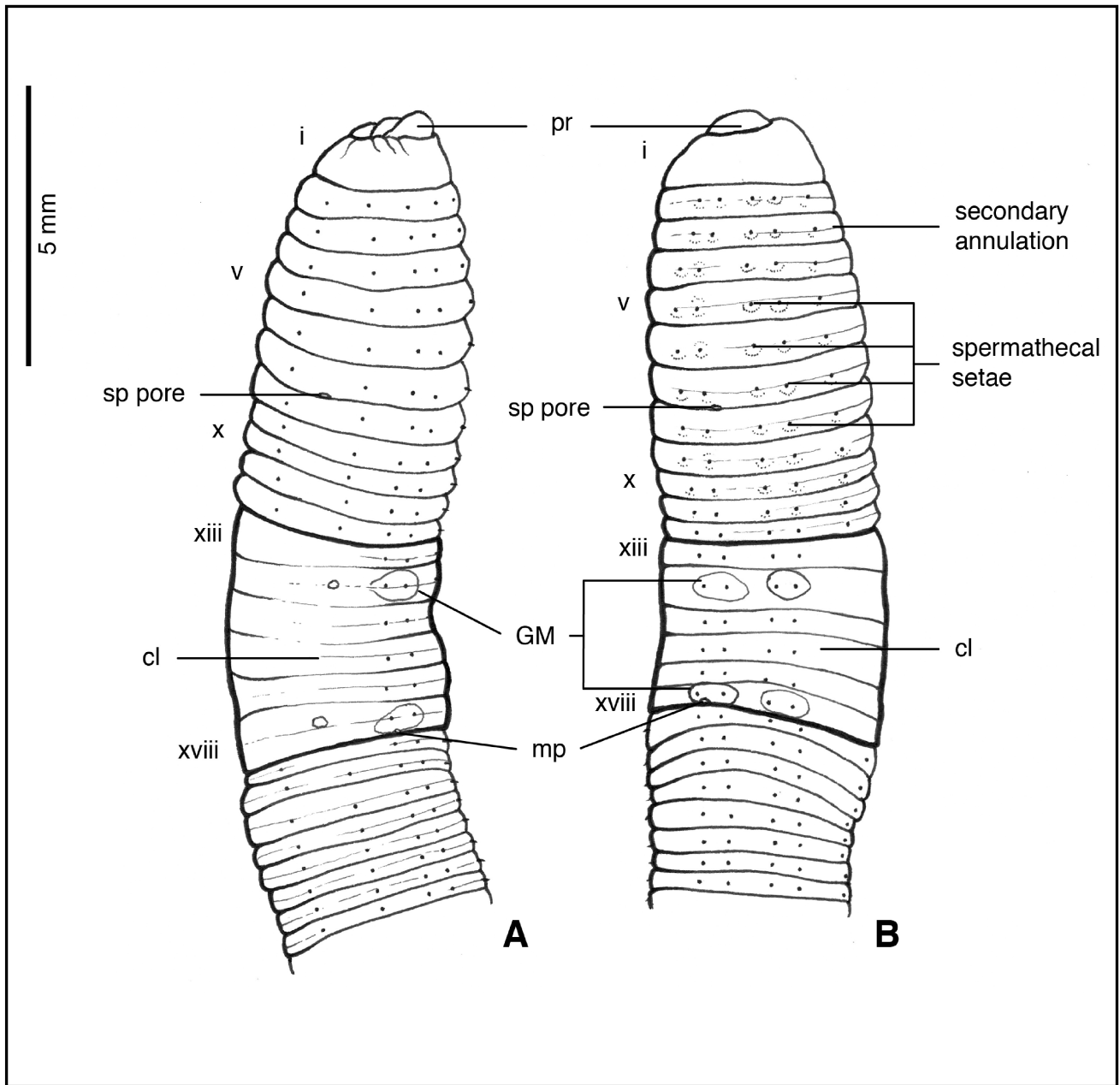


Fig. 34. External longitudinal views of *Arctiostrotus perrieri* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the British Museum of Natural History, London, UK).

***Arctiostrongylus vancouverensis* McKey-Fender, 1994**
Vancouver worm — Ver de Vancouver
(Fig. 35)

- 1994 *vancouverensis*, *Arctiostrongylus* McKey-Fender, 1994; Canadian J. Zool. 72(7): 1332. Type species are in the Canadian Museum of Nature (Aylmer, Quebec) cat. no. 1994-0008 (Reynolds and Wetzel, 2021).
- 2018 *vancouverensis*, *Arctiostrongylus*-Reynolds, Megadrilogica 23(1): 6.

Note: additional detail in diagnosis is presented as this species very rare in Canada (Vancouver Island, British Columbia). The identification of this species may require dissection.

Diagnosis (after McKey-Fender *et al.*, 1994: 1332)

Moderately large worm. Length 167–381 mm, diameter 3.2–4.5 mm, number of segments 147–204. Prostomium tanylobic. Prostomial lobe firm, tongue long, sometimes with cross groove, grooves converging in anterior fourth segment, nearly straight posteriorly. Clitellum annular, basically xiii–xviii, except extending to ix/xii dorsally and lacking ventrally in area of male field. Tubercula pubertatis, lacking. Sexthecal, pores in grooves 6/7, 7/8, and 8/9, anterior to furrows, in or lateral to *B*, minute rounded pits on very small, slightly tumescent, pellucid porophores. Genital markings paired, transverse elongate in 19/20 and 20/21, sometimes unilateral in 21/22, sometimes missing in 20/21, large, centering just median to *A*, largest (anterior pair) nearly convergent mV, occasionally fused to form a single transverse bar. Dorsal pores absent except usually two large pores in caudal bulb. Male field with glandular bands in grooves 17/18 and 18/19 *B* to *B*; male pores on bluntly pyriform porophores with wide ends laterad, connected medially by two transverse creases in xviii. Female pore in xiv. Nephropores inconspicuous, irregularly alternating in *C* or dorsal to *D*, most and 4.3 often in *C* anteriorly, often at the more dorsal sites posteriorly. Complete series of nephropores present. Stretches of regular alternation broken by several consecutively in the same level. Setae separate; $AA:AB:BC:CD:DD = 2.1:1.0:1.5:1.8:8.5$ on x, and $2.7:1.0:1.5:1.9:9.9$ midbody. $DD:U < 0.5$ (0.43–0.44). Penial setae small and delicate, $430\text{--}570 \times 8\text{--}9 \mu\text{m}$; in the Washington material existed, that there are a number of differences between the sculptured over apical fifth by transverse rings of irregular, slender teeth, reduced to scattered teeth and scars apically; in the Vancouver material similar but with sculpture much reduced, from a few teeth scattered over the end of the seta to almost unsculptured, only a few streaks being visible near the distal ends. Proventriculus in iv naked, with thickened wall almost as conspicuous as gizzard, but soft. Gizzard entirely in v or partly in vi, 5/6 adherent or even not dissectible from gizzard posteriorly, moderately muscular, compressible, narrowly campanulate, slightly flat, weak in the middle, divided into anterior and posterior thickened parts; posterior half with several shallow circumferential creases. Esophagus slightly moniliform vii–xv with longitudinal folds up to 4/5 segment length, highly vascular, with brown circumferential striae in external aspect, especially in v iii–xv, where the esophagus is especially enlarged. Pre-intestinal constriction (xvi) with about 10 low white nonvascular continuously longitudinal folds. Typhlosole in segments 31 to 74–83, rudimentary, height at greatest development up to one-tenth of lumen (Washington material), barely a trace in most Vancouver Island specimens examined, there consisting of a definite blood-filled ridge, which is often collapsed, when it appears like a wavy whitish cord. In these cases, the typhlosole, while clearly present and distinctly limited laterally, does not project into lumen of the intestine. No ventral groove in the intestine but the wall is weak midventrally.

Sexthecal, spermathecae in vii, viii, and ix, ampulla ovoid to subglobular, duct one-third length of ampulla, an ovoid to hemispherical multioculated diverticulum narrowly to broadly attached to and covering anterolateral face of duct. Sperm iridescent in adults. Holandric, prostates long, confined to xviii but bulging septa, length of gland at least 20 times width, duct slender, nearly straight or looped in a C or S shape, slightly broader ectally. Nephridial vesicles slender, differing from ental tubules in being rather clear (nonglandular) and firm; most easily distinguished in anteriormost nephridia, very slightly enlarged posteriorly and obviously contractile (observed in life). Terminal ducts simple, nonconfluent. Musculature interrupted at sites of setal follicles but not entirely separated into bands.

Biology

Intestinal contents included an arthropod leg joint, mosses, and rhizoids wrapped in mucus (Vancouver Island). This species is nearly always found in humus and logs, except where wood bits are mixed in with the soil such as in bulldozed areas, the single exception being a Washington specimen found in gravel along a small stream. Observations of a living dissection yielded the following: in the calciferous region of the esophagus, calciferous spherules mixed with mucus were observed. Beginning in posterior xv, they were seen to move back into the pre-intestinal constriction (xv–xvi and anteriormost xvii), where they accumulated. These carbonates effervesced strongly but not rapidly in cold glacial acetic acid, indicating their identity as calcium carbonate.

Variation

It is not surprising, in view of the geographic separation between Vancouver Island and the Olympic Peninsula and the long time (at least 10 000 years) during which separation has existed, that there are a number of differences between the Vancouver Island and Washington populations of this species (McKey-Fender *et al.*, 1994). Washington specimens tend to be paler (only the largest examples are pigmented), the gizzard may be confined to v, the typhlosole is generally more strongly developed, and the spermathecal diverticulum is more irregular and more broadly attached. Penial setae are stronger and sculptured, with interrupted transverse rows of irregular, slender teeth. There are other differences in the vascular system.

In one worm from Vancouver Island (Darling Main Line, 10 May 82), the genital markings on 19/20 and 20/21 are unpaired, transverse, without two centres of development, and internally the typhlosole is better developed than usual, *i.e.*, about as much as is normal in Olympic Peninsula examples of this species. The penial setae, however, are nearly unsculptured, and it is clearly *A. vancouverensis* (McKey-Fender *et al.*, 1994).

Remarks

Arctiostrotus vancouverensis, first known to us from the Olympic Peninsula of Washington, has been found to be characteristic of the forests of Vancouver Island, B.C., where, as a distinctive, robust population, it fills a significant role in humus formation (Spiers *et al.*, 1984, 1986).

Reproduction

Arctiostrotus vancouverensis is presumed amphimictic until there is evidence to the contrary (Fender and McKey-Fender, 1990).

Climatic zone: Temperate.

Ecological type

Arctiostrotus vancouverensis is an epigeic species (Reynolds, 2018).

Origin, range

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This species is very rare in North America.

Canada: British Columbia.

United States: Washington.

Mexico: none.

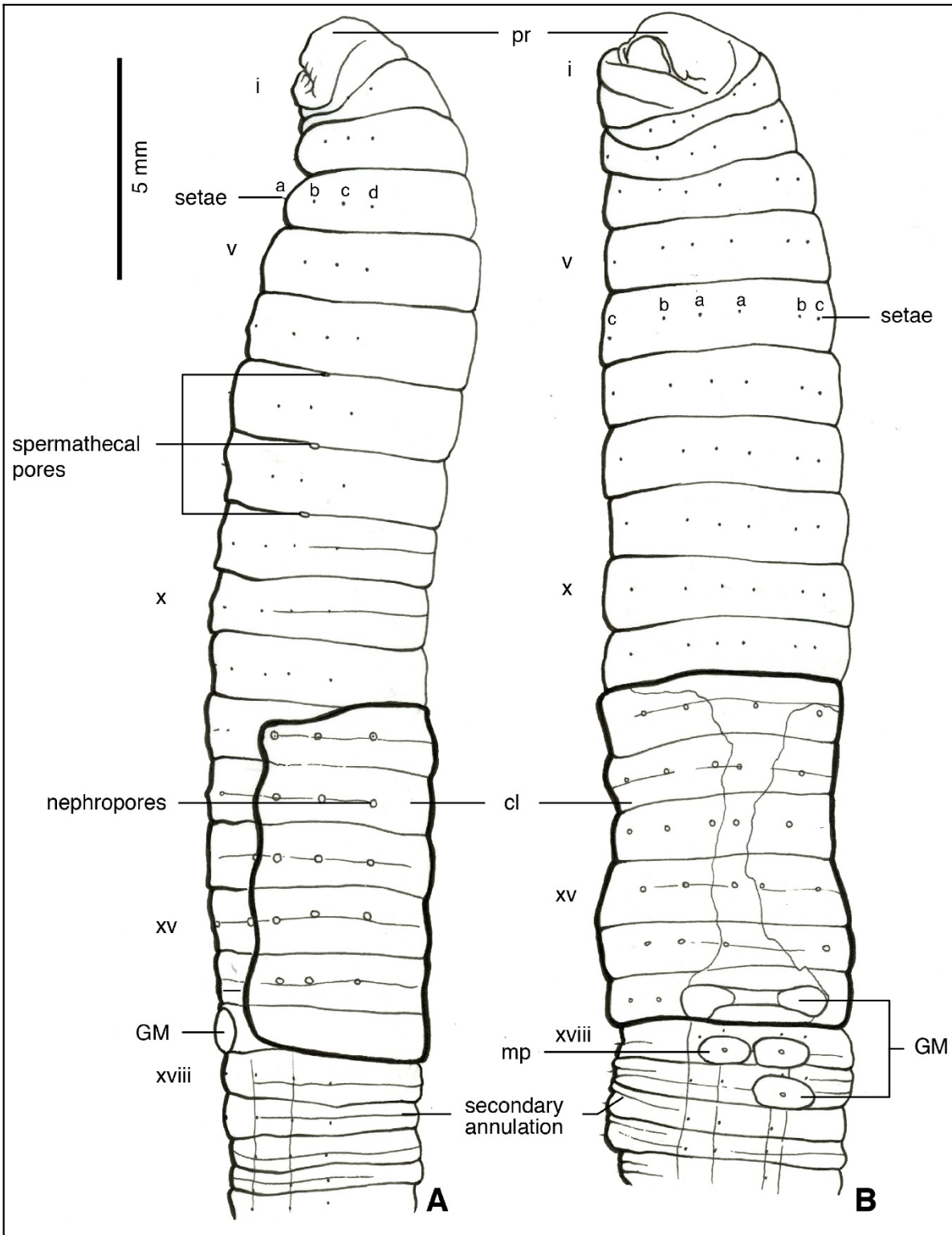


Fig. 35. External longitudinal views of *Arctiostrotus vancouverensis* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the Canadian Museum of Nature, Ottawa, Ontario).

Genus *Toutellus* Fender and McKey-Fender, 1990

- 1942 *Plutellus* (part.)-Gates, American Midl. Nat. 27(1): 89.
1977 *Argilophilus*-Gates, Megadrilogica 3(2): 58.
1990 *Toutellus* Fender and McKey-Fender, Soil Biology Guide, p. 374.
1994 *Toutellus*-McKey-Fender, Fender and Marshall, Canadian J. Zool. 72: 1336.

Type species

Plutellus toutellus Altman, 1936.

Diagnosis (after Fender and McKey-Fender, 1990: 374)

Bulbous anteriorly, slender posteriorly, phallic in contraction. Prostomium epilobic, open. Clitellum annular, in xiii–xviii. Dorsal pores present behind clitellum, usually beginning at 14/15. Holonephric, exonephridia, avesculate, inconspicuous pores alternating very irregularly. Genital markings intersegmental. Quadrithecal, ducts stout, with intramural seminal chambers bulging anterior wall of duct. Prostates confined to xviii. Penial setae strong, curved, ornamented with rows of teeth or scales. Strong gizzard in v, v and vi, or vi. Calciferous lamellae longitudinal, continuous in xv–xvi. Intestine beginning in xviii, with caeca and ventral ciliated groove. Caeca paired dorsolaterally and (or) laterally on intestine, anteriorly several pairs adnate to and supported by anterior septa of their segments, saccate to digitate, form and segmental position varying specifically, a series in region of xxii–lv. Typhlosole lamellar to branched T shape in cross section. Musculature of body wall continuous, thickness nearly uniform. Setae regular, none especially enlarged. Widely paired to separate. Unpigmented or immatures with red epidermal (alcohol soluble) chromophores (specific variation).

Range

Vancouver Island; Washington west of the Cascade Range in the Puget Trough, but south of Olympia; south in Oregon west of the Cascade Range summits and in the central valleys and along the coast to southernmost Curry County. Not yet known from the Washington coast or from California.

Discussion

The genus *Toutellus* is a large and very diverse assemblage, with representatives ranging in size from 50 to 450 mm, rivaling the size of the giant meronephric species of *Driloleirus* Fender, 1990 (= *Megascolides* of some authors) found in the deep soils of Oregon and Washington, varying in heart position, calciferous gland morphology, patterns of genital markings etc., and including many species and variant populations. Vancouver Island materials of this genus thus far include only *Toutellus oregonensis* (Smith, 1937), a species widely spread in Washington and Oregon. This species is not particularly maritime.

The genus *Toutellus* in Washington and Oregon occupies most available niches, from xeric hill sites to stream margins and from heavy soils to humus and duff, with accompanying specific morphological and physiological distinctions. Given the wide variety of habitats available on Vancouver Island, Fender and McKey-Fender suspect other *Toutellus* species may be present (Fender and McKey-Fender, 1990). The greatest diversity in the genus centres in western Oregon.

***Toutellus oregonensis* (Smith, 1937)**

Oregon worm — Ver de l'Oregon

(Fig. 36)

- 1937 *oregonensis*, *Plutellus* Smith, Proc. United States Nat. Mus. 84(3009): 177. Type species in the USNM–Smithsonian Institution cat nos. 20247–52 (Reynolds and Wetzel, 2021).
- 1942 *oregonensis*, *Plutellus*-Gates, American Midl. Nat. 27(1): 90.
- 1977 *oregonensis*, *Argilophilus*-Gates, Megadrilogica 3(2): 58.
- 1990 *oregonensis*, *Toutellus*-Fender and McKey-Fender, Soil biology guide, p. 374.
- 1995 *oregonensis*, *Toutellus*-Fender, Earthworm ecology and biogeography, p. 57.
- 2018 *oregonensis*, *Toutellus*-Reynolds, Megadrilogica 23(1): 6.

Note: additional detail in diagnosis is presented as this species is very rare in Canada (Vancouver Island, British Columbia). The identification of this species may require dissection.

Diagnosis (after Fender and McKey-Fender, 1990: 374)

Large earthworm, length 74–88 mm, diameter 4.5–6.0 mm, number of segments 113–121. Clitellum, annular, in xiii–xviii. Tubercula pubertatis, lacking. Prostomium epilobic $\frac{1}{2}$ half open, sides of tongue converging. Dorsal pores present behind clitellum. Quadriothecal, spermathecal pores in furrows $\frac{7}{8}$ and $\frac{8}{9}$ in setal in *B*, with glandular, puckered lips. Genital markings intersegmental, paired or unilateral $\frac{19}{20}$, short transverse ovals centred in *A* (transverse bar on $\frac{9}{10}$ absent in this population). Male porophores paired, broadly lunate, each with 3 pores (male pore and 2 penisetal pores), covering xviii and encroaching on xvii and xix, centering in *B*, joined medially by a broad glandular strip with several transverse creases. Nephropores inconspicuous, those visible irregularly alternating between loosely defined levels above *D* and between *B* and *C*. Setae separate, dorsal interval wide (setal intervals, taken from Oregon specimens compared with Vancouver Island material, $AA:AB:BC:CD:DD = 2.6:1.0:2.4:2.2:4.0$), $DD:U = \frac{1}{3}$, on *x*, and $2.8:1.0:2.0:1.9:5.3$, $DD:U = \frac{2}{5}$, on *xxx* *AB* much narrower in segments near male pores. Penial setae strong, curved, sculptured, with rows of teeth, $845 \times 26 \mu\text{m}$. Unpigmented.

Proventriculus thin-walled, smooth internally. Gizzard mostly in *v*, $\frac{5}{6}$ thin, gizzard short, strong, cuticular lining plain in posterior half, anterior part with several moderately incised circumferential striae. Anterior oesophagus vii–xiv, with low, irregularly interrupted longitudinal ridges. Posterior calciferous gland region *xv* and *xvi* externally somewhat narrowed at $\frac{15}{16}$, internally lined with about 16 continuously longitudinal thin lamellae not interrupted at $\frac{15}{16}$; pre-intestinal constriction *xvii* and anteriormost *xviii* with low white longitudinal folds. Intestine expands in *xviii*, typhlosole cross section a narrow-limbed T-shape, a lamella with vein either side on free edge, beginning gradually as a simple ridge in *xxi* and *xxii*. Caeca paired on dorsum of intestine, deeply saccate in *xxiii*–*xxviii* plus lesser sacs in *xxix*–*xxx* and bulges in *xxxi*–*xxxiii*.

Quadriothecal, spermathecae in *viii* and *ix* with broadly ovoid ampulla tapering to a short duct with multiloculate diverticular bulge across anterior and lateral face of duct. Holandric, testes and funnels free in *x* and *xi*, seminal vesicles postseptal dorsolaterally in *xi* and *xii*, of many cauliflowerlike lobes.

Dorsolateral hearts present in *xiii*, or occasionally missing on one or both sides, and then most posterior hearts in *xii* (see note on variation).

Variation

Toutellus oregonensis, although readily distinguished from the other species of *Toutellus*, may vary in a number of directions within the species. For example, the anterior genital markings, while usually consisting of a single transverse bar on $\frac{9}{10}$ in *BB*, may include successively shorter bars on $\frac{8}{9}$ and $\frac{7}{8}$. This variant was originally described as *Toutellus oregonensis swiftae* Smith, 1937. Similar superpapillation may be found in other *Toutellus* species. It is therefore not a nameable subspecies. The anterior genital markings may also be lacking, as is the case in the Vancouver Island material. Individuals of this species occasionally lack the hearts of *xiii*, symmetrically or unilaterally, within

populations uniform for other characteristics. There is also variation in the degree of development of the calciferous gland in xv–xvi, though it is always comparatively undeveloped in this species. The Vancouver Island specimens are about as primitive for this feature as any *T. oregonensis*. An occasional worm may have an anomalous origin for the first caecum (e.g., xxii on one side). In fact, one of the Vancouver Island specimens is lacking a heart on one side and so is a "12, 13–23." The other Vancouver Island specimens are "13–23s." Gizzard position (relative to septum 5/6) also varies.

Remarks

Fender and Marshall in 1993 looked unsuccessfully for this species in the Douglas Peak area. They were unable to sample Spiers' locality (original collection site), but considering the variety of habitats they sampled and the area covered, it would seem that *T. oregonensis* is very rare on Vancouver Island.

Biology

Only five specimens (0-1-4) have been collected on Vancouver Island, in soil under *Thuja plicata* (western red cedar Donn ex D. Don in Lambert), on MacMillan Bloedel land (Cameron Division), east of China and west of Douglas Peak.

Reproduction

Toutellus oregonensis is presumed amphimictic until there is evidence to the contrary (Fender and McKey-Fender, 1990).

Climatic zone: Temperate.

Ecological type

Toutellus oregonensis is an endogeic species (Reynolds, 2018).

Origin, range

Toutellus oregonensis is a native North American species and is restricted to the Pacific coastal area, in particular, Vancouver Island; Washington west of the Cascade Range in the Puget Trough, but south of Olympia; south in Oregon west of the Cascade Range summits and in the central valleys and along the coast to southernmost Curry County. It is not yet known from the Washington coast or from California.

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

This is a very rare species in North America.

Canada: British Columbia.

United States: Oregon, Washington.

Mexico: none.

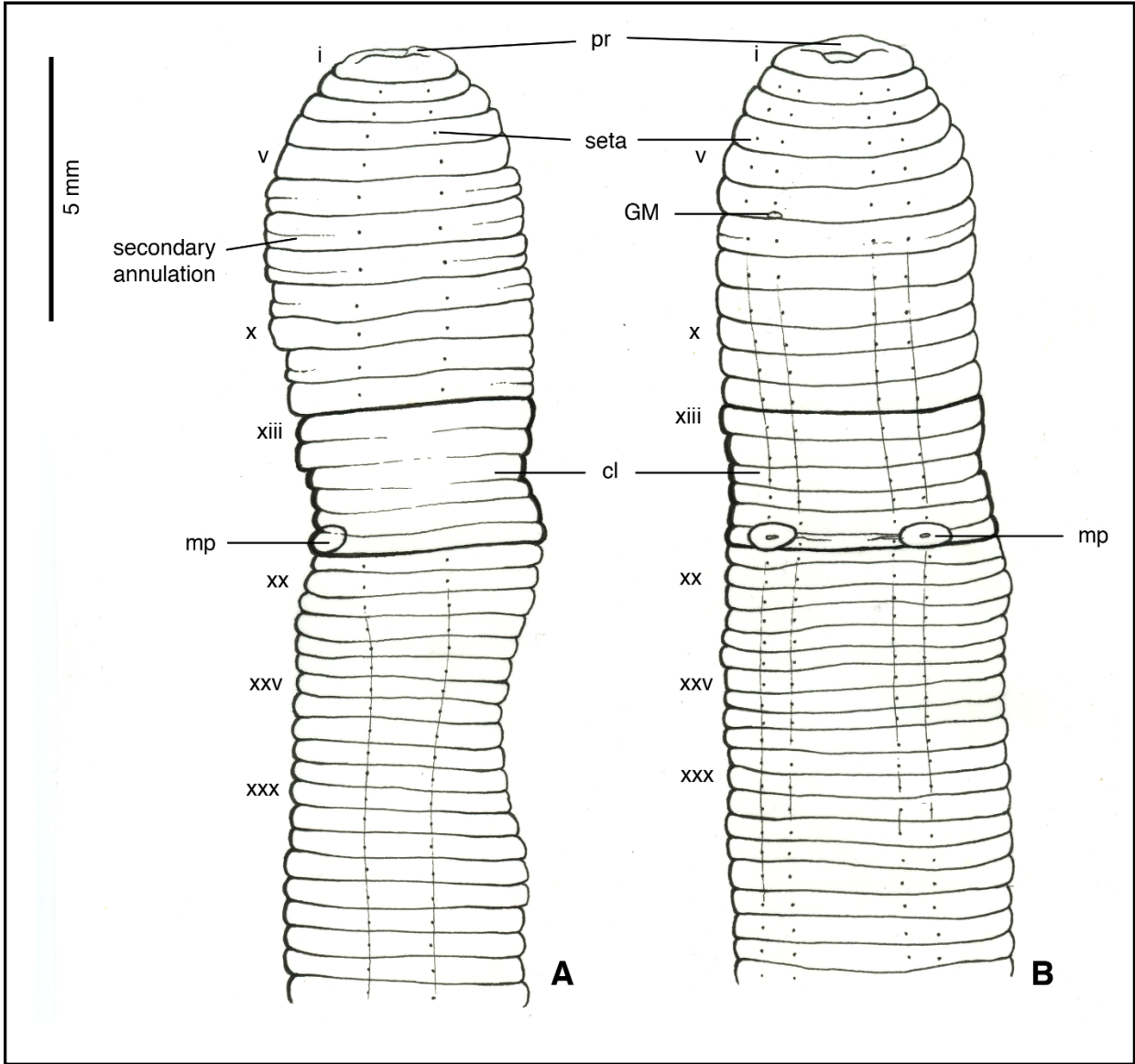


Fig. 36. External longitudinal views of *Toutellus oregonensis* showing taxonomic characters. A. Lateral view. B. Ventral view (specimen graciously furnished by the United States National Museum of Natural History – Smithsonian Institution, Washington, DC).

Family SPARGANOPHILIDAE Michaelsen, 1921

- 1917 Sparganophilinae (Lumbricidae), Michaelsen, Zool. Jb. Abt. Syst., Jena 41: 41: 301.
1921 Sparganophilidae (Lumbricina)-Michaelsen, Arch. Naturg. 86(A-8): 141.
1930 Sparganophilinae (Glossoscolecidae)-Stephenson, The Oligochaeta, p. 899.
1959 Sparganophilidae-Gates, Bull. Mus. Comp. Zool. Harvard College 121: 255.

Diagnosis (after Gates, 1972a: 314)

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, zygalobous. Anus, dorsal. Reproductive apertures: all minute and superficial, female pores in xiv, spermathecal pores in front of testis segments. Clitellum multilayered, including male pore segment. Seminal vesicles, trabeculate. Ovaries, in xiii, each terminating in a single eggstring. Ova, not yolky. Ovisacs, in xiv, small and lobed. Spermathecae, adiverticulate.

Type Genus

Sparganophilus Benham, 1892.

Distribution

In North America there is one genus (*Sparganophilus*) with 11 species and 2 subspecies (Reynolds, 1980, 2008). At least one species, *S. tamesis* (*S. eiseni* is a junior synonym of *S. tamesis*), is widely distributed, and found mainly in limicolous/aquatic habitats, throughout the USA (within and outside of its native range), Mexico, in several European countries (Germany, France, England, Switzerland, Italy, Spain, etc.) (Rota *et al.*, 2014; Bouché and Qiu, 1998).

The description of *S. langi* by Bouché and Qui (1998) based upon specimens collected from Lake Geneva (Switzerland), supports the possibility of an ancient and endemic presence of Sparganophilidae in Europe.

As a subfamily, this taxon was for a time in the Glossoscolecidae but relationships now seem (Gates, 1974c: 2 and 1976: 1) to be closer to the lumbricoid Hormogastridae, Komarekionidae, Lumbricinae and Lutodrilidae. Perhaps even to the Japanese Biwadrilidae, if ovaries of the latter prove to be lumbricoid.

Gates (1982) still considered the Sparganophilidae to be monogeneric, notwithstanding that Righi *et al.* (1978) had described *Areco reco* gen. novo et sp. novo from Brazil. There is still some debate on whether the genus *Areco* belongs in the Sparganophilidae, as recently stated by Brown and Fragoso (2007: 75) "Tanto los autores originales (Righi *et al.*, 1978) como Gavrillov (1981), consideran la colocación de este género en Sparganophilidae es dudosa y esta pendiente de futuras investigaciones." [*translation by JWR*: Even the original authors (Righi *et al.*, 1978) and Gavrillov (1981) questioned whether this genus belonged in Sparganophilidae, but left this up to future investigations.] It is surprising that Gates was not aware (or chose not to consider the validity) of *Areco* when making his comment.

Genus *Sparganophilus* Benham, 1892

- 1892 *Sparganophilus* Benham, Quart. J. Micros. Soc. (n.s.), 34: 155.
1895 *Sparganophilus*-Smith, Bull. Ill. St. Lab. Nat. Hist. 4(5): 142.
1900 *Sparganophilus*-Michaelsen, Das Tierreich, Oligochaeta 10: 463.
1921 *Sparganophilus*-Michaelsen, Arch. Naturg. 86(A): 141.
1930 *Sparganophilus*-Stephenson, Oligochaeta (Oxford), p. 899.
1971 *Sparganophilus*-Brinkhurst and Jamieson, Aquatic Oligochaeta World, p. 810.
1972 *Sparganophilus*-Gates, Trans. Amer. Philos. Soc. 62(7): 314.
1980 *Sparganophilus*-Reynolds, Megadrilogica 3(12): 189.

Type species

Sparganophilus tamesis Benham, 1892.

Diagnosis (after Reynolds, 1977a, 1977c, 1980)

Calciferous gland and gizzard, absent. Hearts, in vii–xi. Nephridia, absent in cephalic region (segments i–xii). Nephropores, inconspicuous, in *AB*. Setae, paired. Prostomium zygotlobic. Lateral lines, absent. Colour, unpigmented.

Discussion

Aside from the original description in England in 1892, it was believed that *Sparganophilus* was restricted to North America. In recent years, this genus has been reported from several countries in Central America and Europe: Guatemala (Brown and Fragoso, 2007), Mexico (Reynolds and Wetzel, 2008, 2012), France (Tétay, 1934; Bouché, 1972; Bouché and Qiu, 1998), Germany (Graefe and Beylich, 2011), Italy (Rota *et al.*, 2016), Switzerland (Zicsi and Vaucher, 1987; Bouché and Qiu, 1998), and Ukraine (Lapied (unpubl. data). Recent papers reported this genus from the Philippines (Magahud *et al.*, 2017; Aspe, 2020).

In 1980, ten new-to-science taxa in this genus were described (Reynolds, 1980); all of these were initially reported from the southeastern United States. The range of several of these new species have been reported from the midwest and west coast of the USA.

Recently, Ikeda *et al.* (2020) reported a comparison of latitudinal species diversity patterns between riverine and terrestrial earthworms from the North American temperate zone involving *Sparganophilus* and *Diplocardia* (a nearctic genus of terrestrial earthworms not currently recorded in Canada). *Sparganophilus* species diversity was higher at mid-latitudes (32° to 40° N) due to a preponderance of species with limited geographical distributions, whereas all specimens collected north of 40° belonged to broadly distributed species. Species with limited geographical distributions were more often collected at higher elevations than broadly distributed species in *Sparganophilus*.

***Sparganophilus tamesis* Benham, 1892**
American mud worm — Ver américain de la base
(Fig. 37)

- 1892 *Sparganophilus tamesis* Benham, 1892: 156; Type species in the British Museum Natural History cat. nos. 1892:12:16:1–2 (Reynolds and Wetzel, 2021).
- 1895 *Sparganophilus eiseni* Smith, Bull. Illinois St. Lab. Nat. Hist. 4(5): 142.
- 1906 *Sparganophilus eiseni*-Moore, Bull. Bur. Fish.. 25: 170.
- 1911 *Helodrilus elongatus* Friend, Zoologist (4), 15: 192.
- 1921 *Sparganophilus elongatus*-Friend, Ann. Mag. Nat. Hist. (9), 7: 137.
- 1934 *Pelodrilus cuenoti* Tétrý, C.R. Acad. Sci. Paris 199: 322.
- 1934 *Eiseniella tetrahedra* (laps.)-Moon, J. Anim. Ecol. 3: 17.
- 1938 *Pelodrilus cuenoti*-Tétrý, Contribution à l'étude faune l'est de France, p. 188.
- 1972 *Sparganophilus tamesis* (part.)-Brinkhurst and Jamieson, Aquatic Oligochaeta of the world, p. 812.
- 1977 *Sparganophilus eiseni*-Reynolds, Roy. Ontario Mus., Life Sci. Misc. Publ., p. 113.
- 1980 *Sparganophilus tamesis*-Reynolds, Megadrilogica 3(12): 190.
- 1980 *Sparganophilus eiseni*-Reynolds, Megadrilogica 3(12): 191.
- 1998 *Sparganophilus langi* Qiu and Bouché, Doc. Pédozool. Intégral 4: 179.
- 2001 *Sparganophilus eiseni*-McAlpine *et al.*, Megadrilogica 8(10): 53.
- 2001 *Sparganophilus eiseni*-Reynolds, Megadrilogica 8(11): 84.
- 2008 *Sparganophilus eiseni*-Reynolds, Megadrilogica 12(9): 125.
- 2021 *Sparganophilus tamesis*-Reynolds, Megadrilogica 26(4): 54.

Diagnosis (after Reynolds, 1977a, 1977c, 1980)

Large and thin earthworm, length 150–200 mm, diameter uniformly about 2.5 mm, number of segments 165–225, prostomium zygotobitic, dorsal pores absent. Clitellum xv–xxv. Tubercula pubertatis xvii–xxii. Setae closely paired, with setae *c* and *d* above mL line. Male pores on xix, female pores on xiv. Seminal vesicles, two pairs, in 11 and 12 with a pair of testes in 10 and 11. Spermathecae, three pairs, in 7, 8, and 9 with ducts opening just ventral to level C in 6/7–8/9. Gizzard, calciferous glands, and typhlosole absent. Prostate-like glands, four pairs, in 13, 14, 15, and 16. Body cylindrical. Colour, unpigmented but sometimes appearing pink with blue and green iridescence.

Biology

This species is limicolous and confined to the muddy banks of streams, rivers, ponds, and lakes. Smith (1915) found it to be abundant in the mud of the bottom and margins of many waters east of the Mississippi River. Olson (1928) reported it along the shores of Lake Erie, and similar habitats are recorded for New York (Lake Ontario) (Olson, 1940), New Jersey (Davies, 1954), Louisiana (Harman, 1965) and Tennessee (Reynolds, 1977c). In waters off the Ontario shores in Lake Erie and Lake Huron was reported by Reynolds (1977a) and in similar habitats in the Saint Lawrence River of Quebec by Reynolds and Reynolds (1992), the St. John River of New Brunswick (McAlpine *et al.*, 2001), the Spednic Lake PNA (McAlpine *et al.*, 2022). This species has also been reported from caves (Holler *et al.*, 2020). At this time, *S. tamesis* has not been recorded from any other Maritime or western province.

Reproduction

Sparganophilus tamesis is assumed to be amphimictic (Reynolds, 1974a).

Climatic zone Temperate.

Ecological type

Sparganophilus tamesis is a limicolous, and some consider it an aquatic, species (Reynolds, 2018).

Origin, range

Sparganophilus tamesis is a native North American species, but is relatively rare in North America except for an area bounded by the Great Lakes, Mississippi River, Atlantic Ocean, and the Gulf States. No *Sparganophilus* species has been reported from Vancouver Island to date, but the family is included for completeness, as it has representatives in Oregon (Macnab and McKey-Fender 1947), though the determination as *S. eiseni* is an error). No recent treatment of western Sparganophilidae exists (Fender and McKey-Fender, 1990); for the eastern distribution of Sparganophilidae see Reynolds (1980, 2008b). Recent records from Europe would support its designation as a peregrine species (see the list under the genus).

North American distribution – a complete listing of species and their first report in Canada and the United States was presented by Reynolds (2018):

Canada: British Columbia (?), Manitoba, New Brunswick, Ontario, Quebec.

United States: Alabama, Arkansas, Colorado, Connecticut, Georgia, Florida, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, Wisconsin.

Mexico: Guerrero, Nayarit and Veracruz States (Fragoso, 2001).

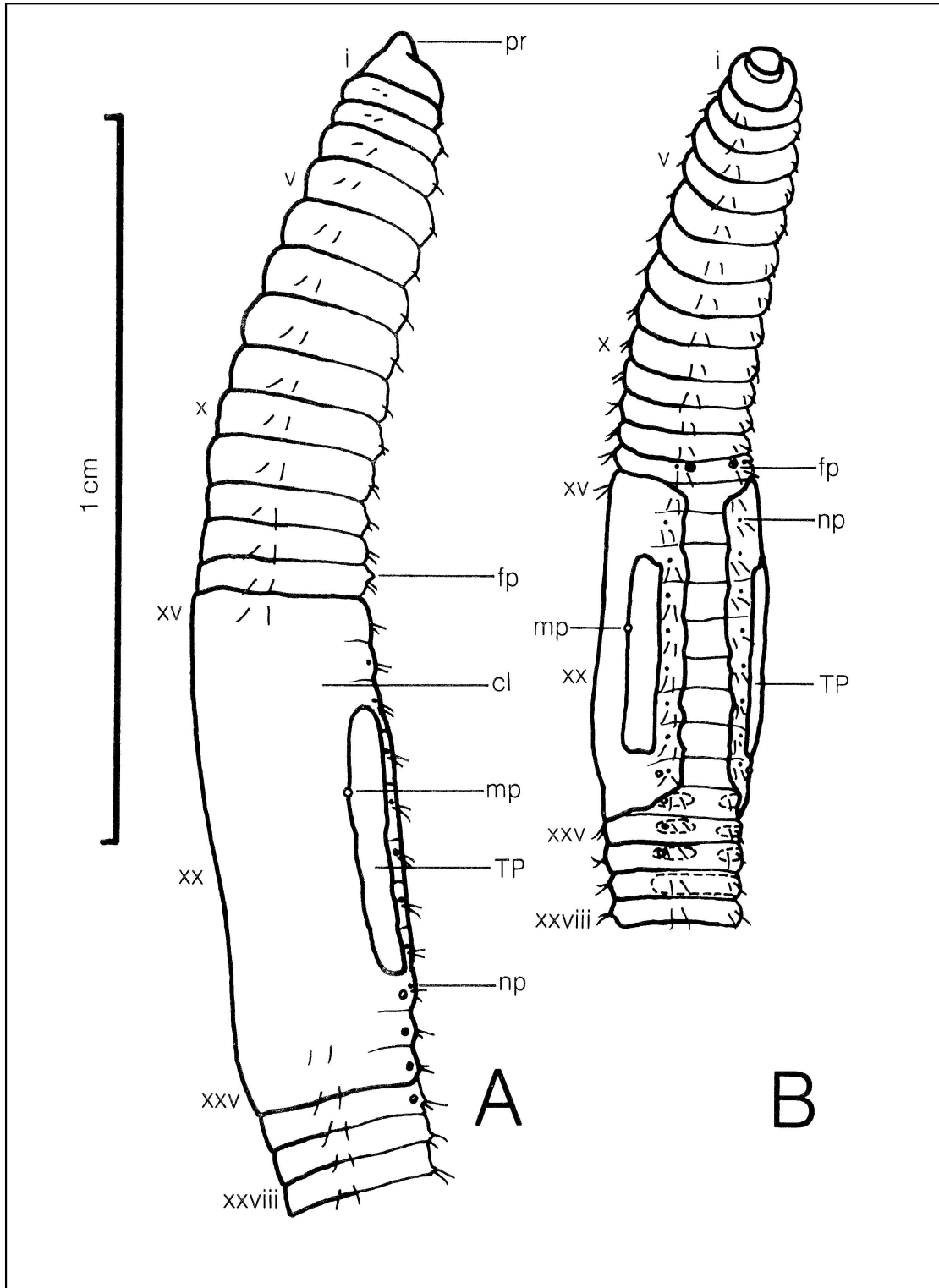


Fig. 37. External longitudinal views of *Sparganophilus tamesis* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a).

Arctic earthworm migration and climate change

I used to think that all earthworms were good and, that there were no negative aspects to their activities in the soil. In recent decades their spread as invasive species and the effect of climate change have caused me to rethink my original position. I have thought of myself as the antithesis of Johnny Appleseed travelling the world taking samples randomly, instead of spreading apple seeds randomly everywhere he went (Hillis, 1917; Means, 2011; Silverman, 2012).

Physical properties of soils have been altered by the invasive pheretimoid earthworms and their casting layer creates a thermal refuge (Görres *et al.*, 2019). Ali and Naaz (2013) have used earthworms as biomarkers for assessing the environmental impact in soils.

Climate change can have a significant effect on organisms above and below the soil surface in terrestrial ecosystems (Singh *et al.*, 2019). Many ecological factors can affect earthworm population densities, biomass and the species complex. Undoubtedly, the obvious and most frequently cited factors include soil moisture, soil temperature and soil acidity – each of which potentially can act as a complete limiting factor. Other factors, such as soil depth and texture, nutrient and food supply (vegetation species), physiographic features (physiographic position, slope, aspect, elevation) and soil colour can interact with the above factors and influence soil conditions; a preliminary model reflecting these interactions was published nearly 50 years ago (Reynolds and Jordan, 1975). We suggested that soil moisture tension was more important than the percentage of moisture in the soil, which seems to have been ignored in most subsequent studies, *e.g.*, Diehl and Williams (1992) and Bessolitsyna (2012). Earthworm communities ebb and flow with the changing precipitation patterns (Tondoh, 2006; Eisenhauer *et al.*, 2009), but if the moisture is not available to the earthworms, this pattern may not be sustainable. Therefore, soil moisture tension gives a better indication of earthworm's ability to reproduce and feed in a given habitat.

I have noticed a change in the earthworm diversity in North America during the past 50 years. In the mid to late 1960's, the Oriental pheretimoid species (*Amyntas*, *Metaphire* and *Polypheretima* spp.) were limited in natural habitats to the southeastern United States, particularly south of Tennessee (Reynolds, 1978, 2019). A change in climate permits a rapid increase in their range due to their parthenogenetic reproduction. In the past 50 years, they have spread into the midwestern and the northeastern American soils (Reynolds, 2010c, 2011a). It was not until recently, that I recorded the first populations of these earthworms in Canada (Reynolds, 2014a). I may not live to see it happen, but as the soils in Canada warm, if precipitation in the form of increased rain, and vegetation diversifies, one day earthworms will become a major component of the soil fauna in the Canadian far north.

Development recreational and industrial activities are rapidly expanding in the boreal forests of western Canada. It has been suggested, that this activity is facilitating the introduction and spread of non-native species such as exotic European earthworms, particularly *Dendrobaena octaedra*, *Dendrodriulus rubidus* and *Lumbricus rubellus* (Cameron *et al.*, 2007; Reynolds *et al.*, 2019b). Since earthworms cannot migrate very far on their own, Cameron *et al.* suggest four mechanisms for their introduction: 1) bait cast-offs, 2) dispersal via vehicles, 3) dispersal via vertebrate predators, and 4) dispersal via waterways. Their research indicates that the first two mechanisms are the most likely. My experience, particularly in the United States, has shown that river flooding is a definite means of dispersal. In the far north where the rivers, streams and lakes flow into the Arctic region, this is a definite possibility.

Today, the Arctic is a treeless plain with only sparse tundra vegetation, such as grasses, sedges and a few flowering plants (Reynolds, 2020b). In contrast, the Russian sediment cores contained pollen from trees such as larch (*Larix* spp.), spruce (*Picea* spp.), fir (*Abies* spp.) and hemlock (*Tsuga* spp.). This shows that boreal forests, which today end hundreds of miles farther south and west in Russia and at the Arctic Circle in Alaska and Canada, once reached all the way to the Arctic Ocean, across much of Arctic Russia and North America. Changes in Arctic vegetation can have important implications for trophic interactions and ecosystem functioning leading to climate feedbacks. Arctic plant communities and species are generally sensitive to warming, but trends over a period of time are heterogeneous and complex (Bjorkman *et al.*, 2019).

The latest evidence of drastic Arctic warming came when scientists recorded extreme summer melt rates across the Greenland Ice Sheet. In early August 2020, Canada's last remaining ice shelf, in the territory of Nunavut,

collapsed into the sea. Parts of Arctic Siberia and Svalbard, a group of Norwegian islands in the Arctic Ocean, reached record-shattering high temperatures 38°C (100°F) in the summer of 2020 (Brigham-Grette and Petsch, 2020; Laba *et al.*, 2020).

The question is whether the invasion of earthworms in the North will effect on the release of carbon in the soil, or increase the concentration of atmospheric CO₂ in the soil (sequestration). However, it is difficult to determine at present, and the results may often contradict each other. As an example, Zhang *et al.* (2013) and Coleman *et al.* (2017) showed how earthworms contribute to net carbon sequestration (a natural or artificial process by which carbon dioxide is removed from the atmosphere and held in solid or liquid form.) in soil.

Earthworms were often found to stimulate CO₂ emission, especially in short-term experiments, but they have also been reported to enhance carbon stabilization in soil aggregates in some longer-term experiments (Coleman *et al.*, 2017). Nevertheless, more experimental data support the view that earthworms reduce carbon sequestration due to the fact that CO₂ emission is easier to detect than carbon stabilization. As a result, a recent meta-analysis study concluded that earthworm presence will increase CO₂ emissions from soil by 33 % (Lubbers *et al.*, 2013). In contrast, Zhang *et al.* (2013) found that earthworms could facilitate net carbon sequestration through unequal amplification of carbon stabilization compared with carbon mineralization. Zhang *et al.* proposed that neither an increase in CO₂ emission nor that in stabilized carbon would entirely reflect the earthworms' contribution to net carbon sequestration; that is, the impacts of earthworms on the two coupled processes of carbon mineralization and carbon stabilization should be studied simultaneously. They found that, firstly, although earthworms accelerate carbon mineralization, the total amount of CO₂ that can potentially escape from the soil with earthworms differs little from soil containing no earthworms, because the capacities of carbon mineralization of earthworms and soil microbiota are similar. Most previously published studies did not note this and, thus, were likely to conclude that earthworms decrease carbon sequestration only because CO₂ emission was often enhanced by earthworms (Lavelle, 1997; Liski *et al.*, 2003). Secondly, given that an increase in carbon mineralization (C_{\min}) and carbon stabilization (C_{sta}) may be a natural consequence of an increased pool of activated carbon, the pool size of the activated carbon (C_{act}) and its allocation pattern into carbon mineralization and carbon stabilization then determine the net carbon sequestration. Thus, Zhang *et al.* introduced the new concept of sequestration quotient (SQ, $C_{\text{sta}}/C_{\text{act}}$) to quantify the earthworms' impact on the balance of carbon mineralization and carbon stabilization (Fig. 38). The study revealed that the presence of earthworms is more likely to create a carbon sink, as the carbon stabilized by earthworms outweighs that converted to CO₂ during carbon mineralization, *i.e.*, SQ values are higher in soil with earthworms.

Earthworms play an essential part in determining the greenhouse-gas balance of soils worldwide, and their influence is expected to grow over the next decades. They are thought to stimulate carbon sequestration in soil aggregates, but also to increase emissions of the main greenhouse gases carbon dioxide and nitrous oxide. Hence, it remains highly controversial whether earthworms predominantly affect soils to act as a net source or sink of greenhouse gases. Lubbers *et al.* (2013) provided a quantitative review of the overall effect of greenhouse gas emissions from soils increased by earthworms.

Another recent study (Blume-Werry *et al.*, 2020) indicated that invasive earthworms unlock arctic plant nitrogen. Arctic plant growth generally has limited nitrogen due to low temperatures and slow soil microbial processes. Their study illustrated that arctic plant-soil N-cycling was constrained by lack of earthworms and their activities. Earthworm activity also increased either the height or number of floral shoots, while enhancing fine root production and vegetation greenness. The effect of earthworms suggested that human spreading of earthworms may lead to substantial changes in the structure and function of Arctic ecosystems. The authors reported the earthworms only as *Aporrectodea* sp. and *Lumbricus* sp. Since they cite Reynolds (2000a), it may be assumed they refer to *Ap. tuberculata* and *L. rubellus* or *L. terrestris*.

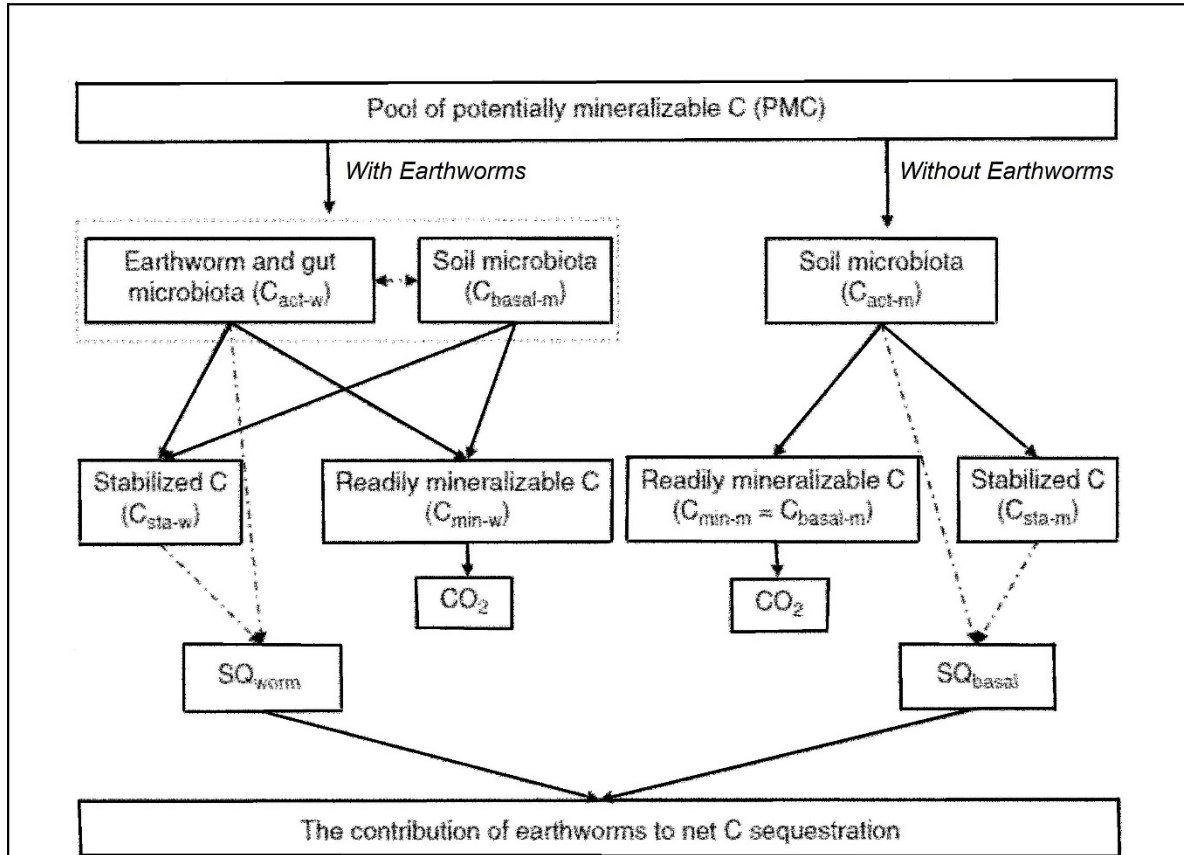


Fig. 38. A conceptual model of how earthworms regulate C sequestration. C_{act-w} and C_{act-m} refer to the earthworm-activated and soil microbiota-activated mineralizable C, respectively. C_{min-w} and C_{sta-w} refer to the pool of readily mineralizable C and pool of stabilized C in soil with earthworms, respectively; C_{min-m} and C_{sta-m} refer to the pool of readily mineralizable C and pool of stabilized C, respectively in soil without earthworms. Given that the soil microbiota-induced readily mineralizable C (C_{min-m}) may also be metabolized and/or stabilized by earthworms, C_{min-m} is also defined as basal C ($C_{basal-m}$). Note that the value of C_{min-m} ($C_{basal-m}$) in a system with and without earthworms may gradually differ as earthworm incubation proceeds. C_{sta-w} and C_{act-w} are the differences between C_{sta} and $C_{sta} + C_{min}$ between soil with and without earthworms, respectively. SQ_{worm} and SQ_{basal} refer to the C sequestration quotient in soil with and without earthworms, respectively. The single-ended dot-dash lines represent the major components for the calculation of SQ values. The double-ended dotted line indicates possible interactions (This figure was from Zhang *et al.* (2013)).

The Arctic hasn't been this warm for 3 million years; geoscientists have great concern on what is going on in the Arctic and the effect it will have on the rest of the world. It has taken humans only 200 years to completely reverse the trajectory begun 50 million years ago and return the planet to CO₂ levels not experienced for millions of years. Scientists project that the Arctic will be completely ice-free in summer within the next two decades, *e.g.*, by 2040 (Brigham-Grette and Petsch, 2020). It is my belief that by 2050, the frequency and diversity of earthworms in Arctic soils will be considerably greater than it is today.

Literature cited

Provincial and Territory References

Alberta:

Hilton, D.F.J. and J.W. Reynolds. 1983. The earthworm (Oligochaeta: Lumbricidae) fauna of the Cypress Hills Provincial Park, Alberta. *Megadrilogica* 4(4): 91–92.

Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.

Reynolds, J.W. and M.J. Clapperton. 1996. New earthworm records for Alberta (Oligochaeta: Lumbricidae) including the description of a new Canadian species. *Megadrilogica* 6(8): 73–82.

British Columbia:

Berkeley, C, 1968. Records of earthworms from Vancouver, British Columbia. *J. Fish. Res. Bd. Canada* 25(1): 205.

Marshall, V.G. and W.M. Fender. 2007. Native and introduced earthworms (Oligochaeta) of British Columbia, Canada. *Megadrilogica* 11(4): 29–52.

Reynolds, J.W. 1977. Le ver québécois (*Lumbricus festivus*) envahit la Colombie-Britannique. *Canadian Field-Nat.* 91(4): 395–396.

Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.

Manitoba:

Chang, P.S.S., D.G. Cobb, J.F. Flannagan and O.E. Saether. 1992. The Oligochaetes from the 1969 Lake Winnipeg baseline survey. *Canadian Data Rep. Fish. Aquat. Sci.* 869: iv + 35 pp.

Reynolds, J.W. 2000. A contribution to our knowledge of the earthworm fauna of Manitoba, Canada (Oligochaeta, Lumbricidae). *Megadrilogica* 8(3): 9–12.

Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.

New Brunswick:

McAlpine, D.F. and J.W. Reynolds. 1977. Terrestrial Oligochaeta of some New Brunswick caves with remarks on their ecology. *Canadian Field-Nat.* 91(4): 360–366.

McAlpine, D.F. and J.W. Reynolds. 2018. Earthworms (Oligochaeta: Lumbricidae) of the Jacquet River Gorge Protected Natural Area and region, New Brunswick, with additions to the Province. *Megadrilogica* 23(7): 103–107.

McAlpine, D.F. and J.W. Reynolds. 2019. Earthworms (Oligochaeta: Lumbricidae) of the Nepisiquit Protected Natural Area, New Brunswick, Canada. *Megadrilogica* 24(4): 39–49.

McAlpine, D.F. and J.W. Reynolds. 2020. Earthworms (Oligochaeta: Lumbricidae) of the Caledonia Gorge Protected Natural Area and region, New Brunswick, with additions to the Province. *Megadrilogica* 25(4): 53–60.

- McAlpine, D.F., J.W. Reynolds and F.W. Schueler. 2019. *Thamnophis sirtalis pallidulus* (Maritime Garter Snake): Diet. Herpetological Review 50(4): 815.
- McAlpine, D.F., J.W. Reynolds, C.R. Graves and M.C. Sollows. 2022. Earthworms (Lumbricidae and Sparganophilidae) of the Spednic Lake Protected Natural Area, New Brunswick, Canada. Megadrilogica 26(11): 169–184.
- McAlpine, D.F., J.W. Reynolds, T.J. Fletcher, J.L. Trecartin and D.L. Sabine. 2001. *Sparganophilus eiseni* (Oligochaeta, Sparganophilidae) in New Brunswick, an addition to the earthworm fauna of Maritime Canada. Megadrilogica 8(10): 53–56.
- McAlpine, D.F., S.A. Sullivan, F.J.T. McAlpine, J.H. Lewis and J.W. Reynolds. 2020. Earthworms (Lumbricidae and Sparganophilidae) of the Grand Lake Protected Natural Area, New Brunswick, Canada. Megadrilogica 25(6): 89–98.
- Reynolds, J.W. 1976. A preliminary checklist and distribution of the earthworms of New Brunswick. New Brunswick Nat. 7(2): 16–17.
- Reynolds, J.W. 2001. The earthworms of New Brunswick (Oligochaeta: Lumbricidae). Megadrilogica 8(8): 37–47.
- Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in the Canadian Maritime Provinces. Megadrilogica 16(11): 137–156.
- Reynolds, J.W. and D.S. Christie. 1977. Additional records of New Brunswick earthworms. New Brunswick Nat. 8(3): 25.
- Reynolds, J.W., A.J. Hasson and D.F. McAlpine. 2015. Earthworms (Oligochaeta: Lumbricidae) of the Nepisiquit Protected Natural Area and region, New Brunswick, with additions to the Province. Megadrilogica 19(1): 1–10.
- Newfoundland and Labrador:**
- Reynolds, J.W. 2000. A contribution to our knowledge of the earthworm fauna of Newfoundland and Labrador, Canada (Oligochaeta, Lumbricidae). Megadrilogica 8(2): 5–8.
- Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in the Canadian Maritime Provinces. Megadrilogica 16(11): 137–156.
- Northwest Territories:**
- Reynolds, J.W. 2002. First earthworm record from Nunavut, Canada and the second from the Northwest Territories. Megadrilogica 9(6): 40.
- Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. Megadrilogica 17(10): 141–156.
- Reynolds, J.W. 2020. New earthworm (Oligochaeta: Lumbricidae) records from opposite ends of the Earth. Megadrilogica 25(9): 113–118.
- Reynolds, J.W. and S.M. Moore. 1996. Note on the first earthworm record from the Northwest Territories, Canada. Megadrilogica 6(10): 96.
- Reynolds, J.W., P.M. Catling and B. Kostiuk. 2020. Earthworms (Annelida: Oligochaeta) and Leeches (Annelida: Hirudinea) of the Northwest Territories, Canada. Megadrilogica 25(7): 99–106.

Reynolds, J.W., P.M. Catling and B. Kostiuk. 2021. List 6.9. Earthworms and Leeches. (pp. 88-93) *In*: Working Group on General Status of NWT Species. 2020. NWT Species 2020-2025 – General Statuses Ranks of Wild Species in the Northwest Territories. Department of Environment and Natural Resources. Government of the Northwest Territories, Yellowknife, NT, 388 pp.

Nova Scotia:

- Reynolds, J.W. 1975. Boiteagan (Oligochaeta: Lumbricidae) Cheap Breatunn. *Megadrilogica* 2(6): 1–7.
- Reynolds, J.W. 1976. The distribution and ecology of the earthworms of Nova Scotia. *Megadrilogica* 2(8): 1–8.
- Reynolds, J.W. 2010. The earthworms (Oligochaeta: Lumbricidae) of Nova Scotia, revisited. *Megadrilogica* 14(6): 77–100.
- Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in the Canadian Maritime Provinces. *Megadrilogica* 16(11): 137–156.

Nunavut:

- Reynolds, J.W. 2002. First earthworm record from Nunavut, Canada and the second from the Northwest Territories. *Megadrilogica* 9(6): 40.
- Reynolds, J.W. 2003. A second earthworm species (Lumbricidae) from Nunavut, Canada. *Megadrilogica* 9(8): 52.
- Reynolds, J.W. 2004. More earthworm (Lumbricidae) collections from Nunavut, Canada. *Megadrilogica* 10(3): 13–14.
- Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.

Ontario:

- Reynolds, J.W. 1972. Earthworms (Lumbricidae) of the Haliburton Highlands, Ontario, Canada. *Megadrilogica* 1(3): 1–11.
- Reynolds, J.W. 1976. *Aporrectodea icterica* (Savigny, 1826) une espèce européenne de vers de terre récemment découverte en Amérique du Nord. *Megadrilogica* 2(12): 3–4.
- Reynolds, J.W. 1977. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. *Life Sci. Misc. Publ., Roy. Ont. Mus.* xi + 141 pp.
- Reynolds, J.W. 2011. The earthworms (Oligochaeta: Lumbricidae) of Pelee Island, Ontario, Canada. *Megadrilogica* 15(3): 23–33.
- Reynolds, J.W. 2014. Earthworms (Oligochaeta: Lumbricidae) invade lawn bowling greens in the Waterloo Region of Ontario, Canada. *Megadrilogica* 16(7): 69–76.
- Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae, Megascolecidae and Sparganophilidae) in Ontario, Canada. *Megadrilogica* 16(10): 111–135.
- Reynolds, J.W. and P.N. Mayville. 1994. New earthworm records from Rainy River District in north western Ontario (Oligochaeta: Lumbricidae). *Megadrilogica* 6(2): 13–16.

Prince Edward Island:

- Jordan, G.A., J.W. Reynolds and A.J. Burnett. 1976. Computer plotting and analysis of earthworm population distribution in Prince Edward Island. *Megadrilogica* 2(10): 1–7.
- Reynolds, J.W. 1975. The earthworms (Oligochaeta: Lumbricidae) of Prince Edward Island. *Megadrilogica* 2(7): 4–10.
- Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in the Canadian Maritime Provinces. *Megadrilogica* 16(11): 137–156.

Quebec:

- Moore, J.-D. 2019. Premières mentions de vers de terre au parc naturel et historique de l'île aux Basques. *Nat. canadien* 143(2): 33–38.
- Moore, J.-D. and J.W. Reynolds. 2003. Premières mentions de vers de terre dans deux écosystèmes forestiers de la rive nord du Saint-Laurent, Québec. *Megadrilogica* 9(9): 53–60.
- Moore, J.-D., R. Ouimet and J.W. Reynolds. 2009. Premières mentions de vers de terre dans trois écosystèmes forestiers du Bouclier canadien. *Nat. canadien* 133(1): 31–37.
- Reynolds, J.W. 1975. Les lombricidés (Oligochaeta) des Îles-de-la-Madeleine. *Megadrilogica* 2(3): 1–8.
- Reynolds, J.W. 1975. Les lombricidés (Oligochaeta) de la Gaspésie, Québec. *Megadrilogica* 2(4): 4–9.
- Reynolds, J.W. 1975. Les lombricidés (Oligochaeta) de l'Île d'Orléans, Québec. *Megadrilogica* 2(5): 8–11.
- Reynolds, J.W. 1976. Catalogue et clé d'identification des lombricidés du Québec. *Nat. canadien* 103(1): 21–27.
- Reynolds, J.W. 1977. Le ver québécois (*Lumbricus festivus*) envahit la Colombie-Britannique. *Canadian Field-Nat.* 91(4): 395–396.
- Reynolds, J.W. 2007. First earthworm records from Wentworth Township, Argenteuil County, Quebec. [Premiers signalements de lombrics dans le canton de Wentworth, comté d'Argenteuil (Québec).] *Megadrilogica* 11(5): 58–62.
- Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in Quebec, Canada. *Megadrilogica* 17(6): 73–103.
- Reynolds, J.W. 2017. The first earthworm (Oligochaeta: Lumbricidae) records from Îles aux Basques, Quebec, Canada. *Megadrilogica* 22(8): 157–159.
- Reynolds, J.W. et K.W. Reynolds. 1992. Les vers de terre (Oligochaeta: Lumbricidae et Sparganophilidae) sur la rive nord du Saint-Laurant (Québec). *Megadrilogica* 4(9): 145–161.
- Reynolds, J.W., D.F. McAlpine, K.J. Vanderwolf and H.M. Huynh. 2014. Earthworm (Oligochaeta: Lumbricidae) occurrences from Anticosti Island, Quebec, Canada. *Megadrilogica* 17(1): 1–6.

Saskatchewan:

- Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.

Reynolds, J.W. and M.N. Khan. 1999. A contribution to our knowledge of the earthworm fauna of Saskatchewan, Canada. *Megadrilogica* 7(12): 81–82.

Yukon:

Berman, D.I. and Y.M. Marusik. 1994. On *Bimastos parvus* (Oligochaeta: Lumbricidae) from Yukon Territory (Canada), with discussion of distribution of the earthworms in northwestern North America and northeastern Siberia. *Megadrilogica* 5(10): 113–116.

Reynolds, J.W. 2015. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.

Reynolds, J.W., B. Godin and D. Horwood. 2019. The first report of *Arctiostrotus fontinalis* (Oligochaeta: Megascolecidae) in Canada. *Megadrilogica* 24(2): 17–22.

Reynolds, J.W., E.K. Cameron, L.M. Sweeney, B. Bennett and B. Godin. 2019. The earthworms (Oligochaeta: Lumbricidae and Megascolecidae) in the Yukon and a first record for Skagway, Alaska, USA. *Megadrilogica* 25(1): 1–17.

Teale, C.L. 2007. A preliminary survey of the Oligochaete fauna of the Yukon Territory, Canada. *Megadrilogica* 11(1): 3–7.

Literature cited

Adams, H. and A. Adams. 1854. The genera of recent Mollusca arranged according to their organization, Volume I. London: van Voorst, 484 pp.

Addison, J.A. 2009. Distribution and impacts of invasive earthworms in Canadian forest ecosystems. *Biol. Invasions* 11(1): 59–79.

Ali, A.S. and I. Naaz. 2013. Earthworm biomarkers: The new tools of environmental impact assessment. *Biosci. Biotech. Res. Comm.* 6(2): 163–169.

Altman, L.C. 1936. Oligochaeta of Washington. *Univ. Washington Publ. Biol.* 4: 1–137.

Ammer, C. 2003. *The American Heritage Dictionary of Idioms*, rev. ed. San Diego, CA: Houghton Mifflin Harcourt, 480 pp.

Amone III, J.A. and J.G. Zaller. 2014. Earthworm effects on native grassland root system dynamics under natural and increased rainfall. *Frontiers Plant Sci.* 5(152): 8 pp.

André, F. 1963. Contribution à l'analyse expérimentale de la reproduction des Lombriciens. *Bull. Biol. France Belgique* 81: 1–101.

Aspe, N. 2020. *Field Guide: Earthworms in heirloom rice fields of the Philippine Cordillera and their integrated management*. Manila: Philippines, Intern. Rice Res. Inst., 26 pp.

Atkinson, R.J.C. 1957. Worms and weathering. *Antiquity* 31: 219–233.

Avel, M. 1959. Classe des Annélides, Oligochètes. *In: Grasse, P.P. (ed.)*. Paris: *Traité de Zool.* 5(1): 224–470.

Babiker, M.S. 2012. Chemical composition of some non-conventionnal and local feed resources for poultry in Sudan. *Int. J. Poultry Sci.* 11(4): 283–287.

Backland, H.O. 1949. Oligochaeta. I. Lumbricidae. *Zool. Iceland* II(20): 1–15.

- Bahl, K.N. 1947. Excretion in Oligochaeta. *Biol. Rev.* 22: 109–147.
- Baird, W. 1869. Description of a new species of earthworm (*Megascolex diffringens*) found in north Wales. *Proc. Biol. Soc. London*, 1869: 40–43. [*Amyntas diffringens* n. sp.]
- Ball, R.C. and L.L. Curry. 1956. Culture and agricultural importance of earthworms. *Michigan St. Univ. Agric. Exp. Stn., Circ. Bull.* 222: 27 pp.
- Bartlett M.D., J.A. Harris, I.T. James and K. Ritz. 2006. Inefficiency of mustard extraction technique for assessing size and structure of earthworm communities in UK pasture. *Soil Biol. Biochem.* 38: 2990–2992.
- Bartlett, M.D., M.J.I. Briones, R. Neilson, O. Schmidt, D. Spurgeon and R.E. Creamer. 2010. A critical review of current methods in earthworm ecology: From individuals to populations. *European J. Soil Biol.* 46(2): 67–73.
- Bellitürk, K., J.H. Görres, J. Kunkle and R.D.S Melnichuk. 2015. Can commercial mulches be reservoirs of invasive earthworms? Promotion of ligninolytic enzyme activity and survival of *Amyntas agrestis* (Goto and Hatai, 1899). *Appl. Soil Ecol.* 87: 27–31.
- Benham, W.B. 1892. Description of three new species of earthworms. *Proc. Zool. Soc., London* 1892, pp. 136–152. [*Arctiostrotus perrier* n. sp.]
- Berkeley, C. 1968. Records of earthworms from Vancouver, British Columbia. *J. Fish. Res. Bd. Canada* 25(1): 205.
- Berman, D.I. and Y.M. Marusik. 1994. On *Bimastos parvus* (Oligochaeta: Lumbricidae) from Yukon Territory (Canada), with discussion of distribution of the earthworms in northwestern North America and northeastern Siberia. *Megadrilogica* 5(10): 113–116.
- Bessolitsyna, E.P. 2012 Ecological and geographic distribution patterns of earthworms (Oligochaeta, Lumbricidae) in landscapes of southern middle Siberia. *Russian J. Ecol.* 43: 82–85.
- Bjorkman, A.D. M.G. Criado, I.H. Myers-Smith, V. Ravolainen, I.S. Jónsdóttir, K.B. Westergaard, J.P. Lawler, M. Aronsson, B. Bennett, H. Gardfjell, S. Heiðmarsson, L. Stewart, S. Normand. 2019. Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. *Ambio* 48(1): 678–692.
- Blackwelder, R.E. 1967. *Taxonomy: a text and reference book*. New York: John Wiley & Sons, Inc., *xiv* + 698 pp.
- Blake, L.H. 1927. A comparison of the animal communities of coniferous forests and deciduous forests. *Illinois Biol. Monogr.* 10(4): 1–148.
- Blakemore, R.J. 2003. Japanese earthworms (Annelida: Oligochaeta): a review and checklist of species. *Organisms Diversity & Evolution, Electronic Suppl.* 11: 1–43.
- Blakemore, R.J. 2006. A series of searchable texts on earthworm biodiversity, ecology and systematics from various regions of the World (Vol. 2). CD-ROM publication by Ito, M.T. and N. Kaneko (*eds.*), *Soil Ecol. Res. Group, Grad. Sch. Environ. Inform. Sci. Tokiwadai: Yokohama National Univ.*
- Blakemore, R.J. 2007a. Scandinavian earthworms - A checklist of species. *In: A series of searchable texts on earthworm biodiversity, ecology and systematics from various regions of the World*, 3rd ed. Blakemore privately published.
- Blakemore, R.J. 2007b. Origin and means of dispersal of cosmopolitan *Pontodrilus litoralis* (Oligochaeta: Megascolecidae). *European J. Soil Biol.* 43: s3–s8.

- Blakemore, R.J. 2008a. Review of Southern Ocean, South Atlantic and Subantarctic earthworm species. *In*: A series of searchable texts on earthworm biodiversity, ecology and systematics from various regions of the World, 3rd ed. Blakemore privately published.
- Blakemore, R.J. 2008b. British and Irish earthworms - A checklist of species. *In*: A series of searchable texts on earthworm biodiversity, ecology and systematics from various regions of the World, 3rd ed. Blakemore privately published.
- Blakemore, R.J. 2008c. Korean earthworm species - updated checklist. *In*: A series of searchable texts on earthworms. Blakemore privately published.
- Blakemore, R.J. 2010. Cosmopolitan earthworms. 4th ed. (CD publication). Yokohama: Japan: VermEcology, 750 pp. Blakemore, R.J. 2013. The major megadrile families of the World reviewed again on their taxonomic types (Annelida: Oligochaeta: Megadrilacea). *Opusc. Zool. Budapest* 44(2): 107–127.
- Blume-Werry, G., E.J. Krab, J. Olofsson, M.K. Sundqvist, M. Väisänen and J. Klaminder. 2020. Invasive earthworms unlock arctic plant nitrogen limitation. *Nat. Commun.* 11(1766): 1–10. <https://doi.org/10.1038/s41467-020-15568-3>
- Bornebusch, C.H. 1930. The fauna of forest soil. *Forstl. Forsøgs. Danmark* 11: 1–224.
- Bottinelli, N., M. Hedde, P. Jouquet and Y. Capowiez. 2020. An explicit definition of earthworm ecological categories – Marcel Bouché's triangle revisited. *Geoderma* 372, <https://doi.org/10.1016/j.geoderma.2020.114361>.
- Bouché, M.B. 1970. Relations entre les structures et fonctionnelles des écosystèmes, illustrées par le rôle pédobiologique des vers de terre. Pp. 187–209. *In*: Pesson, P. (éd.), *La vie dans le sol. Aspects nouveaux. Études expérimentales*. Paris: Gauthiers-Villars (publ. 1971).
- Bouché, M.B. 1972. *Lombriciens de France, écologie et systématique*. *Inst. Nat. Rech. Agron.*, 671 pp.
- Bouché, M.B. 1973. Commentaires: *Lumbricus terrestris* Linnaeus, 1758. *Bull. Zool. Nomencl.* 30(2): 68.
- Bouché, M.B. 1983. The establishment of earthworm communities. *In*: Satchell, J.E. (ed.), *Earthworm ecology from Darwin to vermiculture*. London: Chapman and Hall, pp. 431–448.
- Bouché, M.B. and J.-P. Qiu. 1998. Un nouveau *Sparganophilus*, (Annelida: Oligochaeta) d'Europe, avec considérations paléogéographiques sur les Lumbricina. *Doc Pédozool. Intégrol.* 4: 178–180.
- Bretscher, K. 1899. Beitrag zur Kenntnis der Oligochaeten-Fauna der Schweiz. *Rev. Suisse Zool.* 6: 369–426.
- Bretscher, K. 1901. Beobachtungen über Oligochaeten der Schweiz. *Rev. Suisse Zool.* 9: 189–223.
- Brigham-Grette, J. and S. Petsch. 2020. The Arctic hasn't been this warm for 3 million years – and that foreshadows big changes for the rest of the planet. *The Conversation*, October 5th, 2020.
- Brinkhurst, R.O. 1986. Guide to the freshwater aquatic microdrile oligochaetes of North America. *Canadian Spec. Publ. Fish. Aquat. Sci.*, Minister of Supply and Services Canada 84: 259 pp.
- Brinkhurst, R.O. and B.G.M. Jamieson. 1971. *Aquatic Oligochaeta of the world*. Toronto: University of Toronto Press, xi + 860 pp.
- Brown, D.M. 1944. Cause of death in submerged earthworms. *J. Tennessee Acad. Sci.* 19: 147–149.

- Brown, G.G. and C. Fragoso. 2007. Listado de las especies de lombrices de tierra de América Central (Guatemala, Belice, Honduras, El Salvador, Nicaragua, Costa Rica, Panamá), las "Guyanas" (Surinam, Guyane Française, Guyana), Venezuela y Paraguay. *In*: "Minhocas na América Latina: Biodiversidade e Ecologia", Brown, G.G. and C. Fragoso. (eds.). Londrina: Embrapa Soja, pp. 421–452.
- Brown, G.G., S.W. James, A. Pasini, D.H. Nunes, N.P. Bento, P.T. Martins, and K.D. Sautter. 2006. Exotic, peregrine, and invasive earthworms in Brazil: Diversity, distribution, and effects on soils and plants. *Caribbean J. Sci.* 42(3): 339–358.
- Brunges, H.J., J.P. Dunn, D.R. Helder and S. Otieno. 2020. Effects of invasive earthworm feeding guilds and their interactions with physiographic conditions on the relative abundance and distribution of woodland salamanders. *Herp. Conserv. Biol.* 15(1):16–24.
- Buckley, T.R., S. James, J. Allwood, S. Bartlam, R. Howitt and D. Prada. 2011. Phylogenetic analysis of New Zealand earthworms (Oligochaeta: Megascolecidae) reveals ancient clades and cryptic taxonomic diversity. *Molec. Phylogenet. Evol.* 58: 85–96.
- Byron, E. 2003. The worm turns: off home turf. It's down to no good. *The Wall Street Journal* CCXLII(4): A1; A6. (July 7th issue).
- Callahan, M.A., P.F. Hendrix and R.J. Phillips. 2003. Occurrence of an exotic earthworm (*Amyntas agrestis*) in undisturbed soils of the southern Appalachian Mountains, USA. *Pedobiologia* 47: 466–470.
- Cameron, E.K., E.M Bayne and M.J. Clapperton. 2007. Human-facilitated invasion of exotic earthworms into northern boreal forests. *Écoscience* 14(4): 482–490.
- Cameron, M.L. and W.H. Fogal. 1963. The development and structure of the acrosome in the sperm of *Lumbricus terrestris* L. *Canadian J. Zool.* 41: 753–761.
- Capowiez, Y., N. Bottinelli, S. Sammartino, E. Michel and P. Jouquet. 2015. Morphological and functional characterisation of the burrow systems of six earthworm species (Lumbricidae). *Biol. Fertil. Soils* 51: 869–877.
- Carpenter, D., E. Sherlock, D.T. Jones, J. Chiminoide, T. Writer, R. Neilson, B. Boag, A.M. Keith and P. Eggleton. 2012. Mapping of earthworm distribution for the British Isles and Eire highlights the under-recording of an ecologically important group. *Biodiv. Conserv.* 21(2): 475–485.
- Causey, D. 1952. The earthworms of Arkansas. *Proc. Arkansas Acad. Sci.* 5: 31–42.
- Černosvitov, L. 1930. Studien über die Spermaresorption. I. Teil. Die Samenresorption bei den Oligochaeten. *Zool. Jb. Anat.* 52: 487–538.
- Černosvitov, L., 1938. Zur Kenntnis der Oligochaetenfauna des Balkans. VI. Oligochaeten aus Griechenland. *Zool. Anz.*, 123: 192–200.
- Černosvitov, L. and A.C. Evans. 1947. Lumbricidae. Synopses of the British fauna. 6. *Linn. Soc. London*, 36 pp.
- Chan, K.-Y. and K. Munro. 2001. Evaluating mustard extracts for earthworm sampling. *Pedobiologia* 45(3): 272–278.
- Chandebois, R. 1958. *Dendrobaena rivulicola* n. sp., nouveau lumbricide amphibie de la région méditerranéenne. *Bull. Soc. Zool. France* 83(2-3): 159–162.
- Chang, C-H., B.A. Snyder and K. Szilávecz. 2016. Asian pheretimoid earthworms in North America north of Mexico: an illustrated key to the genera *Amyntas*, *Metaphire*, *Pithemera* and *Polypheretima* (Clitellata: Megascolecidae). *Zootaxa* 4179(3): 495–529.

- Chang, C-H., M.R. Johnston, J.H. Görres, A. Dávalos, D. McHugh and K. Szilávecz. 2018. Co-invasion of three Asian earthworms, *Metaphire hilgendorfi*, *Amyntas agrestis* and *Amyntas tokioensis* in the USA. *Biol. Invasions* 20: 843–848.
- Chang, P.S.S., D.G. Cobb, J.F. Flannagan and O.E. Saether. 1992. The Oligochaetes from the 1969 Lake Winnipeg baseline survey. *Canadian Data Rep. Fish. Aquat. Sci.* 869: iv + 35 pp.
- Claus, C. 1876. *Grundzüge der Zoologie*, 3rd ed., Volume 1., Marburg and Leipzig: Aulf., 1218 pp.
- Claus, C. 1880. *Grundzüge der Zoologie*, 4th ed., Volume 1., Marburg: N.G. Elwert'sche Universität, 530 pp.
- Cognetti de Martiis, L. 1923. Sul genere *Monocystis*. *Monit. Zool. Italiano* 34: 250–253.
- Coleman, D.C., W. Zhang and S. Fu. 2017. Toward a holistic approach to soils and plant growth. Pp. 211–223. *In: Fundamentals of soil ecology*, 3rd ed. Coleman, D.C., M.A. Callahan Jr. and D.A. Crossley Jr. (eds.) London: Academic Press, viii + 369 pp.
- Csuzdi, Cs. 2012. Earthworm species, a searchable database. *Opusc. Zool. Hungaricae* 43(1): 97–99.
- Csuzdi, Cs. and A. Zicsi. 2003. Earthworms of Hungary (Annelida: Oligochaeta; Lumbricidae). *Hungarian Natural History Museum, Budapest*, 271 pp.
- Csuzdi, Cs., V.V. Pop and A.A. Pop. 2011. The earthworm fauna of the Carpathian Basin with new records and description of three new species (Oligochaeta: Lumbricidae). *Zool. Anz.* 250: 2–18.
- Darwin, C. 1881. The formation of vegetable mould through the action of worms, with observations on their habit. New York: Appleton, vii + 326 pp.
- Davies, H. 1954. A preliminary list of the earthworms of northern New Jersey with notes. *Breviora, Mus. Comp. Zool.*, no. 26, 13 pp.
- Deepshikha, V., D. Verma and M. Shweta. 2011. Earthworm resources of western himalayan region, India. *Intern. J. Soil Sci.* 6: 124–133.
- Delamare-Deboutteville, C. 1951. Microfaune du sol des pays tempérés et tropicaux. *In: Actulites scienti figures et industrielles*. Paris: Hermann et Cie 1000: 1–360.
- de Sosa, I., D.J. Díaz Cosín, Cs. Csuzdi, M.G. Paoletti and D.F. Marchán. 2019. Placing *Eophila tellinii* (Oligochaeta, Lumbricidae) in a molecular phylogenetic context advances the century-old controversy around the problematic genus. *European J. Soil Biol.* 94: <https://doi.org/10.1016/j.ejsobi.2019.103114>
- Díaz Cosín, D.J., D. Trigo and R. Mascato. 1992. Earthworms of Iberian Peninsula. Species list and some biogeographical considerations. *Soil Biol. Biochem.* 24: 1351–1356.
- Diehl, W.J. and D.L. Williams. 1992. Interactive effects of soil moisture and food on growth and aerobic metabolism in *Eisenia fetida* (Oligochaeta). *Comp. Biochem. Physiol. Part A: Physiology* 102: 179–184.
- Dindal, D.L. 1970. Feeding behavior of a terrestrial turbellarian *Bipalium adventitium*. *American Midl. Nat.* 83(2): 635–637.
- Dobson, R.M. and J.R. Lofty. 1956. Observations of the effect of BHC on the soil fauna of arable land. *Congr. Int. Sci. Sol., Paris* 3: 203–205.
- Doeksen, J. 1950. An electrical method of sampling soil for earthworms. *Trans. 4th Int. Congr. Soil Sci.*, pp. 129–131.

- Domínguez, J., M. Aira, J. Breinholt, M. Stojanović, S. James and M. Péres-Losada. 2015. Underground evolution. New roots for the old tree of lumbricid earthworms. *Molec. Phylogenet. Evol.* 83: 7–19.
- Dugès, A. 1828. Recherche sur la circulation, la respiration et la reproduction des Annélides abranches sétigères. *Ann. Sci. Nat.* 15(1): 284–336. [*Aporrectodea trapezoides* n. sp.]
- Dugès, A. 1837. Nouvelles observations sur la zoologie et l'anatomie des Annélides abranches sétigères. *Ann. Sci. Nat.* (2), Zool. 8: 15–35.
- Easton, E.G. 1983. A guide to the valid names of Lumbricidae (Oligochaeta). pp. 475–485. *In: Earthworm ecology, from Darwin to vermiculture.* Satchell, J.E. (ed.), London: Chapman and Hall, 495 pp.
- Eaton, T.H. Jr. 1942. Earthworms of the northeastern United States: a key, with distribution records. *J. Washington Acad. Sci.* 32(8): 242–249.
- Edwards, C.A. 1965. Effects of pesticide residues on soil invertebrates and plants. Oxford: 5th Symp. British Ecol. Soc. pp. 239–261.
- Edwards, C.A. 1970. Effects of herbicides on the soil fauna. *Proc. 10th Weed Control Conf.* 3: 1052–1062. Edwards, C.A. 2004. *Earthworm ecology*, 2nd ed. New York: CRC Press, 441 pp.
- Edwards, C.A. and N.Q. Arancon. 2004. The use of earthworms in the breakdown of organic wastes to produce vermicomposts and animal feed protein. pp. 345–379. *In: Earthworm ecology*, 2nd ed. Edwards, C.A. (ed.) New York: CRC Press, 441 pp.
- Edwards, C.A. and P.J. Bohlen. 1996. *The biology and ecology of earthworms* (3rd ed.). New York: Chapman and Hall, 426 pp.
- Edwards, C.A. and J.R. Lofty. 1972. *Biology of earthworms.* London: Chapman and Hall, xv + 283 pp.
- Edwards, C.A., E.B. Dennis and D.W. Empson. 1967. Pesticides and the soil fauna. I. Effects of aldrin and DDT in an arable field. *Ann. Appl. Biol.* 60: 11–22.
- Edwards, C.A., N. Arancon, P.J. Bohlen and P. Hendrix. 2013. *Biology and ecology of earthworms*, 4th ed. Berlin: Springer, xiv + 422 pp.
- Eisen, G.A. 1873. Om Skandinaviens Oligochaeter. *Öfv. Vet-Akad. Förh. Stockholm* 30(8): 43–56. [*Aporrectodea turgida* n. sp.]
- Eisen, G.A. 1874. New Englands och Canadas Lumbricider. *Öfv. Vet-Akad. Förh. Stockholm* 31(2): 41–49. [*Aporrectodea tuberculata* n. sp., *Bimastos parvus* n. sp.]
- Eisen, G.A. 1893. California earthworms of the family Eudrilidae. *Zoe* 4(3): 248–254.
- Eisenhauer, N., A. Milcu, A.C.W. Sabais, H. Bessler, A. Weigelt, C. Engels and S. Scheu. 2009. Plant community impacts on the structure of earthworm communities depend on season and change with time. *Soil Biol. Biochem.* 41: 2430–2443.
- Enckell, P.H., M. Niklasson, B. Stille and P. Douwes. 1986. Insulation and isolation: factors influencing the genetic variation in *Lumbricus rubellus* Hoffm. (Lumbricidae) in the Faroe Islands. *Hereditas* 104: 263–271.
- Ernst, D. (ed.). 1995. *The farmer's earthworm handbook - Managing your underground money-makers.* Brookfield, WI: Lessiter Publ., 112 pp.

- European Environment Agency (EEA). 2002. Environmental signals 2002. Copenhagen 2002.
- Evans, A.C. 1946. A new earthworm of the genus *Allolobophora*. Ann. Mag. Nat. Hist. (11), 13: 98–101.
- Evans, A.C. 1948. Identity of earthworms stored by moles. Proc. Zool. Soc. London 118: 1356–1359.
- Evans, A.C. and W.J.McL. Guild. 1947. Studies on the relationships between earthworms and soil fertility. I. Biological studies in the field. Ann. Appl. Biol. 34(3): 307–330.
- Evans, A.C. and W.J.McL. Guild. 1948. Studies on the relationships between earthworms and soil fertility. IV. On the life cycles of some British Lumbricidae. Ann. Appl. Biol. 35(4): 471–484.
- Ezzatpanah, S. 2010. Earthworms of the Markazi province, Iran (Annelida: Oligochaeta: Lumbricidae). Calodema 122: 1–9.
- Fabricius, O. 1780. Fauna groenlandica, Systematice sistens Animalia Groenlandiae occidentalis hactenus indagata, quad nomen specificum, triviale, vernaculumque ; synonyma auctorum plurium, descriptionem, locura, victum, generationem, mores, usum, capturamque singuli, prout detegendi occasio fuit, maximaque parte secundum proprias observationes. Hafnia (Copenhagen) et Lepsia, 432 pp.
- Fender, W.M. 1982. *Dendrobaena attemsi* in an American greenhouse, with notes on its morphology and systematic position. Megadrilogica 4(1-2): 8–11.
- Fender, W.M. 1985. Earthworms of the western United States. Part I. Lumbricidae. Megadrilogica 4(5): 93–129.
- Fender, W.M. 1995. Native earthworms of the Pacific Northwest: an ecological overview. pp. 53–60. In: Hendrix, P.F. (ed.), Ecology and biogeography of earthworms in North America. Boca Raton, FL: Lewis Publ., 244 pp.
- Fender, W.M., and D. McKey-Fender. 1990. Oligochaeta: Megascolecidae and other earthworms from western North America. pp. 357–378. In: Soil biology guide. Dindal, D.L. (ed.). New York: John Wiley and Sons, 1376 pp.
- Enckell, P.H. and S. Rundgren. 1988. Anthropochorous earthworms (Lumbricidae) as indicators of abandoned settlements in the Faroe Islands. J. Archaeol. Sci. 15(4): 439–451.
- Foerster, A. 1862. Synopsis der Familien und Gattungen der Braconen. Verh. naturh. Ver. preuss. Rheinlande und Westphalens. 19: 225–288.
- Fox, C.J.S. 1964. The effects of five herbicides on the number of certain invertebrate animals in grassland soils. Canadian J. Plant Sci. 44: 405–409.
- Fragoso, C. 2001. Las lombrices de tierra de México (Annelida, Oligochaeta): diversidad, ecología y manejo. Acta Zool. Mexicana (n.s.), Número especial 1: 131–171.
- Fragoso, C. and G.G. Brown. 2007. Ecología y taxonomía de las lombrices de tierra en latinoamérica: El Primer Encuentro Latino-Americano de Ecología y Taxonomía de Oligoquetos (ELAETAO1). pp. 33–75. In: Brown, G.G. and C. Fragoso (eds.). Minhocas na América Latina: Biodiversidade e ecologia. Londrina: Embrapa Soja, 454 pp.
- Fragoso, C. and J.W. Reynolds. 1997. On some earthworms from central and southeastern Mexican mountains, including two new species of the genus *Dichogaster* (Dichogastrini). Megadrilogica 7(2): 9–20.
- Friend, H. 1892. British Annelida. Essex Nat. 6: 30–33, 60–65, 107–111, 169–174, 185–190.

- Friend, H. 1897. Earthworm studies. IV. A check-list of British earthworms. *Zoologist* (4), 1: 453–459.
- Friend, H. 1910. New garden worms. *Gardener's Chron.* (3), 48: 98–99.
- Friend, H. 1911. The distribution of British annelids. *Zoologist* (4), 15: 143–146, 184–191, 367–374.
- Friend, H. 1921. Two new aquatic annelids. *Ann. Mag. Nat. Hist.* (9), 7: 137–141.
- Gates, G.E. 1942. Check list and bibliography of North American earthworms. *American Midl. Nat.* 27(1): 86–108.
- Gates, G.E. 1952. New species of earthworms from the Arnold Arboretum, Boston. *Breviora, Mus. Comp. Zool.*, No. 9: 1–3.
- Gates, G.E. 1953. Further notes on the earthworms of the Arnold Arboretum, Boston. *Breviora, Mus. Comp. Zool.*, Harvard 15: 1–9.
- Gates, G.E. 1954. Exotic earthworms of the United States. *Bull. Mus. Comp. Zool.*, Harvard 111(6): 119–258.
- Gates, G.E. 1958. On some species of the Oriental earthworm genus *Pheretima* Kinberg, 1867, with key to species reported from the Americas. *American Mus. Nov.*, No. 1888, 33 pp.
- Gates, G.E. 1959. On a taxonomic puzzle and the classification of the earthworms. *Bull. Mus. Comp. Zool.*, Harvard, 121: 229–261.
- Gates, G.E. 1961. Ecology of some earthworms with special reference to seasonal activity. *American Midl. Nat.* 66: 61–86.
- Gates, G.E. 1963. *Miscellanea megadrilologica*. VII. Greenhouse earthworms. *Proc. Biol. Soc. Washington* 76: 9–18.
- Gates, G.E. 1966. Requiem – for megadrile utopias. A contribution toward the understanding of the earthworm fauna of North America. *Proc. Biol. Soc. Washington* 79: 239–254.
- Gates, G.E. 1967. On the earthworm fauna of the great American desert and adjacent areas. *Great Basin Nat.* 27: 142–176.
- Gates, G.E. 1968. What is *Enterion ictericum* Savigny, 1826 (Lumbricidae, Oligochaeta)? *Bull. Soc. Linn. Normande* (10), 9: 199–208.
- Gates, G.E. 1969a. On two American genera of the earthworm family Lumbricidae. *J. Nat. Hist. London* 9: 305–307.
- Gates, G.E. 1969b. On the earthworms of Ascension and Juan Fernandez Islands. *Breviora, Mus. Comp. Zool.*, Harvard 323: 1–4.
- Gates, G.E. 1970. *Miscellanea megadrilologica* VIII. *Megadrilologica* 1(2): 1–14.
- Gates, G.E. 1972a. Burmese earthworms. An introduction to the systematics of megadrile oligochaetes with special references to southeast Asia. *Trans. American Philos. Soc. (n.s.)* 62(7): 1–326.
- Gates, G.E. 1972b. Toward a revision of the earthworm family Lumbricidae. IV. The trapezoides species group. *Bull. Tall Timbers Res. Stn.*, No. 12, 146 pp.
- Gates, G.E. 1973a. Contribution on the species name *Lumbricus terrestris*. *Bull. Zool. Nomencl.* 30(2): 34.

- Gates, G.E. 1973b. Contributions to North American earthworms (Annelida) No. 8. The earthworm genus *Octolasion* in America. Bull. Tall Timbers Res. Stn., No. 14: 29–50.
- Gates, G.E. 1973c. Contributions to a revision of the earthworm family Glossoscolecidae. I. *Pontoscolex corethrurus* (Müller, 1856). Bull. Tall Timbers Res. Stn., No. 14: 1–12.
- Gates, G.E. 1974a. On oligochaete gonads. Megadrilogica 1(9): 1–4.
- Gates, G.E. 1974b. Contributions to a revision of the family Lumbricidae. X. *Dendrobaena octaedra* (Savigny, 1826) with special references to the importance of its parthenogenetic polymorphism for the classification of earthworms. Bull. Tall Timbers Res. Stn., No. 15: 15–57.
- Gates, G.E. 1975a. Contributions to a revision of the earthworm family Lumbricidae. XII. *Enterion mammale* Savigny, 1826 and its position in the family. Megadrilogica 2(1): 1–5.
- Gates, G.E. 1975b. Contributions to a revision of the earthworm family Lumbricidae. XVII. *Allolobophora minuscula* Rosa, 1906 and *Enterion pygmaeum* Savigny, 1826. Megadrilogica 2(6): 7–8.
- Gates, G.E. 1976. On earthworm ovaries and their importance in megadrile systematics. Megadrilogica 2(12): 1–2.
- Gates, G.E. 1977a. On the correct generic name for some West Coast native earthworms, with aids for a study of the genus. Megadrilogica 3(2): 54–60.
- Gates, G.E. 1977b. Contributions to a revision of the earthworm family Lumbricidae. XX. The genus *Eiseniella* in North America. Megadrilogica 3(5): 71–79.
- Gates, G.E. 1978a. The earthworm genus *Lumbricus* in North America. Megadrilogica 3(6): 81–116. [*Murchiona* n. gen., type *Allolobophora minima* Muldal, 1952 = *Bimastos muldali* Omodeo, 1956]
- Gates, G.E. 1978b. Contributions to a revision of the earthworm family Lumbricidae. XXII. The genus *Eisenia* in North America. Megadrilogica 3(8): 131–147.
- Gates, G.E. 1979. Contributions to a revision of the earthworm family Lumbricidae. XXIII. The genus *Dendrodrilus* Omodeo, 1956, in North America. Megadrilogica 3(9): 151–162.
- Gates, G.E. 1980. Contributions to a revision of the earthworm family Lumbricidae. XXIV. The genus *Allolobophora* Eisen, 1874, in North America. Megadrilogica 3(11): 177–184.
- Gates, G.E. 1982. Farewell to North American Megadriles. Megadrilogica 4(1/2): 12–77.
- Gates, G.E., *The late* and J.W. Reynolds. 2017. Preliminary key to North American Megadriles (Annelida, Oligochaeta), based on external characters, insofar as possible. Megadrilogica 22(10): 201–219.
- Gavrilov, K. 1935. Contribution à l'étude de l'autofécondation chez les Oligochètes. Acta Zool. Stockholm 16: 111–115.
- Gavrilov, K. 1939. Sur la reproduction de *Eiseniella tetraedra* (Sav.) forma *typica*. Acta Zool. Stockholm 20(2-3): 439–464.
- Gavrilov, K. 1981. Oligochaeta. In: Hurlbert, S.H., G. Rodríguez and N. Dias dos Santos (eds.) Aquatic biota of tropical South America: Being a compilation of taxonomic bibliographies for the fauna and flora of inland waters of the tropical portion of South America, Part 2, Arthropoda: 170–190. San Diego, CA: S.H. Hurlbert, San Diego State Univ., 298 pp.
- Gerard, B. 1964. Synopses of the British fauna. No. 6. Lumbricidae (Annelida) with keys and descriptions. Linn. Soc. London, 58 pp.

- Geraskina, A.P. and N. Shevchenko. 2019. Spatial distribution of the epigeic species of earthworms *Dendrobaena octaedra* and *D. attemsi* (Oligochaeta: Lumbricidae) in the forest belt of the northwestern Caucasus. Turkish J. Zool. 43: 480–489
- Gilin, H. 1943. Ökologie und Lebengemeinschaften der Collembolen im schweizerischen Excursions-Gebiet Basels. Rev. Suisse Zool. 50: 131–224.
- Gish, C.D. and R.E. Christensen. 1973. Cadmium, nickel, lead and zinc in earthworms from roadside soil. Environ. Sci. Tech. 7: 1060–1062.
- Goff, C.C. 1952. Flood-plain animal communities. American Midl. Nat. 47(2): 478–486.
- González, G., M.F. Barberena-Arias, W. Huang and C.M. Ospina-Sánchez. 2020. Sampling methods for soil and litter fauna. Springer: Measuring Arthropod Biodiversity, pp. 495–522.
- Görres, J.H., R.D.S. Melnichuk and K. Bellitürk. 2014. Mortality pattern relative to size variation within *Amyntas agrestis* (Goto & Hatai 1899) (Oligochaeta: Megascolecidae) populations in the Champlain Valley of Vermont, USA. Megadrilogica 16(2): 9–14.
- Görres, J.H., C. Martin, M. Nouri-Alin and K. Bellitürk. 2019. Physical properties of soils altered by invasive pheretimoid earthworms: does their casting layer create thermal refuges? Soil Syst. 3(3): 52–65.
- Goto, S. and S. Hatai. 1899. New or imperfectly known species of earthworms. No. 2. Annot. Zool. Japonenses 3(1): 13–24. [*Amyntas agrestis* n. sp.]
- Graefe, U. and A. Beylich. 2011. First record of the aquatic earthworm *Sparganophilus tamesis* Benham, 1892 (Clitellata, Sparganophilidae) in Germany. Proc. 5th Int. Oligochaete Taxonomy Meeting, Beatenberg, Switzerland, Abstract no. 25.
- Graff, O. 1953. Die Regenwürmer Deutschlands. Schr. Forsch. Landwirtschaft Braunschweig-Völkenrode 7, Schaper, Germany, 81 pp.
- Graff, O. 1957. De Lumbricidis quibusdam in Lusitania habitantibus. Agron. Lusitana 19(4): 299–305.
- Grimm, F.W., R.G. Forsyth, F.W. Schueler and A. Karstad. 2009. Identifying land snails and slugs in Canada: Introduced species and native genera. Ottawa: Canadian Food Insp. Agency, iv + 168 pp.
- Guild, W.J.McL. 1951. The distribution and population density of earthworms (Lumbricidae) in Scottish pasture fields. J. Anim. Ecol. 20(1): 88–97.
- Guo, Q., J.K. Sidhu, T.M.D. Ebbels, F. Rana, D.J. Spurgeon, C. Svendsen, S.R. Stürzenbaum, P. Kille, A.J. Morgan and J.G. Bundy. 2009. Validation of metabolomics for toxic mechanism of action screening with the earthworm *Lumbricus rubellus*. Metabolomics 5(1): 72–83.
- Hale, C.M., L.E. Frelich, P.B. Reich and J. Pastor. 2008. Exotic earthworm effects on hardwood forest floor, nutrient availability and native plants: a mesocosm study. Oecologia 155: 509–518.
- Harman, W.J. 1952. A taxonomic survey of the earthworms of Lincoln Parish, Louisiana. Proc. Louisiana Acad. Sci. 15: 19–23.
- Harman, W.J. 1955. Earthworms of commercial importance and their effect on distribution. Proc. Louisiana Acad. Sci. 18: 54–57.

- Harman, W.J. 1965. Life history studies of the earthworm *Sparganophilus eiseni* in Louisiana. *SWest. Nat.* 10(1): 22–24.
- Hendrix, P.F. (ed.) 1995. Earthworm ecology and biogeography in North America. London: Lewis Publ., 244 pp.
- Hesse, E. 1909. Contribution à l'étude des monocystidées des oligochètes. *Arch. Zool. Exp. Gén.* 43: 27–301.
- Hillis, N.D. 1917. The quest of John Chapman: The story of a forgotten hero. New York: The Macmillan Co., 308 pp.
- Hilton, D.F.J. and J.W. Reynolds. 1983. The earthworm (Oligochaeta: Lumbricidae) fauna of the Cypress Hills Provincial Park, Alberta. *Megadrilogica* 4(4): 91–92.
- Hoffmeister, W. 1843. Beiträge zur Kenntnis deutscher Landanneliden. *Arch. Naturg.* 9(1): 183–198. [*Lumbricus rubellus* n. sp.]
- Hoffmeister, W. 1845. Die bis jetzt bekannten Arten aus der Familie der Regenwürmer. Als Grundlage zu einer Monographie dieser Familie. Braunschweig: Vieweg, 43 pp.
- Holler, C. Jr., J.D. Mays and M.L. Niemiller. 2020. The fauna of caves and other subterranean habitats of North Carolina. *J. Cave Karst Stud.* 82(4): 221–260.
- Howell, C.D. 1939. The response to light in the earthworm *Pheretima agrestis* Goto and Hatai, with special reference to the function of the nervous system. *J. Exp. Zool.* 81(2): 231–259.
- Huang, J., Q. Xu, Z.J. Sun, C. Wang and D.M. Zhen. 2006. Research on earthworm resources of China. Checklist and distribution. *J. China Agric. Univ.* 11(3): 9–20.
- Hunt, L.B. and R.J. Sacho. 1969. Response of robins to DDT and methoxychlor. *J. Wild. Manage.* 33: 267–272.
- ICZN. 1999. International Code on Zoological Nomenclature, 4th ed. London: Intern. Trust Zool. Nomencl., xxix + 306 pp.
- Ikeda, H., M.A. Callahan, Jr., J.J. O'Brien, B.S. Hornsby and E.S. Wenk. 2015. Can the invasive earthworm, *Amyntas agrestis*, be controlled with prescribed fire? *Soil Biol. Biochem.* 82: 21–27.
- Ikeda, H., M.A. Callahan Jr., R.P. Shefferson and E.S. Wenk. 2020. A comparison of latitudinal species diversity patterns between riverine and terrestrial earthworms from the North American temperate zone. *J. Biogeog.* 47:1373–1382.
- Jackson, A. 1931. The Oligochaeta of southwestern Australia. *J. Roy. Soc. West. Australia* 17: 71–136.
- James, S.W. 2011. Earthworms. *In: Simberloff, D. and M. Rejmánek (eds.), Encyclopaedia of biological invasions.* Berkeley: Univ. California Press, pp. 177–183.
- James, S.W. and P.F. Hendrix. 2004. Invasion of exotic earthworms into North America and other regions. pp. 85–88. *In: Earthworm ecology*, 2nd ed. Edwards, C.A. (ed.), Boca Raton: St. Lucie Press, 441 pp.
- James, S.W., D. Porco, T. Decaëns, B. Richard, R. Rougerie and C. Erséus. 2010. DNA barcoding reveals cryptic diversity in *Lumbricus terrestris* L., 1758 (Clitellata): Resurrection of *L. herculeus* (Savigny, 1826). *PLoS One* 5(12): 1–8.
- Jamieson, B.G.M. 2000. Native earthworms of Australia (Megascolecidae, Megascolecinae). Science Publishers, Inc., Enfield, NH, U.S.A. (CD ROM).

- Jamieson B.G.M. and M. Ferraguti. 2006. Non-leech Clitellata. pp. 235–392. *In*: Reproductive biology and phylogeny of Annelida. Jamieson, B.G.M., G. Rouse and F. Pleijel (eds.), Enfield, NH: Science Publishers, 698 pp.
- Jamieson B.G.M., S. Tillier, A. Tillier, J.-L. Justine, E. Ling, S. James, K. McDonald and A.F. Hugall. 2002. Phylogeny of the Megascolecidae and Crassiclitellata (Annelida, Oligochaeta): combined versus partitioned analysis using nuclear (28S) and mitochondrial (12S, 16S) rDNA. *Zoosystema* 24(4): 707–734.
- Jaenike, J. 1982. "*Eisenia foetida*" is two biological species. *Megadrilogica* 4(1-2): 6–8.
- Jänsch, S., L. Steffens, H. Höfer, F. Horak, M. Roß-Nickoll, B. Russell, A. Toschki and J. Römbke. 2013. State of knowledge of earthworm communities in German soils as a basis for biological soil quality assessment. *Soil Organisms* 85(3): 215–233.
- Johnson, G. 1865. A catalogue of the British non-parasitical worms in the collection of the British Museum. London: Taylor and Francis, 365 pp.
- Johnstone-Wallace, D.B. 1937. The influence of wild white clover on the seasonal production and chemical composition of pasture herbage and upon soil temperatures. Soil moistures and erosion control. 4th Int. Grassl. Congr. Rept. pp. 188–196.
- Jordan, G.A., J.W. Reynolds and A.J. Burnett. 1976. Computer plotting and analysis of earthworm population distribution in Prince Edward Island. *Megadrilogica* 2(10): 1–7.
- Julin, E. 1949. De svenska dagmaskarterna. *Ark. Zool.* 42A(17): 1–58.
- Kevan, D.K.McE. 1962. Soil animals. New York: Philosophical Library, 237 pp.
- Kinberg, J.G. 1867. *Annulata nova*. *Öfv. Vetensk. Akad. Förh. Stockholm* 23: 97–103, 356–357.
- King, R.A., I.P. Vaughan, J.R. Bell, D.A. Bohan and W.O.C. Symondson. 2010. Prey choice by carabid beetles feeding on an earthworm community analysed using species- and lineage-specific PCR primers. *Mol. Ecol.* 19: 1721–1732.
- Labe, Z.M., Y. Peings and G. Magnúsdóttir. 2020. Warm Arctic, cold Siberia pattern: role of full Arctic amplification versus sea ice loss alone. *Geophysical Res. Lett.*, DOI:10.1029/2020GL088583.
- Lardo, L., P. Coll, E. Le Cadre, A.M. Palese, C. Villenave, C. Xiloyannis and G. Celano. 2012. Electromagnetic induction (EMI) measurements as a proxy of earthworm presence in southern French vineyards. *Appl. Soil Ecol.* 61: 76–84.
- Lavelle, P. 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Adv. Ecol. Res.* 27: 93–132.
- Le Bayon, R.C., G. Bullinger-Weber, J.-M. Gobat and C. Guenat. 2013. Earthworm communities as indicators for evaluating floodplain restoration success. *In*: Environmental Management, Restoration and Ecological Implications, Enner Herenio Alcântara, Hauppauge, NY: Nova Science Publishers, pp. 47–68.
- Legg, D.C. 1968. Comparison of various worm-killing chemicals. *J. Sports Turf Res. Inst.* 44: 47–48.
- Lemtiri, A., G. Colinet, T. Alabi, D. Cluzeau, L. Zirbes, E. Haubruge and F. Francis. 2014. Impacts of earthworms on soil components and dynamics. A review. *Biotechnol. Argon. Soc. Environ.* 18(1): 121–133.

- Linnaeus, C. 1758. *Systema naturae per regna tris naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*, Edition decima, reformata. Tom I. Holmiae (Stockholm): Laurentii Salvii, 824 pp. [*Lumbricus terrestris* n.sp.]
- Linnaeus, C. 1767. *Systema naturae*, Edition duodecima, reformata. Tom. I, Pars II. Holmiae (Stockholm): Laurentii Salvii, 1317 pp. + Appendices. (Classis VI Vermes pp. 1069–1269)
- Lipa, J.J. 1958. Effect on earthworm and Diptera populations of BHC dust applied to soil. London: Nature 181: 863.
- Liscinsky, S. 1965. The American woodcock in Pennsylvania. Harrisburg: Pennsylvania Game Comm., 32 pp.
- Liski, J., A. Nissinen, M. Erhard and O. Taskinen. 2003. Climatic effects on litter decomposition from arctic tundra to tropical rainforest. *Global Change Biol.* 9: 575–584.
- Liu, T., X. Chen, X. Gong, I.M. Lubbers, Y. Jiang, W. Feng, X. Li, J.K. Whalen, M. Bonkowski, B.S. Griffiths, F. Hu and M. Liu. 2019. Earthworms coordinate soil Biota to improve multiple ecosystem functions. *Curr. Biol.* 29: 3420–3429.
- Ljungström, P.-O. 1970. Introduction to the study of earthworm taxonomy. *Pedobiologia* 10: 265–285.
- Ljungström, P.-O. and A.J. Reinecke. 1969. Variation in the morphology of *Microchaetus modestus* (Microchaetidae: Oligochaeta) from South Africa with notes on its biology. *Zool. Anz.* 182: 216–224.
- Logier, E.B.S. 1958. The snakes of Ontario. Toronto: Univ. Toronto Press, x + 94 pp.
- Lubbers, I.M., K.J. Van Groenigen, S.J. Fonte, and J. Six. 2013. Greenhouse gas emissions from soils increased by earthworms. *Nat. Climate Change* 3: 87–194.
- Macnab, J.A. and D. McKey-Fender. 1947. An introduction to Oregon earthworms with additions to the Washington list. *NWest. Sci.* 21(2): 69–75.
- Magahud, J.C., S.L.P. Dalumpines, N.M. Aspe and C.C. Cabusora. 2017. Responses of paddy earthworm, *Sparganophilus* sp., to butachlor herbicide. *IAMURE Intern. J. Ecol. Conserv.* 21: 50–87.
- Mahmoud, H.M. 2007. Earthworm (*Lumbricus terrestris*) as indicator of heavy metals in soils. *Online J. Vet. Res.* 11(2): 23–37.
- Malm, A.W. 1877. Om dagmasker, Lumbricina. *Öfv. Salsk. Hortik. Förh. Göteborg* 1: 34–47.
- Makin, A.A., M.F. Miah, S.K. Yadav, M. Deb and Z.K. Khan. 2014. Ecological diversity and abundance of earthworms in Sylhet Metropolitan Area of Bangladesh. *Adv. Zool. Botany* 2(4): 63–68.
- Marshall, V.G. and W.M. Fender. 2007. Native and introduced earthworms (Oligochaeta) of British Columbia, Canada. *Megadrilogica* 11(4): 29–52.
- Mazur-Pączka, A., G. Pączka, J. Kostecka, A. Podolak and M. Garczyńska. 2020. Effectiveness of Lumbricidae extracting with an environmentally friendly method. *J. Ecol. Engineering* 21(5): 114–119.
- McAlpine, D.F. and J.W. Reynolds. 1977. Terrestrial Oligochaeta of some New Brunswick caves with remarks on their ecology. *Canadian Field-Nat.* 91(4): 360–366.
- McAlpine, D.F. and J.W. Reynolds. 2018. BiotaNB 2009-2010 earthworms (Oligochaeta: Lumbricidae) of the Jacquet River Gorge Protected Natural Area and region, New Brunswick, with additions to the province. *Megadrilogica* 23(7): 103–107.

- McAlpine, D.F. and J.W. Reynolds. 2019. Earthworms (Oligochaeta: Lumbricidae) of the Nepisiquit Protected Natural Area, New Brunswick, Canada. *Megadrilogica* 24(4): 39–49.
- McAlpine, D.F. and J.W. Reynolds. 2020. Earthworms (Oligochaeta: Lumbricidae) of the Caledonia Gorge Protected Natural Area and region, New Brunswick, with additions to the province. *Megadrilogica* 25(4): 53–60.
- McAlpine, D.F., J.W. Reynolds and F.W. Schueler. 2019. *Thamnophis sirtalis pallidulus* (Maritime Garter Snake): Diet. *Herpetological Review* 50(4): 815.
- McAlpine, D.F., J.W. Reynolds, C.R. Graves and M.C. Sollows. 2022. Earthworms (Lumbricidae and Sparganophilidae) of the Spednic Lake Protected Natural Area, New Brunswick, Canada. *Megadrilogica* 26(11): 169–184.
- McAlpine, D.F., J.W. Reynolds, T.J. Fletcher, J.L. Trecartin and D.L. Sabine. 2001. *Sparganophilus eiseni* (Oligochaeta, Sparganophilidae) in New Brunswick, an addition to the earthworm fauna of Maritime Canada. *Megadrilogica* 8(10): 53–56.
- McAlpine, D.F., S.A. Sullivan, F.J.T. McAlpine, J.H. Lewis and J.W. Reynolds. 2020. Earthworms (Lumbricidae and Sparganophilidae) of the Grand Lake Protected Natural Area, New Brunswick, Canada. *Megadrilogica* 25(6): 89–98.
- McCay, T.S., G. Brown, M.A. Callahan Jr., C.-H. Chang, A. Dávalos, A. Dobson, J.H. Görres, B.M. Herrick, S.W. James, M.R. Johnston, D. McHugh, T. Minter, J.-D. Moore, M. Nouri-Aiin, M. Nov., J. Ortiz-Pachar, R.A. Pinder, J.B. Richardson, B.S.A. Snyder and K. Szlávecz. 2020. Tools for monitoring and study of peregrine pheretid earthworms (Megascolecidae). *Pedobiologia – J. Soil Ecol.* 83: 1–12. [doi.org/10.1016/j.pedobi. 2020.150669]
- McKey-Fender, D. and W.M. Fender. 1982. *Arctiostratus* (gen. nov.). Part I. The identity of *Plutellus perrieri* Benham, 1892 and its distribution in relation to glacial refugia. *Megadrilogica* 4(3): 81–85. [*Arctiostratus* n. gen.]
- McKey-Fender, D., W.M. Fender and V.G. Marshall. 1994. North American earthworms native to Vancouver Island and the Olympic Peninsula. *Canadian J. Zool.* 72: 1325–1339. [*Arctiostratus fontinalis* n.sp., *Ar. vancouverensis* n.sp. and *Bimastos lawrenceae* n. sp.]
- McLeod, J.H. 1954. Note on a staphylinid (Coleoptera) predator of earthworms. *Canadian Entomol.* 86(5): 236.
- Means, H. 2011. *Johnny Appleseed: The man, the myth, the American story*. New York: Simon & Schuster, 19 pp.
- Meindinger, D. and J. Pojar (eds.). 1991. *Ecosystems of British Columbia*. Victoria: British Columbia Ministry of Forests, 330 pp.
- Michaelsen, W. 1891. Oligochaeten des Naturhistorischen Museums in Hamburg. IV. *Jb Hamb. wiss. Anst.* 8: 3–42. [*Bimastos beddardi* n. sp.]
- Michaelsen, W. 1892. Terricolen der Berliner Zoologischen Sammlung. II. *Arch. Naturg.* 58(2): 209–261. [*Amyntas hilgendorfi* n. sp.]
- Michaelsen, W. 1894. Die Regenwurm-Fauna von Florida und Georgia. *Zool. Jb. Syst, Jena* 10:177–194.
- Michaelsen, W. 1899. Beiträge zur Kenntnis der Oligochäten. *Zool. Jb., Ab. Syst., Jena* 12: 105–144.
- Michaelsen, W. 1900a. *Das Tierreich*. 10, Oligochaeta. Berlin: R. Friedländer und Sohn, xxix + 575 pp.
- Michaelsen, W. 1900b. Die Lumbriciden-Fauna Nordamerikas. *Abh. Ges., Hamburg* 16, 22 pp.

- Michaelsen, W. 1901. Neue Oligochaeten und neue Fundorte alt-bekannter. Mitt. Naturhist. Mus. Hamburg 19: 1–54. [*Dendrobaena attemsi* n. sp.]
- Michaelsen, W. 1907. Oligochaeten von Madagaskar, den Comoren und anderen Inseln des westlichen Indischen Ozeans. In: Reise in Ostafrika. Voeltzkow, V.A. (ed.), Bd. 2. Stuttgart: E. Schweizerbart, 1907: 39–50.
- Michaelsen, W. 1910. Zur Kenntnis der Lumbriciden und ihrer Verbreitung. Ann. Mus. Zool. Acad. Imp. Sci., St.-Petersburg 15: 1–74.
- Michaelsen, W. 1917. Die Lumbriciden, mit besonderer Berücksichtigung der Bisher als Familie Glossoscolecidae zusammengefassten Unterfamilien. Zool. Jb. Abt. Syst., Jena 41: 1–398.
- Michaelsen, W. 1921. Zur Stammesgeschichte und Systematik der Oligochaeten, insbesondere der Lumbriculiden. Arch. Naturg. 86(A-8): 130–141.
- Miesen, G. 2005. Live bait fishing: including doughbait and scent. Chanhassen: MN: Creative Publ. International, 127 pp.
- Mihailova, P. 1966. Dzdovni cervi Lumbricidae (Oligochaeta) v Trakija. Fauna na Trakja. Bulgarian Acad. Sci. 3: 181–200. [In Bulgarian: Lumbricidae (Oligochaeta) Earthworms in Thrace. Fauna of Thrace].
- Mischis, C.C. 2007. Catálogo de las Lombrices de tierra de la Argentina (Annelida, Oligochaeta). pp. 247–252. In: Minhocas na América Latina: Biodiversidade e ecologia. Brown, G.G. and C. Fragoso (eds.), Embrapa Soja, Londrina, 545 pp.
- Misırlioğlu, İ.M. 2018. Earthworms from Bursa Uludağ Mountain, with the first record of *Octolasion cyaneum* (Savigny, 1826) from Turkey. Zootaxa 4394(1): 141–143.
- Misırlioğlu, İ.M. and M. Stojanović. 2020. *Dendrobaena attemsi* (Michaelsen, 1902) (Clitellata, Megadrili) on the Balkan Peninsula and Anatolia: distribution and biogeographical significance. Opusc. Zool. Budapest 51(2): 123–131.
- Misırlioğlu, İ.M., M. Stojanović and R. Tsekova. 2018. Species richness of the earthworm fauna (Clitellata: Acanthodrilidae, Lumbricidae) of the Marmara Region in Turkey: Zoogeographical overview. North-Western J. Zool. 14(2): 259–264.
- Misırlioğlu, M., J.W. Reynolds, G.G. Brown, M. Stojanović, T. Trakić and J. Sekulić. 2021. An overview of the distribution of earthworm (Clitellata, Megadrili) families in the world. Biol. Invasions (in press).
- Moment, G.B. 1979. Growth, posterior regeneration and segment number in *Eisenia foetida*. Megadrilologica 3(10): 167–175.
- Moon, H.P. 1934. An investigation of the littoral region of Windermere. J. Anim. Ecol. 3: 8–28. Moore, A.R. 1923. Muscle tension and reflexes in the earthworm. J. Gen. Physiol. 5: 327–333.
- Moore, H.F. 1893. Preliminary account of a new genus of Oligochaeta. Zool. Anz. 16: 333.
- Moore, J.P. 1906. Hirudinae and Oligochaeta collected in the Great Lakes region. Bull. Bur. Fish.. 25: 153–171.
- Moore, J.-D. and J.W. Reynolds. 2003. Premières mentions de vers de terre dans deux écosystèmes forestiers de la rive nord du Saint-Laurent, Québec. Megadrilologica 9(9): 53–60
- Moore, J.-D., J.H. Görres and J.W. Reynolds. 2018. Colonization front and potential effects of forest ecosystem invasions by exotic Asian pheretimoid earthworms (*Amyntas* spp., *Metaphire* spp.) in eastern Canada. Environ. Rev. DOI: 10.1139/er-2017-0066.

- Moore, J.-D., R. Ouimet and J.W. Reynolds. 2009. Premières mentions de vers de terre dans trois écosystèmes forestiers du Bouclier canadien. *Nat. canadien* 133(1): 31–37.
- Morgan, C. 1970. Profitable earthworm farming, 12th ed. Elgin: Shields Publ., 93 pp.
- Morgan, A.J., S.R. Stürzenbaum, C. Winters, G.W. Grime, N.A. Aziz and P. Kille. 2004. Differential metallothionein expression in earthworm (*Lumbricus rubellus*) tissues. *Ecotox. Environ. Safety* 57: 11–19.
- Morrison, F.O. 1950. The toxicity of BHC to certain microorganisms. Earthworms and arthropods. *Ontario Ent. Soc. Ann. Rep.* 80: 50–57.
- Mršić, N. 1991. Monograph on earthworms (Lumbricidae) of the Balkans I, II. *Slovenska Akad. Znanosti in Umetnosti, Razred za Naravoslovne Vede, Opera, Ljubljana* 31: 1–757.
- Mršić, M. and J. Šapkarov. 1988. Revision of the genus *Allolobophora* Eisen, 1874 (emend. Pop, 1941) (Lumbricidae, Oligochaeta). *Acta Mus. Macedonia Sci. Nat.* 1(154): 1–38.
- Muldal, S. 1952. The chromosomes of the earthworms. I. The evolution of polyploidy. *Heredity* 6: 55–76.
- Müller, O.F. 1774. *Vermium terrestrium et fluviatilium seu Animalium Infusoriorum, Helminthicorum et Testaceorum non marinorum succincta Historia*. Copenhagen et Leipsik 1(2): 1–72.
- Munroe, G. 2008. Manual of on-farm vermi-composting and vermiculture. Organic Agriculture Centre Canada, v + 51 pp.
- Murchie, W.R. 1956. Survey of Michigan earthworm fauna. *Pap. Michigan Acad. Sci. Arts. Lett.* 41: 53–72.
- Muys, B. 2013. Earthworm populations of hardwood stand in northern Belgium. *Silva Gandavensis* 52: 29–55.
- Myers, R. 1969. The ABC's of the earthworm business. Elgin: Shields Publ., 60 pp.
- Novak, T. 2005. Terrestrial fauna from cavities in northern and central Slovenia, and a review of systematically ecologically investigated cavities. *Acta Carsol. Ljubljana* 34/1(10): 169–210.
- Oliver, J.H. Jr. 1962. A mite parasitic in the cocoons of earthworms. *J. Parasit.* 48(1): 120–123.
- Olson, H.W. 1928. The earthworms of Ohio, with a study of their distribution in relation to hydrogen-ion concentration, moisture and organic matter content in the soil. *Bull. Ohio Biol. Surv.* 4(2), *Bull.* 17: 47–90.
- Olson, H.W. 1936. Earthworms of Missouri. *Ohio J. Sci.* 36(2): 102–113.
- Olson, H.W. 1940. Earthworms of New York state. *American Mus. Nov.*, No. 1090, 9 pp.
- Omodeo, P. 1952. Oligochetidi della Turchia. *Annuaire. Ist. Mus. Zool. Univ. Napoli* 4(2): 1–10.
- Omodeo, P. 1952. Particolarità della Zoogeografia dei lombrichi. *Boll. Zool. Napoli* 19: 349–369.
- Omodeo, P. 1955. Cariologia dei Lumbricidae. II. Contributo. *Caryologia* 8: 137–178.
- Omodeo, P. 1956. Contributo alla revisione dei Lumbricidae. *Arch. Zool. Italiano* 41: 129–212.
- Omodeo, P. 1961. Le peuplement des îles méditerranéennes et le problème de l'insularité. *Colloques Intern. Cent. Natn. Rech. Scient.* 94: 128–133.
- Omodeo, P. 1962. Oligochètes des Alpes. I. *Mem. Mus. Civ. Sto. Verona* 10: 71–96.

- Omodeo, P. 1988. The genus *Eophila* (Lumbricidae, Oligochaeta). *Boll. Zool. Napoli* 55: 73–88.
- Omodeo, P. and G. Martinucci, 1987. Earthworms of Maghreb. *In: On earthworms*. Bonvicini Pagliani, A.M. and P. Omodeo (eds.), Selected synopsia and monographs, Mucci Modena, pp. 235–250.
- Omodeo, P., E. Rota and M. Baha. 2003. The megadrile fauna (Annelida: Oligochaeta) of Maghreb: a biogeographical and ecological characterization. *Pedobiologia* 47(5–6): 458–465.
- Örley, L. 1881a. A magyarországi Oligochaeták faunája. I. Terricolae. *Mathematikai és Természettudományok Közlemények* 16: 562–611.
- Örley, L. 1881b. Beiträge zur Lumbricinen-Fauna der Balearen. *Zool. Anz.* 4: 284–287.
- Örley, L. 1885. A palaearktikus övben élő Terrikoláknak revíziója és elterjedése. *Értekezések a Természettudományok Köréből, Magyar Akad.* 15(18): 1–34.
- Owen, J., B.A. Hedley, C. Svendsen, J. Wren, M.J. Jonker, P.K. Hankard, L.J. Lister, S.R. Stürzenbaum, A.J. Morgan, D.J. Spurgeon, M.L. Blaxter and P. Kille. 2008. Transcriptome profiling of developmental and xenobiotic responses in a keystone soil animal, the oligochaete annelid *Lumbricus rubellus*. *BMC Genomics* 9: 266.
- Paliwal, R. and J.M. Julka. 2005. Checklist of earthworms of Western Himalaya, India. *Zoo's Print J.* 20(9): 1972–1976.
- Paoletti, M.G., D. Sommaggio and S. Fusaro. 2013. Proposta di indice di qualità biologica del suolo (QBS-e) basato sui lombrichi e applicato agli agroecosistemi. *Biologia Ambientale* 27(2): 25–43.
- Pavlíček, T., Y. Hadid, T. Cohen, M. Glasstetter, S. Snir, M. Mısırlıoğlu, O. Pearlson, S. Yadav, Cs. Csuzdi and P. Král. 2014. Opening Pandora's Box: II. Segmentation and evolution of hermaphroditic annelids. Pp. 38–49. Pavlíček, T., P. Cardet, M.T. Almeida, C. Pascoal and F. Cássio (eds.): *Advances in earthworm taxonomy VI (Annelida: Oligochaeta)*. – Proc. 6th Intern. Oligochaete Taxonomy Meeting (6th IOTM), Palmeira de Faro, Portugal, 22–25 April, 2013.
- Peech, M. 1965. Exchange acidity, hydrogen-ion activity and lime requirements. *In: Black, C.A. (ed.) Methods of soil analysis. Part 2. Chemical and Microbiological Properties*. Madison, WS: no. 9: 905–932.
- Pelosi, C., S. Joimel and D. Makowski. 2013. Searching for a more sensitive earthworm species to be used in pesticide homologation tests – a meta-analysis. *Chemosphere* 90: 895–900.
- Pelosi, C., M. Bertrand, J. Thénard and C. Mougin. 2015. Earthworms in a 15 years agricultural trial. *Appl. Soil Ecol.* 88(1): 1–8.
- Pelosi, C., S. Barot, Y. Capowiez, M. Hedde and F. Vandenbuclcke. 2014. Pesticides and earthworms. A review. *Agron. Sustain. Devel.* 34: 199–228.
- Pelosi, C., C. Bertrand, G. Daniele, M. Coeurdassier, P. Benoit, S. Nelieu, F. Lafay, V. Bretagnolle, S. Gaba, E. Vulliet and C. Fritsch. 2021. Residues of currently used pesticides in soils and earthworms: A silent threat? *Agric. Ecosyst. Environ.* 305: 1–13.
- Perel, T.S. 1979. Rasprostranenie i zakonomernosti raspredelenia doždevyh červej fauny SSSR. *Nauka Moskva*, 268 pp.
- Perrier, E. 1872. Recherches pour servir à l'histoire des lombriciens terrestres. *Nouv. Arch. Mus. Hist. Nat., Paris* 8: 5–198.

- Perrier, E. 1873. Études sur un genre nouveau du lombriciens (genre *Plutellus*). Arch. Zool. Exp. Gén. 2: 245–268.
- Pickford, G.E. 1932. Oligochaeta, Part II. Discovery Reports 4: 265–290.
- Pižl, V. 2001. Earthworm succession in afforested colliery spoil heaps in the Sokolov region, Czech Republic. Restoration Ecol. 9: 359–364.
- Plisko, J.D. 1973. Lumbricidae dżdżownice (Annelida: Oligochaeta). Fauna Polski, no. 1, Warszawa, 156 pp.
- Pokhrel, P. 2016. Reproductive system of earthworm. URL: <http://www.microbiologynotes.com/reproductive-system-of-earthworm/>
- Pop, V.V. 1941. Zur Phylogenie und Systematik der Lumbriciden. Zool. Jb. Syst. 74: 487–522.
- Pop, V.V. 1947. *Allolobophora dugesi* (Rosa) var. *getica*, une nouvelle variété de Lombricidé de la Roumanie. Compt. Rend. Zool. Cluj. 8: 9.
- Pop, V.V. 1948. Lumbricidele din România. Ann. Acad. Repub. Române, Sect. Știint. Geol. Geogr. Biol. (A), 1(9): 383–507.
- Protz, A. 1895. Bericht über meine vom 11. Juni bis zum 5. Juli 1894 ausgeführte zoologische Forschungsreise im Kreise Schwetz. Schr. natur. Ges. Danzig 9: 254–268.
- Purrini, K. and V. Pižl. 1982. Studies on a new sporozoon, *Monocystis* n. sp. (Sporozoa, Gregarinida) parasitizing in the earthworms *Lumbricus rubellus* (Hoffm.) and *Nicodrilus caliginosus* (Sav.) (Annelida, Lumbricidae) [Ein neues Sporentierchen, *Monocystis* n. sp. (Sporozoa, Gregarinida). Anz. Schädlingsk. Pflanz. Umwelt. 55: 131–134.
- Qiu, J.P., and M.B. Bouché. 1998a. Le genre *Allolobophora* Eisen, 1874 (Oligochaeta: Lumbricidae), ses avatars et sa définition moderne. Institut National de la Recherche Agronomique (*ed.*). Doc. Pédozool. Intégrol. 4: 86–97.
- Qiu, J.P. and M.B. Bouché. 1998b. Un nouveau *Sparganophilus*, (Annelida: Oligochaeta) d'Europe, avec considérations paléogéographiques sur les Lumbricina. Institut National de la Recherche Agronomique (*ed.*). Doc. Pédozool. Intégrol. 4: 178–180.
- Qiu, J.P. and M.B. Bouché. 1998c. Liste classée des taxons valides de lombriciens (Oligochaeta: Lumbricoidea) après l'étude des trois cinquièmes d'entre-eux. Institut National de la Recherche Agronomique (*ed.*). Doc. Pédozool. Intégrol. 4: 181–200.
- Qiu, J.P. and M.G. Turner. 2017. Effects of non-native Asian earthworm invasion on temperate forest and prairie soils in the midwestern US. Biol. Invasions 19(1): 73–88.
- Rabe, D. L., H.H. Prince and D.L. Beaver. 1983. Feeding- site selection and foraging strategies of American woodcock. The Auk 100(3): 711–716.
- Rafinesque-Schmaltz, C.S. 1815. Analyse de la nature ou Tableau de l'univers et des corps organisés. Palerme, 1–224.
- Rajmohan, K.S., R. Chandrasekaran and S. Varjani. 2020. A review on occurrence of pesticides in environment and current technologies for their remediation and management. Indian J. Microbiol. 60: 125–138.
- Ramadan, N., S. Fawzy, A. Medhat, M. Ali and N. Ahmed. 2019. Description of a novel aseptate gregarine *Zygocystis* Stein, 1848 (Apicomplexa: Monocystinae) from earthworms (Annelida: Oligochaeta) of Egypt. Egyptian J. Exp. Biol. (Zool.) 15(2): 237–245.

- Raw, F. 1959. Estimating earthworm populations by using formalin. *Nature*, London 184: 1661–1662.
- Raw, F. and J.R. Lofty. 1959. Earthworm populations in orchards. *Rep. Rothamstead Exp. Stn.* 1958: 134–135.
- Reeves, W.K. and J.W. Reynolds. 1999. New records of cave-dwelling earthworms (Oligochaeta: Lumbricidae, Megascolecidae and Naididae) and other annelids (Aeolosomatida, Banchiobdellida and Hirudinea) in the Southeastern United States, with notes on their ecology. *Megadrilogica* 7(10): 65–71.
- Reynolds, J.W. 1972a. Earthworms (Lumbricidae) of the Haliburton Highlands, Ontario. *Megadrilogica* 1(3): 1–11.
- Reynolds, J.W. 1972b. Répartition et biomasse des lombricidés (Oligochaeta: Lumbricidae) dans trois bois de la France (Département d'Essonne). *Megadrilogica* 1(4): 1–6.
- Reynolds, J.W. 1972c. The relationship of earthworm (Oligochaeta: Acanthodrilidae and Lumbricidae) distribution and biomass in six heterogeneous woodlot sites in Tippecanoe County, Indiana. *J. Tennessee Acad. Sci.* 47(2): 63–67.
- Reynolds, J.W. 1972d. A contribution to the earthworm fauna of Montana. *Proc. Montana Acad. Sci.* 32(1): 6–13.
- Reynolds, J.W. 1973a. The earthworms of Delaware (Oligochaeta: Acanthodrilidae and Lumbricidae). *Megadrilogica* 1(5): 1–4.
- Reynolds, J.W. 1973b. Earthworm (Annelida, Oligochaeta) ecology and systematics. Pp. 95–120 *In*: Dindal, D. L. (ed.) *Proc. First Microcommunities Conf. CONF 711076*, U.S.A.E.C., Natn. Tech. Inform. Serv., U.S. Dept. Com. Springfield, VA 22151, 285 pp.
- Reynolds, J.W. 1974a. Are oligochaetes really hermaphroditic amphimictic organisms? *Biologist* 56(2): 90–99.
- Reynolds, J.W. 1974b. Checklist, distribution and key to the Lumbricidae in Tennessee. *J. Tennessee Acad. Sci.* 49(1): 16–20.
- Reynolds, J.W. 1975a. Les lombricidés (Oligochaeta) des Îles-de-la-Madeleine. *Megadrilogica* 2(3): 1–8.
- Reynolds, J.W. 1975b. Les lombricidés (Oligochaeta) de la Gaspésie, Québec. *Megadrilogica* 2(4): 4–9.
- Reynolds, J.W. 1975c. Les lombricidés (Oligochaeta) de l'Île d'Orléans, Québec. *Megadrilogica* 2(5): 8–11.
- Reynolds, J.W. 1976a. The distribution and ecology of the earthworms of Nova Scotia. *Megadrilogica* 2(8): 1–8.
- Reynolds, J.W. 1976b. Un aperçu vers de terre dans les forêts nord-américaines, leurs activités et leurs répartition. *Megadrilogica* 2(9): 1–11.
- Reynolds, J.W. 1976c. *Aporrectodea icterica* (Savigny, 1826) une espèce de vers de terre récemment découverte en Amérique du Nord. *Megadrilogica* 2(12): 3–4.
- Reynolds, J.W. 1976d. Catalogue et clé d'identification des lombricidés du Québec. *Nat. canadien* 103(1): 21–27.
- Reynolds, J.W. 1976e. A preliminary checklist and distribution of the earthworms of New Brunswick. *N.B. Nat.* 7(2): 16–17.
- Reynolds, J.W. 1977a. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. *Life Sci. Misc. Publ., Roy. Ontario Mus.*, xi + 141 pp.
- Reynolds, J.W. 1977b. Le ver québécois (*Lumbricus festivus*) envahit la Colombie-Britannique. *Canadian Field-Nat.* 91(4): 395–396.

- Reynolds, J.W. 1977c. The earthworms of Tennessee (Oligochaeta). II. Sparganophilidae, with the description of a new species. *Megadrilogica* 3(3): 61–64.
- Reynolds, J.W. 1977d. Earthworms utilized by the American woodcock. *Proc. Woodcock Symp.* 6: 161–169.
- Reynolds, J.W. 1978. The earthworms of Tennessee (Oligochaeta). IV. Megascolecidae, with notes on distribution, biology and a key to the species in the state. *Megadrilogica* 3(7): 117–129.
- Reynolds, J.W. 1980. The earthworm family Sparganophilidae (Annelida, Oligochaeta) in North America. *Megadrilogica* 3(12): 189–204.
- Reynolds, J.W. 1994a. Earthworms of the World. *Global Biodiversity* 4(1): 11–16.
- Reynolds, J.W. 1994b. The distribution of the earthworms (Oligochaeta) of Indiana: a case for the Post Quaternary Introduction Theory of megadrile migration in North America. *Megadrilogica* 5(3): 13–32.
- Reynolds, J.W. 1994c. The earthworms of Bangladesh (Oligochaeta: Megascolecidae, Moniligastridae and Octochaetidae). *Megadrilogica* 5(4): 33–44.
- Reynolds, J.W. 1995. The status of exotic earthworm systematics and biogeography in North America. Pp. 1–27 *In*: Hendrix, P.F. (ed.), *Ecology and biogeography of earthworms in North America*. Boca Raton, FL: Lewis Publ., 244 pp.
- Reynolds, J.W. 1996a. Determination of illness and death in *Lumbricus terrestris* from certain collections of OK Bait Ltd., Lindsay: Oligochaetology Laboratory, 5 pp. [privately printed, but available free on Researchgate]
- Reynolds, J.W. 1996b. On some cave earthworms (Oligochaeta: Lumbricidae) from the Isle of Man, U.K. *Megadrilogica* 6(9): 89–90.
- Reynolds, J.W. 2000a. A contribution to our knowledge of the earthworm fauna of Newfoundland and Labrador, Canada (Oligochaeta, Lumbricidae). *Megadrilogica* 8(2): 5–8.
- Reynolds, J.W. 2000b. A contribution to our knowledge of the earthworm fauna of Manitoba, Canada (Oligochaeta, Lumbricidae). *Megadrilogica* 8(3): 9–12.
- Reynolds, J.W. 2001a. The earthworms of New Brunswick (Oligochaeta: Lumbricidae). *Megadrilogica* 8(8): 37–47.
- Reynolds, J.W. 2001b. Sparganophilidae — are terrestrial oligochaetologists missing the habitat in North America! *Megadrilogica* 8(11): 84–86.
- Reynolds, J.W. 2003a. First earthworm record from Nunavut, Canada and the second from the Northwest Territories. *Megadrilogica* 9(6): 40.
- Reynolds, J.W. 2003b. A second earthworm species (Lumbricidae) from Nunavut, Canada. *Megadrilogica* 9(8): 52.
- Reynolds, J.W. 2004. More earthworm (Lumbricidae) collections from Nunavut, Canada. *Megadrilogica* 10(3): 13–14.
- Reynolds, J.W. 2007. First earthworm records from Wentworth Township, Argenteuil County, Quebec. [Premiers signalements de lombrics dans le canton de Wentworth, comté d'Argenteuil (Québec).] *Megadrilogica* 11(5): 58–62.
- Reynolds, J.W. 2008a. The earthworms (Oligochaeta, Lumbricidae) of Vermont, USA. *Megadrilogica* 12(2): 19–27.

- Reynolds, J.W. 2008b. Sparganophilidae (Annelida, Oligochaeta) distribution in North America and elsewhere, revisited. *Megadrilogica* 12(9): 125–143.
- Reynolds, J.W. 2009. Species distribution maps for Gates' Burmese earthworms and current nomenclatural usage. *Megadrilogica* 13(6): 53–83.
- Reynolds, J.W. 2010a. The earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) of Quebec, Canada, revisited. *Megadrilogica* 14(1): 1–46.
- Reynolds, J.W. 2010b. The earthworms (Oligochaeta: Lumbricidae) of Nova Scotia, revisited. *Megadrilogica* 14(6): 77–100.
- Reynolds, J.W. 2010c. The earthworms (Oligochaeta: Acanthodrilidae, Lumbricidae, Megascolecidae and Sparganophilidae) of northeastern United States, revisited. *Megadrilogica* 14(7): 101–157.
- Reynolds, J.W. 2011a. The earthworms (Oligochaeta: Acanthodrilidae, Eudrilidae, Glossoscolecidae, Komarekionidae, Lumbricidae, Lutodrilidae, Ocnodrilidae, Octochaetidae, Megascolecidae and Sparganophilidae) of southeastern United States. *Megadrilogica* 14(9–12): 175–318.
- Reynolds, J.W. 2011b. The earthworms (Oligochaeta: Lumbricidae) of Pelee Island, Ontario, Canada. *Megadrilogica* 15(3): 23–33.
- Reynolds, J.W. 2014a. A checklist by counties of earthworms (Oligochaeta: Lumbricidae, Megascolecidae and Sparganophilidae) in Ontario, Canada. *Megadrilogica* 16(10): 111–135.
- Reynolds, J.W. 2014b. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in Quebec, Canada. *Megadrilogica* 17(6): 73–103.
- Reynolds, J.W. 2014c. Earthworms (Oligochaeta: Lumbricidae) invade lawn bowling greens in the Waterloo Region of Ontario, Canada. *Megadrilogica* 16(7): 69–76.
- Reynolds, J.W. 2014d. A checklist by counties of earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) in the Canadian Maritime Provinces. *Megadrilogica* 16(11): 137–156.
- Reynolds, J.W. 2015a. A checklist of earthworms (Oligochaeta: Lumbricidae, Megascolecidae, and Sparganophilidae) in western and northern Canada. *Megadrilogica* 17(10): 141–156.
- Reynolds, J.W. 2015b. A checklist by counties of earthworms (Oligochaeta: Glossoscolecidae, Lumbricidae, Megascolecidae, Ocnodrilidae, and Octochaetidae) in Hawaii, USA. *Megadrilogica* 19(7): 115–122.
- Reynolds, J.W. 2016. Earthworms (Oligochaeta: Lumbricidae) of the Elveden Forest Center Parcs, Suffolk County, England. *Megadrilogica* 21(2): 9–20.
- Reynolds, J.W. 2017. Earthworms (Oligochaeta: Lumbricidae) of "The Broads" Norfolk and Suffolk Counties, England. *Megadrilogica* 22(8): 151–156.
- Reynolds, J.W. 2017a. The first earthworm (Oligochaeta: Lumbricidae) records from Îles aux Basques, Quebec, Canada. *Megadrilogica* 22(8): 157–159.
- Reynolds, J.W. 2017b. A summary of the status of earthworms (Annelida: Oligochaeta) in ecoregions of the United States of America. *Megadrilogica* 22(9): 161–200.
- Reynolds, J.W. 2018. First earthworm (Annelida: Oligochaeta) species' collections in Canada and the continental United States. *Megadrilogica* 23(1): 1–50.

- Reynolds, J.W. 2019. A summary of the status of earthworms (Annelida: Oligochaeta) in checklists of the United States of America and Canada. *Megadrilogica* 24(5): 51–65.
- Reynolds, J.W. 2020a. New earthworm (Oligochaeta: Lumbricidae) records from opposite ends of the Earth. *Megadrilogica* 25(9): 113–118.
- Reynolds, J.W. 2020b. Earthworms (Annelida: Oligochaeta) in Canadian ecozones. *Megadrilogica* 26(1): 1–35.
- Reynolds, J.W. 2020c. Earthworms in American Ecoregions. Mauritius: OmniScriptum Publ. Group, 430 pp.
- Reynolds, J.W. 2021. Earthworm (Annelida: Oligochaeta) parasites, parasitoids and predators: a review. *Megadrilogica* 26(4): 51–60.
- Reynolds, J.W. and M.J. Clapperton. 1996. New earthworm records for Alberta (Oligochaeta: Lumbricidae) including the description of a new Canadian species. *Megadrilogica* 6(8): 73–82. [*Aporrectodea bowcrowensis* n. sp.]
- Reynolds, J.W. and D.G. Cook. 1976. *Nomenclatura Oligochaetologica*: a catalogue of the names, descriptions and type specimens of the Oligochaeta. Fredericton: University of New Brunswick, x + 217 pp.
- Reynolds, J.W. and G.A. Damoff. 2011. More earthworms (Oligochaeta: Lumbricidae and Sparganophilidae) from Colorado, USA. *Megadrilogica* 14(8): 159–172.
- Reynolds, J.W. and A.B. Eggen. 1993a. Earthworm biology and vermi - composting I. Course Manual. Lindsay: Sir Sandford Fleming College, 72 pp.
- Reynolds, J.W. and A.B. Eggen. 1993b. Earthworm biology and vermi - composting II. Course Manual. Lindsay: Sir Sandford Fleming College, 78 pp.
- Reynolds, J.W. and C. Fragoso. 2004. The earthworms (Oligochaeta: Acanthodrilidae, Eudrilidae, Glossoscolecidae, Lumbricidae, Megascolecidae and Ocnerodrilidae) of Bermuda. *Megadrilogica* 10(4): 17–26.
- Reynolds, J.W. and C. Hänel. 2005. The earthworms (Oligochaeta: Lumbricidae) of Tristan da Cunha and Nightingale Islands, South Atlantic Ocean. *Megadrilogica* 10(7): 47–56.
- Reynolds, J.W., A.G. Jones. 2005. The earthworms (Oligochaeta: Acanthodrilidae, Glossoscolecidae, and Lumbricidae) of the Falkland Islands, South Atlantic Ocean. *Megadrilogica* 10(10): 75–86.
- Reynolds, J.W. and G.A. Jordan. 1975. A preliminary conceptual model of megadrile activity and abundance in the Haliburton Highlands. *Megadrilogica* 2(2): 1–9.
- Reynolds, J.W. and M.N. Khan. 1999. A contribution to our knowledge of the earthworm fauna of Saskatchewan, Canada. *Megadrilogica* 7(12): 81–82.
- Reynolds, J.W. and P.N. Mayville. 1994. New earthworm records from Rainy River District in north western Ontario (Oligochaeta: Lumbricidae). *Megadrilogica* 6(2): 13–16.
- Reynolds, J.W. and İ.M. Mısırlıoğlu. 2018. Preliminary key to Turkish megadriles (Annelida, Clitellata, Oligochaeta), based on external characters, insofar as possible. *Megadrilogica* 23(11): 141–160.
- Reynolds, J.W. and S.M. Moore. 1996. Note on the first earthworm record from the Northwest Territories, Canada. *Megadrilogica* 6(10): 96.
- Reynolds, J.W. and W.K. Reeves. 2019. New earthworm (Oligochaeta: Lumbricidae) records in the United States and Morocco, plus a key to Moroccan earthworms. *Megadrilogica* 24(9): 107–127.

- Reynolds, J.W. and A.J. Reinecke. 1977. A preliminary survey of the earthworms of the Kruger National Park, South Africa (Oligochaeta: Glossoscolecidae, Megascolecidae and Octochaetidae). *Wet. Bydraes, P.U. vir C.H.O. (B)*, No. 89, 19 pp.
- Reynolds, J.W. and D.W. Reynolds. 2004a. Las Grandes Carreras X–XII Mundales deombrices de tierra y experiencias adicionales de aprendizaje. *Megadrilologica* 10(4): 27–28.
- Reynolds, J.W. and D.W. Reynolds. 2004b. Nuevos registros de las grandes carreras VI–VIII mundiales de lombrices de tierra desde Nuevo León, (México). *Megadrilologica* 10(2): 6–13.
- Reynolds, J.W. and K.W. Reynolds. 1992. Les vers de terre (Oligochaeta: Lumbricidae et Sparganophilidae) sur la rive nord du Saint-Laurant (Québec). *Megadrilologica* 4(9): 145–161.
- Reynolds, J.W. and W.M. Reynolds. 1972. Earthworms in medicine. *American J. Nurs.* 72(7): 1273.
- Reynolds, J.W. and W.M. Reynolds. 1979. Earthworms in medicine. *The Vermiculture Journal* 2(1): 6–7.
- Reynolds, J.W. and M.J. Wetzel. 2004. Terrestrial Oligochaeta in North America north of Mexico. *Megadrilologica* 9(11): 71–98.
- Reynolds, J.W. and M.J. Wetzel. 2008. Terrestrial Oligochaeta (Annelida: Clitellata) in North America, including Mexico, Puerto Rico, Hawaii, and Bermuda. *Megadrilologica* 12(12): 157–208.
- Reynolds, J.W. and M.J. Wetzel. 2012. Terrestrial Oligochaeta (Annelida: Clitellata) in North America, including Mexico, Puerto Rico, Hawaii, and Bermuda. III. *Megadrilologica* 15(8): 191–211.
- Reynolds, J.W. and M.J. Wetzel. 2021. *Nomenclatura Oligochaetologica – A catalogue of names, descriptions and type specimens. Editio Secunda*. URL: <http://www.inhs.illinois.edu/people/mjwetzel/nomenoligo> (accessed: 10 March 2021).
- Reynolds, J.W., P.M. Catling and B. Kostiuk. 2020a. Earthworms (Annelida: Oligochaeta) and Leeches (Annelida: Hirudinea) of the Northwest Territories, Canada. *Megadrilologica* 25(7): 99–106.
- Reynolds, J.W., E.E.C. Clebsch and W.M. Reynolds. 1974. The earthworms of Tennessee (Oligochaeta). I. Lumbricidae. *Contributions to North American Earthworms*, No. 3, Bull. Tall Timbers Research Station, No. 17, viii + 133 pp.
- Reynolds, J.W., B. Godin and D. Horwood. 2019a. The first report of *Arctiostrotus fontinalis* (Oligochaeta: Megascolecidae) in Canada. *Megadrilologica* 24(2): 17–22.
- Reynolds, J.W., J.H. Görres and M.E. Knowles. 2015. A checklist by counties of earthworms (Oligochaeta: Acanthodrilidae, Lumbricidae and Megascolecidae) in the states of Maine, New Hampshire and Vermont, USA. *Megadrilologica* 17(9): 125–140.
- Reynolds, J.W., A.J. Hasson and D.F. McAlpine. 2015. Earthworms (Oligochaeta: Lumbricidae) of the Nepisiquit Protected Natural Area and region, New Brunswick, with additions to the Province. *Megadrilologica* 19(1): 1–10.
- Reynolds, J.W., J.M. Julka and M.N. Khan. 1995. Additional earthworm records from Bangladesh (Oligochaeta: Glossoscolecidae, Megascolecidae, Moniligastridae, Ocnodrilidae and Octochaetidae). *Megadrilologica* 6(6): 51–60.
- Reynolds, J.W., W.B. Krohn and G.A. Jordan. 1977. Earthworm populations as related to woodcock habitat usage in central Maine. *Proc. Woodcock Symp.* 6: 135–146.

- Reynolds, J.W., D.R. Linden and C.M. Hale. 2002. The earthworms of Minnesota (Oligochaeta: Acanthodrilidae, Lumbricidae and Megascolecidae). *Megadrilogica* 8(12): 85–99.
- Reynolds, J.W., E.K. Cameron, L.M. Sweeney, B. Bennett and B. Godin. 2019b. The earthworms (Oligochaeta: Lumbricidae and Megascolecidae) in the Yukon and a first record for Skagway, Alaska, USA. *Megadrilogica* 25(1): 1–17.
- Reynolds, J.W., W.K. Reeves, O.P. Olayemi, S.J. Fonte, M.M. Miller and W.S. Cranshaw. 2020b. A new look at earthworms (Oligochaeta: Lumbricidae) in Colorado, USA as hosts of the cluster fly *Pollenia rudis* F. (Diptera: Calliphoridae). *Megadrilogica* 25(8): 107–112.
- Ribaucourt, E. de. 1896. Étude de la faune lombricienne de la Suisse. *Rev. Suisse Zool.* 4: 1–110.
- Ribaucourt, E. de and A. Combault. 1906. Utilité des vers de terre en agriculture. *Rev. Gen. Agron.* 1: 374–384.
- Richardson, D.R., B.A. Snyder and P.F. Hendrix. 2009. Soil moisture and temperature tolerances and optima for a non- native earthworm species, *Amyntas agrestis* (Oligochaeta: Opisthopora: Megascolecidae). *SWest. Nat.* 8: 325–334.
- Righi, G., I. Ayres and E.R.C. Bittencourt. 1978. Oligochaeta (Annelida) do Instituto Nacional de Pesquisas da Amazônia. *Acta Amazonica* 8: 1–49. Suplemento 1. [new species described in this paper: *Areco reco* Righi, Ayres, and Bittencourt, 1978]
- Risso, A. 1810. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes. Paris: Levrault, vol. 4, vii + 439 pp. + 12 pls. (Les Lombrics, pp. 426–427).
- Rogers, D.C. and J.H. Thorp (*ed.*). 2019. Thorp and Covich's Freshwater Invertebrates, Volume 4: Keys to Palaearctic Fauna, 4th ed., Chapter 12 – Phylum Annelida, pp. 357–518. New York: Academic Press, 944 pp.
- Roots, B.I. 1956. The water relations of earthworms. II. Resistance in desiccation and immersion, and behaviour when submerged and when allowed a choice of environment. *J. Exp. Biol.* 33: 29–44.
- Rosa, D. 1882. Descrizione di due nuovi Lumbrici. *Atti Acc. Torino* 18: 169–173. Rosa, D. 1884. Lumbricidi del Piemonte. *Torino* 1884, pp. 5–54.
- Rosa, D. 1886. Note sui lombrici del Veneto. *Atti Reale Ist. Veneto Sci.* 4: 673–687.
- Rosa, D. 1891. Die exotischen Terricolen des k.k. naturhistorischen Hofmuseums. *Ann. Hofmus. Wien* 6: 399–406.
- Rosa, D. 1893. Revisione dei Lumbricidi. *Mem. Acc. Torino* (2), 43: 399–476.
- Rota, E. and C. Erséus. 1997. First record of *Dendrobaena attemsi* (Michaelsen) (Oligochaeta, Lumbricidae) in Scandinavia, with a critical review of its morphological variation, taxonomic relationships and geographical range. *Annal. Zool. Fennici* 34: 89–104.
- Rota, E. and Y. de Jong. 2015. Fauna Europaea: Annelida - Terrestrial Oligochaeta (Enchytraeidae and Megadrili), Aphanoneura and Polychaeta. *Biodiversity Data J.* 3: e5737.
- Rota, E., M. Bartoli and A. Laini. 2014. First time in Italy. Is the elusive aquatic megadrile *Sparganophilus Bemham*, 1892 (Annelida, Clitellata) accelerating its dispersal in Europe? *J. Limnol.* 73(3): 482–489.

- Rota, E., S. Martinsson, M. Bartoli, A. Beylich, U. Graefe, A. Laini, M.J. Wetzel and C. Erséus. 2016. Mitochondrial evidence supports a Nearctic origin for the spreading limicolous earthworm *Sparganophilus tamesis* Benham, 1892 (Clitellata, Sparganophilidae). *Contr. Zool.* 85(1): 113–119.
- Salmon, T.P., D.A. Whisson and R.E. Marsh. 2006. *Wildlife pest control around gardens and homes*, 2nd ed. Oakland: Univ. California Agric. Nat. Res. Publ. 21385.
- Šapkarev, J. 1975. Contribution to the knowledge the earthworms (Lumbricidae) and leeches (Hirudinea) of Kosovo, Yugoslavia. *Ann. Fac. Sci. Université de Skopje* 27: 39–54.
- Satchell, J.E. 1955. Some aspects of earthworm ecology. *In: Kevan, D.McE. (ed.)*. Soil zoology. London: Butterworths, pp. 180–203.
- Satchell, J.E. 1961. An electrical method of sampling earthworm populations. pp. 89–97. *In: Rodale, R. (ed.)* The challenge of earthworm research. Emmaus, PA: Soil and Health Foundation, 102 pp.
- Savigny, J.C. 1822. Description de l'Égypte, ou Recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française (Description of Egypt, or the collection of observations and researches which were made in Egypt during the expedition of the French Army). Paris: L'Imprimerie Impériale, Part 3, Order 3, pp. 99–128.
- Savigny, J.C. 1826. Analyses des travaux de l'Académie Royale des Sciences pendant l'année 1821, partie physique. Cuvier, M. le Baron G. (ed.) *Mém. Acad. Sci. Inst. France* 5: 176–184. [*Dendrobaena octaedra* n.sp., *Eisenia foetida* n.sp., *Eiseniella tetraedra* n. sp.]
- Schread, J.C. 1952. Habits and control of the oriental earthworm. *Connecticut Agric. Exp. Stn.* 556: 5–15.
- Schwert, D.P. 1977. The first North American record of *Aporrectodea icterica* (Savigny, 1826) (Oligochaeta, Lumbricidae), with observations on the colonization of exotic earthworm species in Canada. *Canadian J. Zool.* 55(1): 245–248. [actually the 2nd North American record]
- Segun, A.O. 1978. Monocystid gregarine parasites of Nigerian earthworms. *J. Protozool.* 25(2): 157–162. Shields, E.B. 1971. *Raising earthworms for profit*, 9th ed. Elgin: Shields Publ., 128 pp.
- Sigovini, M., E. Keppel and D. Tagliapietra. 2016. Open Nomenclature in the biodiversity era. *Methods in Ecology and Evolution* 7: 1217–1225.
- Silverman, R. 2012. *The core of Johnny Appleseed: The unknown story of a spiritual trailblazer*. Pennsylvania: Swedenborg Foundation Press, 73 pp.
- Sims, R.W. 1973. *Lumbricus terrestris* Linnaeus, 1758 (Annelida, Oligochaeta): designation of a neotype in accordance with accustomed usage. Problems arising from the misidentification of the species by Savigny (1822 and 1826) *Bull. Zool. Nomencl.* 30(1): 27–33.
- Sims, R.W. 1980. A classifications and the distribution of earthworms, suborder Lumbricina (Haplotaxida: Oligochaeta). *Bull. British Mus. Nat. Hist. (Zool.)* 39(2): 103–124.
- Sims, R.W. and E.G. Easton. 1972. A numerical revision of the earthworm genus *Pheretima* auct. (Megascolecidae: Oligochaeta) with the recognition of new genera and an appendix on the earthworms collected by the Royal Society North Borneo Expedition. *Biol. J. Linn. Soc.* 4(3): 169–268.
- Sims, R.W. and B.M. Gerrard. 1999. *Earthworms: keys and notes for the identification and study of the species*, rev. ed. *Synopses of the British fauna (New series)*, Shrewsbury: Field Studies Council, viii + 169 pp.
- Singh, J, S. Singh and A.P. Vig. 2015. Extraction of earthworm from soil by different sampling methods: a review. *Environ. Dev. Sustain.* DOI 10.1007/s10668-015-9703-5

- Singh, J., M. Schädler, W. Demetrio, G.G. Brown and N. Eisenhauer. 2019. Climate change effects on earthworms—a review. *Soil Organisms* 91(3): 113–137.
- Singh, S., J. Singh, A.P. Vig, F. Verma, and S. Suthar. 2020. Earthworm communities and soil structural properties. Pp. 333–350. *In: Bhat S., A.P. Vig, F. Li and B. Ravindran (eds.) Earthworm assisted remediation of effluents and wastes.* Singapore: Springer, 363 pp.
- Skoczeń, S. 1970. Gromadzenie zapasów pokarmowych przez niektóre ssaki owadożerne (Insectivora). *Przegląd Zool.* 14(2): 243–248.
- Smith, F. 1895. A preliminary account of two new Oligochaeta from Illinois. *Bull. Illinois St. Lab. Nat. Hist.* 4(5): 138–148. [*Sparganophilus eiseni* n. sp.]
- Smith, F. 1917. North American earthworm of the family Lumbricidae in the collections of the United States National Museum. *Proc. United States Natl. Mus.* 52(2174): 157–182.
- Smith, F. 1937. North American species of earthworms of the family Megascolecidae. *Proc. United States Natl. Mus.* 84(3009): 157–181. [*Toutellus oregonensis* n.sp]
- Smith, F. and E.M. Gittins. 1915. Two new species of Lumbricidae from Illinois. *Bull. Illinois St. Lab. Nat. Hist.* 10(7): 545–550.
- Smith, F. and B.R. Green. 1916. The Porifera, Oligochaeta, and certain other groups of invertebrates in the vicinity of Douglas Lake, Michigan. *Michigan Acad. Sci., Ann. Rept.* 17: 81–84.
- Smith, W.W. 1887. Notes on New Zealand earthworms. *Trans. New Zealand Inst.* 19: 122–139.
- Smith, W.W. 1894. Further notes on New Zealand earthworms. *Trans. New Zealand Inst.* 26: 155–175.
- Snyder, B.A., M.A. Callaham Jr. and P.F. Hendrix. 2011. Spatial variability of an invasive earthworm (*Amyntas agrestis*) population and potential impacts on soil characteristics and millipedes in the Great Smoky Mountains National Park, USA. *Biol. Invasions* 13: 349–358.
- Snyder, B.A., M.A. Callaham Jr., C.N. Lowe and P.F. Hendrix. 2013. Earthworm invasion in North America: Food resource competition affects native millipede survival and invasive earthworm reproduction. *Soil Biol. Biochem.* 57: 212–216.
- Spiers, G.A., D. Gagnon, G.E. Nason, E.C., Packee and J.D. Lousier. 1986. Effects and importance of indigenous earthworms on decomposition and nutrient cycling in coastal forest ecosystems. *Canadian J. For. Res.* 16: 983–989.
- Stafford, J. 1902. Notes on worms. *Zool. Anz.* 25: 481–483.
- Starking, M.D. and G.J. Roloff. 2019. Evaluating a mustard extraction technique for sampling earthworms. *Wildlife Soc. Bull.* 43(4): 760–765.
- Stebbins, J.H. 1962. Endemic-exotic earthworm competition in the American Midwest. *Nature, London* 196(4857): 905–906.
- Steckley, J. 2020. Cash cropping worms: How the *Lumbricus terrestris* bait worm market operates in Ontario, Canada. *Geoderma* 363, 9 pp. <https://doi.org/10.1016/j.geoderma.2019.114128>
- Stephenson, J. 1930. *The Oligochaeta.* Oxford: Clarendon Press, xvi + 978 pp.

- Stone, P.C. and D.G. Ogles. 1953. *Uropoda agitans*, a mite pest in commercial fishworm beds. J. Econ. Ent. 46(4): 711.
- Stürzenbaum, S.R., P. Kille and A.J. Morgan. 1998. Identification of heavy metal induced changes in the expression patterns of the translationally controlled tumor protein (TCTP) in the earthworm *L. rubellus*. Biochim. Biophys. Acta 1398: 294–304.
- Szederjesi, T. and Cs. Csuzdi. 2016. Review of the species allocated to the genus *Satchellius* (Oligochaeta: Lumbricidae) with description of a new species. Biologia 71(2): 169–175.
- Talavera, J.A. 1987. Lombrices de tierra presentes en la laurisilva de Tenerife (Islas Canarias). Misc. Zool. 11: 93–103. Talavera, J.A. 1996. Madeira earthworm fauna. Italian J. Zool. 63(1): 81–86.
- Talavera, J.A. 2007. Gomera earthworm fauna (Canary Islands). Italian J. Zool. 74(2): 203–207.
- Talavera, J.A. 2011. New earthworm records for Macaronesia with observations on the species, ecological characteristics and colonization history. Pedobiologia 54(5–6): 301–308.
- Tandy, R.E. 1969. The earthworm genus *Pheretima* Kinberg, 1866 in Louisiana. Unpublished Ph.D. dissertation. Baton Rouge: Louisiana State University, 155 pp.
- Teale, C.L. 2007. A preliminary survey of the Oligochaeta fauna of the Yukon Territory, Canada. Megadrilologica 11(1): 3–7.
- Templeton, R. 1836. A catalogue of the species of annulose animals, and of rayed ones, found in Ireland, as selected from the papers of the late J. Templeton, Esq., of Cranmore, with localities, description and illustration. Mag. Nat. Hist. London 9: 233–240.
- Templeton, R. 1844. Description of *Megascolex caeruleus*. Proc. Zool. Soc. London 12(1844): 89–91.
- Terhivuo, J. 1988. The Finnish Lumbricidae (Oligochaeta) fauna and its formation. Ann. Zool. Fenn., 25: 229–320.
- Tétry, A. 1934. Description d'une espèce française du genre *Pelodrilus*. C.R. Acad. Sci. Paris 199: 322.
- Tétry, A. 1938. Contribution à l'étude de la faune de l'est de la France (Lorraine). Nancy: Georges Thomas, 453 pp.
- Thompson, A.R. 1971. Effects of nine insecticides on the numbers and biomass of earthworms in pastures. Bull. Environ. Contr. Toxicol. 5(6): 577–586.
- Thomson, A.J. and D.M. Davies. 1973a. The biology of *Pollenia rudis*, the cluster fly (Diptera: Calliphoridae). I. Host location by first instar larvae. Canadian Ent. 105: 335–341.
- Thomson, A.J. and D.M. Davies. 1973b. The biology of *Pollenia rudis*, the cluster fly (Diptera: Calliphoridae). II. Larval feeding behaviour and host specificity. Canadian Ent. 105: 985–990.
- Thornson, M.J. 1857–8. Archives entomologiques. Paris: Au Bureau du Trésorier de la Société entomologique de France, Tomes 1–2, 508 pp.
- Tiunov, A.V., C.M. Hale, A.R. Holdsworth and T.S. Vsevolodova-Perel. 2006. Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the western Great Lakes region of North America. Biol. Invasions 8: 1223–1234.
- Tixier, T., W.U. Blankenhorn, J. Lahr, K. Floate, A. Scheffczyk, R.-A. Düring, M. Wohde, J. Römbke, and J.-P. Lumaret. 2016. A four-country ring test of nontarget effects of Ivermectin residues on the function of coprophilous communities of arthropods in breaking down livestock dung. Environ. Toxicol. Chem. 35(8): 1953–1958.

- Tondoh, J.E. 2006. Seasonal changes in earthworm diversity and community structure in Central Côte d'Ivoire. *European J. Soil Biol.* 42: 334–340.
- Trakić, T., H. Valchovski and M. Stojanović. 2016. Endemic earthworms (Oligochaeta: Lumbricidae) of the Balkan Peninsula: a review. *Zootaxa* 4189: 251–274.
- Turbanov, I.S., D.M. Palatov and S.I. Golovatch. 2016. The state of the art of biospeleology in Russia and other countries of the former Soviet Union: a review of the cave (endogean) invertebrate fauna. 1. Introduction - Crustacea. *Ent. Rev.* 96(7): 926–963.
- Turetsky, M.R., B.W. Abbott, M.C. Jones, K.W. Anthony, D. Olefeldt, E.A.G. Schuur, C. Koven, A.D. McGuire, G. Grosse, P. Kuhry, G. Hugelius, D.M. Lawrence, C. Gibson and A.B.K. Sannel. 2019. Permafrost collapse is accelerating carbon release. *Nature* 569: 32–34.
- Tuzet, O. 1946. Sur la spermatogenèse atypique des lombriciens. *Arch. Zool. Exp. Gén.* 84: 135–168.
- Tiwari, R.K., S. Singh, R.S. Pandey and B. Sharma. 2016. Enzymes of earthworm [*sic*] as indicators of pesticide pollution in soil. *Advances in Enzyme Res.* 4: 113–124.
- Ude, H. 1885. Über die Rückenporen der Terricolen Oligochäten, nebst Beiträgen zur Histologie des Leibschlauches und zur Systematik der Lumbriciden. *Z. Wiss. Zool.* 43: 87-143. [*Aporrectodea longa* n. sp.]
- Vail, V.A. 1974. Observations on the hatchlings of *Eisenia foetida* and *Bimastos tumidus* (Oligochaeta: Lumbricidae). *Cont. North American Earthworms (Annelida)*. No. 11. *Bull. Tall Timbers Res. Stn.*, No. 16: 1–8.
- Vaillant, L. 1889. Histoire naturelle des annelés marins et d'eau douce - lombriciniens, hirudiniens, bdellomorphes, térétrulariens et planariens. *Collection des suites à Buffon*. Tome 3, partie 1. Paris: Librairie Encyclopédique de Roret, 356 pp.
- Valchovski, H.I. 2012. Checklist of earthworms (Oligochaeta: Lumbricidae) from Bulgaria - a review. *In: Global diversity of earthworms and other Oligochaeta (Annelida)*. Schmelz, R.M. (ed.). *Zootaxa* 3458: 86–102.
- Van Gansen, P. 1963. Structures et fonctions du tube digestif du Lombricien *Eisenia foetida* Savigny. *Ann. Soc. Zool. Belgique* 93: 1–120.
- van Gestel, C.A.M., J.E. Koolhaas, T. Hamers, M. van Hoppe, M. van Roover, C. Korsman and S.A. Reinecke. 2009. Effects of metal pollution on earthworm communities in a contaminated floodplain area: Linking biomarker, community and functional responses. *Environ. Pollution* 157: 895–903.
- Wall, D.H., M.A. Bradford, M.G. St. John, J.A. Trofymow, V. Behan-Pelletier, D.E. Bignell, J. M. Dangerfield, W.J. Parton, J. Rusek, W. Voigt, V. Wolters, H.Z. Gardel, F.O. Ayuke, R. Bashford, O.I. Beljakova, P.J. Bohlen, Brauman, S. Flemming, J.R. Henschel, D.L. Johnson, T.H. Jones, M. Kovarova, J.M. Kranbetter, L. Kutny, K.C. Lin, M. Maryati, D. Masse, A. Pokarzhevskii, H. Rahman, M.G. Sabará, J.-A. Salamon, M.J. Swift, A. Varela, H.L. Vasconcelos, D. White and X. Zou. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biol.* 14: 2661–2677.
- Wallwork, J.A. 1970. *Ecology of soil animals*. London: McGraw-Hill, 283 pp.
- Walton, W.R. 1933. The reaction of earthworms to alternating currents of electricity in the soil. *Proc. Ent. Soc. Washington* 35(2): 24–27.
- Waters, R.A.S. 1955. Numbers and weights of earthworms under a highly productive pastures. *New Zealand J. Sci. Tech., Sect. A, Agric. Res.* 36: 516–525.

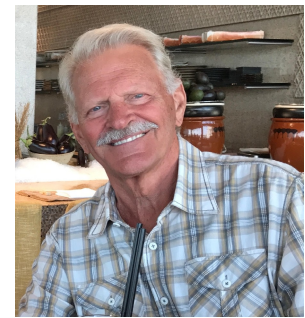
- Wollaston, T.V. 1865. *Coleoptera Atlantidum*, being an enumeration of the coleopterous insects of the Madeiras, Salvages and Canaries. London: Taylor and Francis. x + 526 pp.
- Wironen, M. and T.R. Moore. 2006. Exotic earthworm invasion increases soil carbon and nitrogen in an old-growth forest in southern Quebec. *Canadian J. For. Res.* 36: 845–854.
- Zajonc, I. 1970. Synúzie dážďoviek (Lumbricidae) na lúkach Karpatskej oblasti Československa. *Biol. Práce* 16(8): 1–99.
- Zhang, W., P.F. Hendrix, B.A. Snyder, M. Molina, J. Li, X. Rao, E. Siemann and F. Fu. 2010. Dietary flexibility aids Asian earthworm invasion in North American forests. *Ecology* 91: 2070–2079.
- Zhang, W., P.F. Hendrix, L.E. Dame, R.A. Burke, J. Wu, D.A. Neher, J. Li, Y. Shao, and S. Fu. 2013. Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nat. Comms.* 4(2576): 1–9.
- Zicsi, A. 1982. Verzeichnis der bis 1971 beschriebenen und revidierten Taxa der Familie Lumbricidae (Oligochaeta). *Acta Zool. Hungaricae* 28(3–4): 421–454.
- Zicsi, A. 2007. An annotated checklist of the earthworms of Ecuador (Oligochaeta). Earthworms from South America pp. 167–191. *In*: Brown, G.G. and C. Fragoso. (eds.) *Minhocas na América Latina: Biodiversidade e Ecologia*. Londrina: Embrapa, 545 pp.
- Zicsi, A. and Cs. Csuzdi. 2007. An annotated checklist of the earthworms of Chile (Oligochaeta). Earthworms from South America. pp. 235–252. *In*: Brown, G.G. and C. Fragoso (eds.), *Minhocas na América Latina: Biodiversidade e Ecologia*. Londrina: Embrapa Soja, 545 pp.
- Zicsi, A. and C. Vaucher. 1987. A propos de la présence de *Sparganophilus tamesis* Benham dans le lac Léman à Geneve (Oligochaeta: Sparganophilidae). *Rev. Suisse Zool.* 94: 861–864.

Acknowledgements

I am indebted to Wilma M. Reynolds of the Oligochaetology Laboratory, my longtime editor and critic for her review of the manuscript, her comments and suggestions. Special thanks to Mark J. Wetzel, formerly of the Illinois Natural History Survey, Champaign, Illinois, for editing a section of this book on a subject where he has more knowledge. I am grateful to Martin Damus (Senior Risk Assessor (entomology), Plant Health Risk Assessment Unit Canadian Food Inspection Agency/Government of Canada) for proof-reading the text and providing suggestions which greatly improved the book. Thanks to Dr. Daniel L. Dindal, formerly of the Forestry Faculty of Syracuse University who provided the drawings for the forerunner and model for this book – *The earthworms of Ontario*. I am most pleased with Jessica Hsiung, illustrator for the Entomology Department at Agriculture and Agri-food Canada (Ottawa) who has done a marvellous job of providing the drawings for the additional 14 species included in this book. Also, Julie-Anne Dorval of the Entomology Department at Agriculture and Agri-food Canada (Ottawa), Kristin Moore (Elmira), Philippe Ste-Marie (Canadian Museum of Nature, Ottawa), Dr. Donald F. McAlpine (New Brunswick Museum, Saint John), and Bruce Miller (Elmira) for photographing the missing species. I wish to thank Dr. Tim McCay of Colgate University (Hamilton, New York) and Marie R. Johnson of the University of Wisconsin Arboretum (Madison) for permission to use their drawing of the *Amyntas* life cycle. I also thank Dr. Jean-Marc Gagnon (Canadian Museum of Nature, Ottawa), Dr. Donald F. McAlpine (New Brunswick Museum, Saint John), Emma Sherlock, Ph.D. (British Museum of Natural History, London, UK), and Drs. Bill Moser and Anna J. Phillips (National Museum of Natural History–Smithsonian Institution, Washington, DC) for providing the specimens for the drawings of the additional species.

About the Author

JOHN WARREN REYNOLDS was born in Montreal, Quebec and now resides in Kitchener, Ontario. He received his biological training at Ontario Agricultural College, Guelph, and Wilmington College, Ohio (B.Sc., 1966), Purdue University, West Lafayette, Indiana (M.Sc., 1969), University of Tennessee, Knoxville (Ph.D., 1973), and earned other professional degrees from the University of New Brunswick, Fredericton (LL.B., 1981), Holland College, Charlottetown, Prince Edward Island (Dipl. Police Sci., 1982), and Fellow of the College of Freemasonry, Hamilton, Ontario (F.C.F., 2010). John has received grants and research support from the United States Department of Agriculture, the National Aeronautics and Space Administration, the United States Atomic Energy Commission, the National Institutes of Health and the National Sciences and Engineering Research Council of Canada to support his research activities. His study of earthworms was under the mentorship of the late Dr. Gordon E. Gates the Dean of American Oligochaetology. He is the author of more than 500 publications in 12 disciplines, the majority of which are in the field of oligochaetology. He has been the Editor-in-Chief of the journal, *Megadrilologica*, since its beginning in 1972. John was in charge of oligochaete research at Tall Timbers Research Station, Florida (1972–1976) and a professor in the Faculty of Forestry at the University of New Brunswick (Fredericton) from 1974–1977. From 1991 through 1996, John was the Chairman of the Resource Technology Division, School of Natural Resources of Sir Sandford Fleming College, Lindsay, Ontario. Since 1989, John has served as a member of the Annelida Subcommittee of the American Fisheries Society on Names of Aquatic Invertebrates. He was a member of the New Brunswick Bar, and served as a Barrister, Solicitor, and Notary Public (1982–1993). He has been a journal referee for papers in the following journals: *African Invertebrates*, *Animal Biodiversity and Conservation*, *Journal of Threatened Taxa*, *Journal of Biogeography*, *Acta Zoologica Academiae Scientiarum Hungaricae*, *Canadian Field Naturalist*, *Megadrilologica*, *Northeastern Naturalist*, *Southeastern Naturalist*, and *Uttar Pradesh Journal of Zoology*. John has been a visiting scientist and guest lecturer at various universities and institutions in Argentina, Bangladesh, Brazil, Canada, Dubai, Japan, South Africa, and the United States. He is regularly an external examiner for Masters theses and Doctoral dissertations in various universities around the world. For several years, he served as a Governor/Trustee for Frontier College and Sir Sandford Fleming College, as well as a mentor for the Company Program of Junior Achievement (Waterloo). Over the years, he has developed programs to excite students and members of the general community about the role of earthworms in the environment – primarily through mini lectures, and 18 Great Global Earthworm Races in Canada (6), Mexico (6), Japan (3), Dubai (1) and India (2). He is a member of the Genome Project Canada. John is the Director of the Oligochaetology Laboratory, Kitchener, Ontario, and a Research Associate at the New Brunswick Museum, Saint John, Canada since 2007.



Subject Index

Acknowledgements 172
About the author 172
Arctic earthworm migration and climate change 136
Environmental requirements and the effects of
 pesticides 3
External structures 9
Figure coding 9
General activity 2
General biology 1
General morphology 9
Glossary 13
Identification of the earthworms of Canada 25
Internal structures 10
Introduction 1
Key to sexually mature earthworms found in Canada
 26
Literature cited 139
List of figures 174
Methods of study 5
Parasites and predators 2
Plates of earthworm species 176
Preface i
Preservation techniques 7
Rearing and culturing earthworms 8
Sampling techniques 5
Scientific and common names 12
Systematic section 28

Taxonomic Index

agrestis, *Amyntas* 110
Allolobophora (Genus) 31
Amyntas (Genus) 110
Aporrectodea (Genus) 34
Arctiostrotus (Genus) 117
attemsi, *Dendrobaena* 64
beddardi, *Bimastos* 57
Bimastos (Genus) 56

bowcrowensis, *Aporrectodea* 35
castaneus, *Lumbricus* 87
chlorotica, *Allolobophora* 31
cyaneum, *Octolasion* 99
Dendrobaena (Genus) 64
Dendrodrilus (Genus) 72
Eisenia (Genus) 76
Eiseniella (Genus) 82
festivus, *Lumbricus* 89
fetida, *Eisenia* 77
fontinalis, *Arctiostrotus* 118
hilgendorfi, *Amyntas* 114
hortensis, *Eisenia* 80
icterica, *Aporrectodea* 37
lawrenceae, *Bimastos* 59
limicola, *Aporrectodea* 39
longa, *Aporrectodea* 41
Lumbricidae (Family) 29
Lumbricus (Genus) 86
lusitana, *Dendrobaena* 67
mammalis, *Satchellius* 106
Megascolecidae (Family) 109
octaedra, *Dendrobaena* 69
Octolasion (Genus) 98
oregonensis, *Toutellus* 128
parvus, *Bimastos* 62
perrieri, *Arctiostrotus* 121
rosea, *Aporrectodea* 44
rubellus, *Lumbricus* 91
rubidus, *Dendrodrilus* 73
Satchellius (Genus) 105
Sparganophilidae (Family) 131
Sparganophilus (Genus) 132
tamesis, *Sparganophilus* 134
terrestris, *Lumbricus* 94
tetraedra, *Eiseniella* 83
Toutellus (Genus) 127
trapezoides, *Aporrectodea* 47
tuberculata, *Aporrectodea* 50
turgida, *Aporrectodea* 53
tyrtaeum, *Octolasion* 102
vancouverensis, *Arctiostrotus* 124

List of Figures

- Fig. 1. The location of the earthworm ecological types (*modified from* Reynolds, 1977d). 4
- Fig. 2. Diagrammatic longitudinal section of a lumbricid earthworm showing internal organs (from Reynolds, 1977a). 11
- Fig. 3. Diagrammatic cross section of a lumbricid earthworm (from Reynolds, 1977a). 12
- Fig. 4. External longitudinal views of *Allolobophora chlorotica* showing taxonomic characters. A. Dorsolateral view. B. Ventrolateral view (from Reynolds, 1977a). 33
- Fig. 5. External longitudinal views of *Aporrectodea bowcrowensis* showing taxonomic characters. A. Lateral view. B. Ventral view. 36
- Fig. 6. External longitudinal views of *Aporrectodea icterica* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 38
- Fig. 7. External longitudinal views of *Aporrectodea limicola* showing taxonomic characters. A. Lateral view. B. Ventral view. 40
- Fig. 8. External longitudinal views of *Aporrectodea longa* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 43
- Fig. 9. External longitudinal views of *Aporrectodea rosea* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 46
- Fig. 10. External longitudinal views of *Aporrectodea trapezoides* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 49
- Fig. 11. External longitudinal views of *Aporrectodea tuberculata* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 52
- Fig. 12. External longitudinal views of *Aporrectodea turgida* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 55
- Fig. 13. External longitudinal views of *Bimastos beddardi* showing taxonomic characters. A. Dorsolateral view. B. Ventrolateral view. 58
- Fig. 14. External longitudinal views of *Bimastos lawrenceae* showing taxonomic characters. A. Lateral view. B. Ventral view. 61
- Fig. 15. External longitudinal views of *Bimastos parvus* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 63
- Fig. 16. External longitudinal views of *Dendrobaena attemsi* showing taxonomic characters. A. Lateral view. B. Ventral view. 66
- Fig. 17. External longitudinal views of *Dendrobaena lusitana* showing taxonomic characters. A. Lateral view. B. Ventral view. 68
- Fig. 18. External longitudinal views of *Dendrobaena octaedra* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 71
- Fig. 19. External longitudinal views of *Dendrodrilus rubidus* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 75
- Fig. 20. External longitudinal views of *Eisenia fetida* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 79
- Fig. 21. External longitudinal views of *Eisenia hortensis* showing taxonomic characters. A. Lateral view. B. Ventral view. 81

- Fig. 22. External longitudinal views of *Eiseniella tetraedra* showing taxonomic characters. A, Lateral View, B. Ventral view (from Reynolds, 1977a). 85
- Fig. 23. External longitudinal views of *Lumbricus castaneus* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 88
- Fig. 24. External longitudinal views of *Lumbricus festivus* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a). 90
- Fig. 25. External longitudinal views of *Lumbricus rubellus* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a). 93
- Fig. 26. External longitudinal views of *Lumbricus terrestris* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a). 97
- Fig. 27. External longitudinal views of *Octolasion cyaneum* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 101
- Fig. 28. External longitudinal views of *Octolasion tyrtaeum* showing taxonomic characters. A. Lateral view, B. Ventral view (from Reynolds, 1977a). 104
- Fig. 29. External longitudinal views of *Satchellius mammalis* showing taxonomic characters. A. Lateral view, B. Ventral view. 108
- Fig. 30. The life cycle of *Amyntas agrestis* and *A. hilgendorfi*. 112
- Fig. 31. External longitudinal views of *Amyntas agrestis* showing taxonomic characters. A. Lateral view. B. Ventral view. 113
- Fig. 32. External longitudinal views of *Amyntas hilgendorfi* showing taxonomic characters. A. Lateral view. B. Ventrolateral view. 116
- Fig. 33. External longitudinal views of *Arctiostrotus fontinalis* showing taxonomic characters. A. Lateral view. B. Ventral view. 120
- Fig. 34. External longitudinal views of *Arctiostrotus perrieri* showing taxonomic characters. A. Lateral view. B. Ventral view. 123
- Fig. 35. External longitudinal views of *Arctiostrotus vancouverensis* showing taxonomic characters. A. Lateral view. B. Ventral view. 126
- Fig. 36. External longitudinal views of *Toutellus oregonensis* showing taxonomic characters. A. Lateral view. B. Ventral view. 130
- Fig. 37. External longitudinal views of *Sparganophilus tamesis* showing taxonomic characters. A. Lateral view. B. Ventral view (from Reynolds, 1977a). 135
- Fig. 38. A conceptual model of how earthworms regulate C sequestration. 138

Colour plates of earthworm species

LUMBRICIDAE

Allolobophora chlorotica



Aporrectodea longa



Aporrectodea bowcrowensis



Aporrectodea rosea



Aporrectodea icterica



Aporrectodea turgida



Aporrectodea limicola



Bimastos beddardi



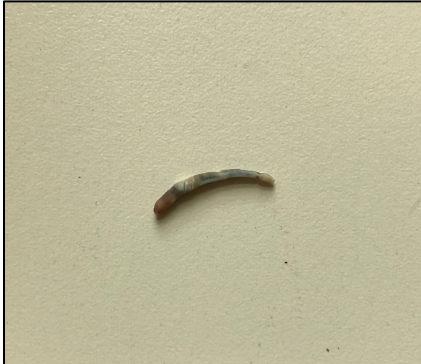
Bimastos lawrenceae



Dendrobaena octaedra



Bimastos parvus



Dendrodrilus rubidus



Dendrobaena attemsi



Eisenia fetida



Dendrobaena lusitana



Eisenia hortensis



Eiseniella tetraedra



Lumbricus terrestris



Lumbricus castaneus



Octolasion cyaneum



Lumbricus festivus



Octolasion tyrtaeum



Lumbricus rubellus



Satchellius mammalis



MEGASCOLECIDAE

Amyntas agrestis



Amyntas hilgendorfi



Arctiostrotus fontinalis



Arctiostrotus perrieri



Arctiostrotus vancouverensis



Toutellus oregonensis



SPARGANOPHILIDAE

Sparganophilus tamesis





Kluane National Park and Reserve, Yukon, alpine pond, 61°09' 59.9", -139° 7' 26.9"; wet moss in soil, alpine tundra meadow in depression 10 July 2019, John W. Reynolds and Sarah Chisholm (Park Ranger). The second site of *Arctiostrotus fontinalis* in Canada.

In a country where native earthworms are mostly inconspicuous and make up 27% of the species, the vast majority are introduced aliens from Europe (67%) or the Orient (6%). Most of the introduced European species are now ubiquitous over large areas of Canada, although six species are considered rare, and have scarcely spread from where they were introduced. Except for two species, the native earthworms are restricted to British Columbia and the Yukon.

Based on fieldwork covering more than 50 years, and the author's knowledge of the fauna, this book describes and illustrates the 33 species reported in Canada. For each species, genus and family, - synonymy, type species, diagnosis, biology, reproduction, climatic zone, ecological type, origin, range, and North American distribution are described. The book also includes an extensive literature section, illustrated glossary and a key to the 33 species.

