Title: Two distinct ecological behaviours within anecic earthworm species in temperate climates

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Abstract

Earthworm species in temperate climates have usually been classified into three main ecological categories according to their morpho-anatomical, physiological and ecological traits: epigeic, endogeic and anecic. However, since these ecological categories were first defined, many studies on the ecological traits of widespread anecic species: *Lumbricus centralis* (Bouché, 1972), *Lumbricus terrestris* (Linnaeus, 1758), *Aporrectodea longa longa* (Ude, 1885) and *Aporrectodea giardi* (Ribaucourt, 1901) have revealed two distinct feeding behaviours, as well as differences in their growth rates and burrowing behaviour. In this review we highlight that within anecic earthworms, *Lumbricus* anecic species (here after "LAS") mainly consume fresh plant-derived materials on the soil surface modifying the quantity and spatial organisation of said materials. In contrast, *Aporrectodea* anecic species (here after "AAS") consume mainly aged plant-derived materials already incorporated into the soil and only a small proportion of surface-available plant-derived materials. Furthermore, the AAS have a denser and more complex burrow network than LAS. This suggests that AAS burrow into the soil to search for soil organic matter incorporated in the soil whereas the LAS essentially focus on burying the surface litter into their burrow. Consequently, LAS seem to benefit from easily assimilated substrates, grow faster and reach maturity in a shorter time span than AAS species. This distinction between anecic *Lumbricus* and *Aporrectodea* earthworms is expected to have different consequences for soil trophic network and soil functioning such as carbon and nutrient cyclings, water regulation and soil structure maintenance.

Keywords

Burrow; feeding guild; growth; plant-derived material; soil organic matter

1. Introduction

During the last half century, earthworm species in temperate climates have usually been classified into three main ecological categories (i.e. epigeic, anecic and endogeic; [1]) given their general distinct contribution to soil processes [2–4]. However, these studies highlighted that, within ecological categories, species contribution to soil processes is highly heterogeneous, underlining that the ecological categories are not sufficient to assess the functional role of earthworms [5].

Earthworm species were first qualitatively categorized into ecological categories using morpho-anatomical, physiological and ecological traits by Bouché [1,6]. Bottinelli et al. [7] quantitatively revised these ecological categories, but did not include ecological traits explicitly in consideration of the anecic group, although several reports are available on the ecological traits of anecic species [8–11]. Usually, it is assumed that anecic earthworms feed on surface plant litter, and bury this material into their vertical or near vertical burrows [12–14] to accelerate the decomposition processes performed by soil microorganisms [15,16]. The plant litter ingested and digested during gut transit is assimilated by anecic earthworms, allocated to maintenance, growth and reproduction [17,18]. However, under a temperate climate, two widespread eartworms genera are classified within the anecic ecological categories *Lumbricus* and *Aporrectodea* anecic species (hereafter "LAS" and "AAS" respectively) and have been grouped together until now [1,7]. A large body of evidence supports the idea that these two anecic genera have distinct ecological traits and should be distinguished according to their feeding and burrowing behaviours, as well as growth rate [19,10,20].

Here, we present a comprehensive review of the scientific literature and synthesize the relationships between anecic earthworms and plant-derived materials in temperate climates, focusing on the distinctions between *Lumbricus centralis* (Bouché, 1972), *Lumbricus terrestris*

(Linnaeus, 1758), *Aporrectodea longa longa* (Ude, 1885) and *Aporrectodea giardi* (Ribaucourt, 1901), four of the most widespread and studied anecic species. We focus on their feeding behaviour and possible consequences on their growth rates and burrowing behaviour, given the relevant relationships between these traits [18,9,13].

2. Procedure

A literature review of the feeding behaviour (location and age preference of plant-derived materials consumed), growth rate and burrowing behaviour (shape of the burrow network) of four anecic species (*L. centralis, L. terrestris, A. longa longa* and *A. giardi*) used the ISI-Web of Science research database. These anecic species are widespread [1,21] where many studies refer to *L. centralis* [22–24], *L. terrestris* [23,25,26], *A. longa* [25–27] and *A. giardi* [22,25,28,29] and were recorded in agricultural, natural and urban fields, although it is not possible yet to distinguish preferences of one or another for a specific land use. In addition, we selected these anecic species due to their morphological and anatomical similarity within LAS (between *L. centralis* and *L. terrestris*) and within AAS (between *A. longa* and *A. giardi*) [1]. The following combinations of keywords were used in Topics: ((“lumbricus centralis” OR “lumbricus terrestris” OR “aporrectodea longa” OR “aporrectodea giardi”) AND (feed* OR plant* OR organic matter* OR mass* OR weight* OR growth* OR burrow* OR gallery*)) which returned 1272 publications. After carefully checking all generated results, 102 references published between 1963 and 2022 were selected (Supplementary material 1). To complete the review, peer-reviewed publications in the references of the selected publications were also studied when they fitted our selection criteria.

3. *Lumbricus* anecic species consume more surface plant litter than *Aporrectodea* anecic species

Both LAS and AAS ingest either living or dead plant-derived materials, microorganisms and mineral soil (Table 1). Nevertheless, several qualitative and quantitative differences exist between the two anecic genera *Lumbricus* and *Aporrectodea* and are summarized below.

Under controlled conditions, *L. centralis* and *L. terrestris* contributed significantly to surface litter mass loss, at rates varying from 2.4 [30] to 84 mg g^{-1} day^{-1} [31]. In line with these results, several studies observed that the digestive tract of *L. terrestris* contained high amounts of plant-derived materials, ranging from 39 % [32] to 80 % [33,34] of the total gut content. The well recognized enrichment of *L. terrestris* casts in C content compared with surrounding soil is due to the presence of plant-derived materials [35,36,19,37,38] which is not observed in the absence of such materials on the soil surface [39–43]. Additionally, few authors have observed that *L. terrestris* and *L. centralis* only consume plant-derived materials located on the soil surface and not when buried in the soil profile [44,45]. Indirectly, this was also observed in other studies in which the growth of *L. terrestris* was likely limited by the absence of surface litter [46,47,41,48,49]. The soil surface feeding behaviour of LAS could hamper their feeding when litter is buried through arable ploughing or soil engineering in artificial soils. In sum, these observations indicate that LAS seem to be sapro-geophagous, consuming preferentially plant-derived materials on the soil surface.

The few studies that focused on *A. longa longa* and *A. giardi*, quantified rates of surface litter mass loss under controlled conditions varying from 0.0 mg g^{-1} day^{-1} [10,20,28,50] to 57 mg g^{-1} day^{-1} [51]. It has thus been observed that even when litter was available on the soil surface, AAS did not feed upon it [10,20,28,50]. Moreover, studies that involved both *Lumbricus* and *Aporrectodea* consistently showed that LAS consumed more plant-derived materials than AAS [52,10,20,50]. This suggests that AAS species either have a lower metabolism compared to LAS or that there are other food sources, besides plant-derived surface material suitable for these species, most likely native and incorporated soil organic matter. In line with the latter, the digestive tract of *A. longa longa* showed a lower content of plant-derived material compared with *L. terrestris* [8], by as much as 38% [32]. The effect on C-litter enrichment in casts of AAS was either not observed or was lower than for LAS [36,19]. The C content in the casts of *Aporrectodea* does not seem to depend on the presence of litter at the soil surface. Alekseeva et al. [53] observed that when no litter was provided on the soil surface, the C content of *A. giardi* casts was still higher than the bulk soil (5.3% for *A. giardi* casts, 3.8 % for soil at 0-20 cm and 1.2% for soil at 40-60 cm). Similarly, Jégou et al. [9] observed that, compared with the surrounding soil, casts of *A. giardi* were not significantly enriched in C when litter was available on the soil surface. Thus, AAS seem to be geo-saprophagous, consuming a high proportion of plant-derived materials already incorporated into the soil with a slight proportion of plant-derived materials from the soil surface.

4. Fresh *vs.* aged plant-derived materials: two distinct food resources for *Lumbricus* and *Aporrectodea* anecic species

Plant-derived materials within the digestive tract of *L. terrestris* consisted of 50% [32,33] to 65% [8] of fresh (i.e. still recognizable) plant litter or roots. Martin et al. [54], using isotopic markers, also observed that the C assimilated by *L. terrestris* originates in fresh fractions of plant-derived materials, with a turnover time in soil of a few years. This observation was also confirmed for *L. centralis* [56]. Moreover, using isotopic markers, the source of C and nitrogen (N) in the casts of *L. terrestris* was found to originate from fresh plant-derived materials [9,57]. Thus, LAS seem to mainly consume fresh plant-derived materials on the soil surface and thus contribute to the burial of organic matter from the surface into the soil profile. Consequently, LAS are highly involved in modifying the quantity and spatial organisation of plant-derived material once deposited on the soil surface [58,14,59]. Interestingly, among anecic species, only *Lumbricus* species were observed to select or consume living plants [6,60,61,48], but the authors did not quantify the importance of these observations, which suggests that it represented a minor part of their diet.

Aged, plant-derived materials are common in the digestive tract of *A. longa longa*, i.e., vegetal matter that is no longer recognisable as a particular plant organ or tissue [8,34]. Accordingly, Larsen et al. [16] observed that *A. longa longa* fed preferentially on aged soil C sources with an assimilated C of between five and seven years old [62] which supported findings of previous studies performed on *A. giardi* [28,63,64]. Moreover, Cortez et al. [28], using isotopic markers, observed that C and N in the casts of *A. giardi* originated mainly from incorporated soil organic matter and little from the litter provided on the soil surface. Andriuzzi et al. [56], using isotopic markers, observed that *A. longa longa* incorporated less fresh C into its burrows than *L. centralis*. Several studies with isotopic markers [65–68,62,16] have shown that the resource spectrum of AAS is located between those of endogeic species (e.g., *Allolobophora chlorotica*, *Aporrectodea caliginosa* and *Allolobophora rosea*) and LAS species, while the resource spectrum of LAS seems to be more restricted. Overall, AAS consume a high proportion of aged plant-derived materials requiring a fairly advanced state of decomposition.

Since fresh plant-derived materials are richer in C and N than aged plant-derived material from the soil, it can be assumed that the C and N contents in the casts of LAS are likely to be higher than those of AAS. This was confirmed by Jégou et al. [9,19] who observed that the C and N enrichment in the casts compared with the bulk/surrounding soil was higher for *L. terrestris* than for *A. giardi*. Similarly, Vos et al. [69] observed that the dissolved C content in the casts of *L. terrestris* was higher than in those produced by *A.giardi*, however, the total C content in the casts of *L. terrestris* and *A. longa longa* were similar. Thus, we speculate that the aged C content in the casts of AAS is deeply incorporated and not easily available for organic matter decomposition by soil microorganisms.

5. Faster growth of *Lumbricus* anecic species compared to *Aporrectodea* anecic species

Lumbricus anecic species, by preferentially feeding on fresh plant-derived materials, can therefore benefit from easily assimilated nutrients compared with AAS that prefer to feed on aged plant-derived materials. These distinctive feeding behaviours lead us to speculate that growth rate or time to maturity (days to reach full clitellum development) are respectively slower and longer for AAS than for LAS. This was confirmed by several studies under controlled conditions [70,71], and, for example, Lowe and Butt [72] observed that the growth rate of *L. terrestris* was 2.2 times faster than that of *A. longa longa* (0.15 and 0.07 g worm^{-1} week^{-1}, respectively), and Butt [73] observed that the time to maturity was longer for *A. longa longa* than for *L. terrestris* under identical conditions (4 and 3 months, respectively).

6. Denser and more complex burrow networks for *Aporrectodea* anecic species

Although their burrow networks are more or less vertical, *L. terrestris* normally has one to two main galleries, with very little branchings, whereas the burrow networks of *A. longa longa* and *A. giardi* are much denser, and tortuous with branched burrows [74–76,19,12,77,78,13,79]. As an illustration, under controlled conditions, Bastardie et al. [12] observed that the total length of the burrow network of *A. giardi* was 3.2 times greater than that of *L. terrestris* (52 and 168 cm, respectively). Accordingly, Briones and Álvarez-Otero [80] observed a thicker tegument in *A. longa longa* than in *L. terrestris*, suggesting a better resistance to abrasion for AAS and consequently a higher burrowing behaviour. In the light of this review, these results may suggest that AAS burrow into the soil searching for native and aged soil organic matter, whereas LAS essentially focus on burying the surface litter in their burrow. Interestingly, it is well known that *L. centralis* and *L. terrestris* form middens at the entrance of their burrows [81,14] which are a surface structure made up of a mix of soil, casts, mucus and buried plant-derived materials but this has never been reported for *A. longa longa* and *A. giardi*. In addition, the permanent burrow systems of *L. centralis* and *L. terrestris* lead to a high and constant enrichment of the entire burrow network by fresh plant-derived materials, whereas the denser system of burrows developed by *A. longa longa* and *A. giardi* result in C-litter dilution in the complex and numerous structures formed [36,82,57,83,56].

7. Knowledge gaps

Differences in feeding behaviour between AAS and LAS could be supported by further studies focussing on morpho-anatomical, histological and physiological traits [1,7]. For example, in the digestive tract, the typhlosole (dorsal involution of the intestine wall) increases the epithelial area without increasing the gut volume [84,85]. Thus the shape of typhlosole could indicate the efficiency to absorb nutrients, with a more complex shaped typhlosole increasing the ability to absorb nutrients [86,87]. Thus, it could be speculated that the typhlosole of AAS is much more developed than that of LAS. Unfortunately, the shape of thyphlosole within anecic earthworms is poorly described, and if so, not often quantitatively [1,26]. Gates [21] observed that the typhlosole of *A. longa longa* is much more developed, complex and with more branches than that of *L. terrestris*, but this remains to be quantified. Another example of some anatomical differences between the two anecic genera demonstrated by Bolton [88] is that *L. terrestris* have very active calciferous glands, while those of *A. longa longa* are very poorly developed. Piearce [89] formulated several hypotheses to explain this differentiation of calciferous glands between both genera, such as the neutralization of dietary acids, the fixation of respiratory carbon dioxide or the excretion of excess calcium in the diet. Although it remains speculative, these anatomical differences could be interpreted as an adaptation to a distinct feeding behaviour. Thereafter, if differences in feeding behaviour and consequences on growth or burrowing behaviour are confirmed, further studies are warranted on the consequences of soil functioning (e.g. decomposition of organic matter, primary production, water regulation...) as they are sorely lacking especially for AAS.

Finally, differences in feeding behaviour, growth rate and burrowing behaviour highlighted in this review have often been observed using the same anecic earthworm species of *Lumbricus* (i.e., *L. centralis*, *L. terrestris*) or *Aporrectodea* (i.e., *A. longa longa*, *A. giardi*) genera. Further studies with other *Lumbricus* and *Aporrectodea* species in addition to other anecic genera, such as *Scherotheca*, *Octodrilus*, *Fitzingeria*, could be useful to confirm distinct ecological behaviours within the anecics. It would allow us to investigate whether this distinction is genus-related or whether other genera of anecic earthworms may cluster together to form an ecological sub-category.

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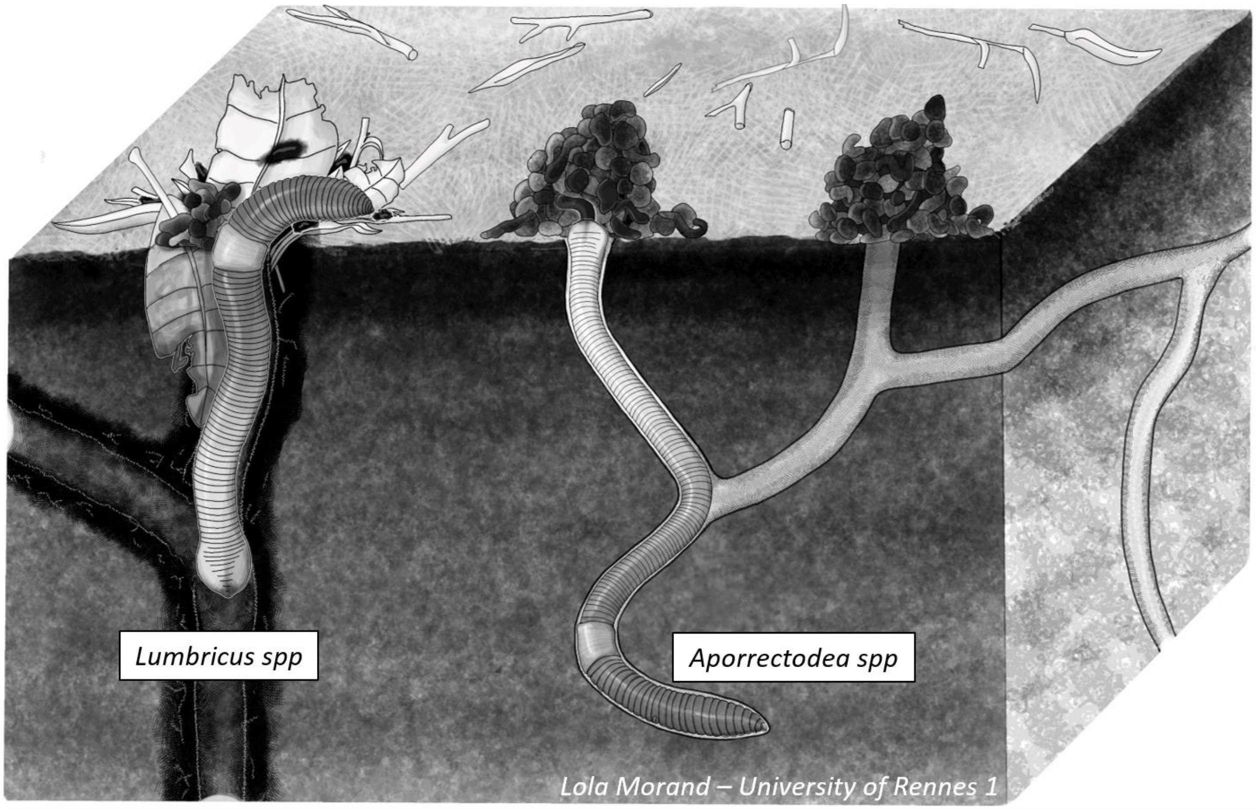
TABLE

Table 1: Resource spectrum of the selected temperate anecic earthworm species (*Lumbricus centralis*, *Lumbricus terrestris*, *Aporrectodea longa longa* and *Aporrectodea giardi*) found in this review (non-exhaustive table, useful for illustrative purposes).

Resource spectrum		***Lumbricus* anecic species**	***Aporrectodea* anecic species**
PLANTS	Shoots	**Dead:** [90,91,33,52,92,34,93,10,94,11,45,20] **Alive:** [6,60,61,48]	**Either dead or alive:** [95,52,28,92–94,11,96]
PLANTS	Roots	**Either dead or alive:** [32,95,8,34,37] **Alive:** [97]	**Either dead or alive:** [95,98]
PLANTS	Seeds	[99,95,100,10,101–104]	[95,10]
PLANTS	Other	**Pollen and moss:** [34]	
Dung		[92,70,72,47,71,105]	[92,70,72,106,47,71,107]
Soil		[95,92,34,108,93,41]	[95,28,92,93]
Micro-organisms		**Fungi:** [109,110,34,52,111,16] **Bacteria:** [90,16] **Algae:** [34]	**Fungi:** [95,52,16] **Bacteria:** [16] **Protozoa:** [95] **Algae:** [95]
Others materials		**Paper sludge:** [73,112,113] **Sewage sludges:** [114,115]	**Earthworm cocoons:** [116] **Nodes and arthropod cuticle:** [95]



SUPPLEMENTARY MATERIAL

TITLE: TWO DISTINCT ECOLOGICAL BEHAVIOURS WITHIN ANECIC EARTHWORM SPECIES IN TEMPERATE CLIMATES

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Supplementary material 1: Papers found in ISI Web of Knowledge database published between 1963 and 2021, dealing with the feeding behaviour, growth rate and burrowing behaviour of one or further selected temperate anecic species (*Lumbricus centralis, Lumbricus terrestris, Aporrectodea longa longa* and *Aporrectodea giardi*).

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