Pedobiologia - Journal of Soil Ecology 67 (2018) 26–34

Contents lists available at ScienceDirect

Pedobiologia - Journal of Soil Ecology

journal homepage: www.elsevier.com/locate/pedobi

Body wall thickness as a potential functional trait for assigning earthworm species to ecological categories

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ARTICLE INFO

Keywords:
Earthworm tegument
Cuticle
Epidermis
Ecological groupings
Burrowing
Morphometry

ABSTRACT

Because earthworm species and ecological groupings could represent adaptive responses to unique climate and geographical characteristics and that their first nonspecific barrier is their tegument, a morphometric assay was performed to relate cuticle and epidermis thickness to specific habitat adaptations. Nine species belonging to three ecological categories (epigeics, anecics and endogeics) were investigated using conventional histological staining methods (haematoxylin-eosin, periodic acid-Schiff's reagent (PAS), Alcian Blue and PAS-AB), followed by quantitative analyses of the measurements of each of tegument layer. Results showed that, on average, both cuticle and epidermis were significantly thinner at the post-clitellar region than at the pre-clitellar one. Furthermore, the morphometric values obtained for these two tegument strata clearly indicated that the epidermis of the anecic worms was 30% thicker than that of epigeics and 22% of endogeics, whereas cuticle thickness decreased in the order anecics > epigeics > endogeics. However, when comparing individual species within each ecological grouping, the underlying variability in cuticle and epidermis thickness evidenced the different sensitivities to desiccation and burrowing behaviours of the different species (e.g. exploratory *versus* sheltering anecic burrowers). Importantly, the discrimination function derived from these analyses allowed the successful assignation of an additional number of earthworm species with intermediate burrowing behaviour (epi-endogeics) and different age groups of *L. friendi* (juvenile and semi-mature worms). It is concluded that earthworm tegument is a reflection of both species ecology (in terms of burrowing activities) and specific life-traits (here ontogenetic changes) and hence, it has the potential to be used in establishing functional and taxonomical classifications of earthworms.

1. Introduction

Earthworms are ectotherm invertebrates and the lack of protective external hard structures or exoskeletons makes them highly vulnerable to changes in abiotic conditions and pollutants in their surrounding environment. Furthermore, they need to keep their skin constantly moist for enabling gas exchange through diffusion. This together with other traits associated with their freshwater lineage (e.g. production of dilute urine, inability to modify the water permeability of the integument, etc.) pose severe restrictions to their terrestrial life (Carley, 1978) and explains their strong preference for wet habitats. However, the current accepted number of 3627 valid species of earthworms (Kooch and Jalilvand, 2008) are spread worldwide, covering natural landscapes (from the arctic to the tropics), agricultural and urban lands. To be able to colonise such a diverse latitudinal gradient, some kind of water and ion regulation capability is expected (Carley, 1983). Indeed, several physiological studies have shed some light on earthworm abilities to withstand different environmental hazards: i) winter freezing and contact with ice crystals by dehydrating and subsequent equilibration of internal fluids melting point to the ambient temperature (Holmstrup et al., 2002; Holmstrup and Overgaard, 2007), but also by adjustments in the phospholipid fatty acids of the membranes (Holmstrup et al., 2007; Bindesbøl et al., 2009); (ii) severe and/or long drought periods, through aestivation (Lee, 1985), but also through increasing internal osmotic pressure by accumulating urea and alanine (Bayley et al., 2010; Holmstrup et al., 2016). The shared mechanism in both types of environmental tolerance seems to be their ability to endure extensive dehydration (50%–80% in aestivating *Aporrectodea caliginosa* and up to 88% in *Lumbricus terrestris*; see Grant, 1955).

The resistance to desiccation is known to vary among earthworm species (Roots, 1956; El-Duweiny and Ghabbour, 1968) and does not seem to be related to the water content stored in their bodies, which is more or less similar across earthworms (82–88%; reviewed by Grant, 1955). Therefore, other structural, physiological and behavioural

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https://doi.org/10.1016/j.pedobi.2018.02.001
Received 4 December 2017; Received in revised form 5 February 2018; Accepted 6 February 2018

Table 1
Earthworm species included in this study. The collection sites together with the average body length and the cuticle and epidermal thickness (mean ± standard deviation) measured in this study are shown. In addition, information about their ecological grouping, body length and width intervals and the length:diameter ratio (L/D) values reported in the literature are also included. Different letters indicate significant ($p < 0.05$) differences in cuticle and epidermal thickness between species given by Wilcoxon with Duncan's Multiple Range Test (3 replicates x 2 body regions x 15 technical replicates per body region).

Species	Putative ecological group[*]	Locality (Country)	Reported body length (mm)[*,a,d,e]	Measured body length (mm)	Reported body diameter (mm)[*a,d,e]	L/D[*,f]	Cuticle (µm)		Epidermis (µm)	
Dendrobaena octaedra (Savigny 1826)	Epigeic[a]	Pontevedra (Spain)	(17) 30–40 (60)	45	2–5	10.00	1.51 ± 0.45	cd	24.78 ± 5.22	a
Dendrodrilus rubidus (Savigny 1826)	Epigeic[a]	Lancaster, UK	20–100	47.5	2–5	15.43	1.97 ± 0.58	e	29.75 ± 12.13	bc
Lumbricus rubellus (Hoffmeister 1843)	Epigeic[a]	Gondomar (Spain)	(25) 60–130 (140)	95	3–4	11.97	3.21 ± 1.56	f	39.42 ± 14.50	e
Aporrectodea longa (Ude 1885)	Anecic[a]	Lancaster (UK)	90–170	130	4–9	35.00	5.72 ± 1.77	i	45.39 ± 21.56	fg
Lumbricus terrestris (Linnaeus 1758)	Anecic[a]	Lancaster (UK)	90–350	220	6–10	31.72	4.03 ± 1.66	g	42.47 ± 16.71	ef
Scherotheca aquitania (Bouché 1972)	Anecic[a]	Olite (Spain)	260–320	275	6–8	41.42[g]	5.64 ± 1.97	i	46.36 ± 9.77	g
Aporrectodea caliginosa (Savigny 1826)	Endogeic[a]	Lyons, Ireland	40–180	70	3.5–7	21.80	0.46 ± 0.15	a	34.19 ± 6.04	d
Octolasion lacteum (Orley, 1885)	Endogeic[a]	Coruña (Spain)	40–160	100	2.5 – 5	19.16	0.88 ± 0.39	b	31.17 ± 7.51	cd
Octolasion cyaneum (Savigny 1826)	Endogeic[a]	Coruña (Spain)	(40) 80–140 (180)	110	5–8	27.79	1.22 ± 0.52	bc	38.94 ± 10.52	e
Allolobophora chlorotica 'green morph' (Savigny 1826)	Epiendogeic[a]	Dublin (Ireland)	30–80		3–7	23.79	1.60 ± 0.56	d	27.39 ± 7.38	abc
Amyntas corticis (Kinberg 1867)	Epiendogeic[b]	Tarragona (Spain)	45–270		3–6	22.72	4.71 ± 1.93	h	34.61 ± 18.17	d
Dendrobaena madeirensis (Michaelsen 1891)	Epiendogeic[c]	Pontevedra (Spain)	42–47		4–5	9.88[g]	3.30 ± 1.05	f	26.19 ± 9.77	ab
Lumbricus friendi (Cognetti, 1904)	Anecic[a]	Pontevedra (Spain)	45–120		4–8	25.12				
immature							2.54 ± 0.58	a	38.86 ± 12.34	a
semimature							2.63 ± 0.59	a	38.58 ± 10.47	a
mature							2.30 ± 0.51	b	49.64 ± 15.26	b

[*]as reported in the literature:
[a](Bouché, 1972, 1977).
[b](Uribe, 2004).
[c](Trigo et al., 1989).
[d](Sims and Gerard, 1999).
[e](Alvarez, 1971).
[f](Kurth and Kier, 2015).
[g] (estimatedhere based on reported values).