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Review

Charles Darwin, earthworms and the natural sciences: various lessons from past to future

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Abstract

In 1881, Darwin (1809–1882) published his last scientific book entitled "The formation of vegetable mould through the action of worms with observations on their habits", the result of several decades of detailed observations and measurements on earthworms and the natural sciences. The work was considered a "best-seller" at the time, with 3500 copies sold immediately and 8500 in less than 3 years which, at the time, rivaled the sale of his most well known book "On the origin of species". The book covers the importance of earthworm activity on a variety of topics: pedogenesis and weathering processes, soil horizon differentiation and the formation of vegetable mould (topsoil), the role of earthworm burrowing and casting (bioturbation) in soil fertility and plant growth, the burial of organic materials and soil enrichment with mineral elements, the global cycle of erosion–sedimentation with hydrologic and aerial transfers of fine particles brought up to the soil surface by earthworms and the protection of archaeological remains through their burial. Finally, Darwin also performed a series of original experiments to determine if earthworms possessed, or not, a certain "intelligence". This part of the book was, among others, one of the main reasons for its success. In this article we analyze the success (past and present) of this book, Darwin's own opinion of his book and the general contents of the work. Throughout, we discuss the main lessons to be learned from his 'little' (as he called it) book and provide brief historic reviews of major literary works on earthworms, both contemporary and posterior to Darwin, emphasizing his role as precursor and/or founder of various scientific disciplines (ethology, soil ecology and pedology). However, despite Darwin's clear demonstrations of the importance of biological activities (earthworms) in the maintenance of soil fertility, his book on worms has been mostly neglected by agronomists and soil scientists, primarily due to the predominant soil fertility and management paradigms of the 19th and 20th centuries.

Keywords: Charles Darwin; Earthworms; Pedology; Agronomy; Ethology; Soil ecology; Geology; Archaeology

1. Introduction

After a period of more than 40 years of observations (generally sporadic but over some periods very intense) on earthworms and their habits, Charles

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Darwin (1809–1882) finished writing and published his last scientific book, namely "The formation of vegetable mould through the action of worms with observations on their habits". The book was published on 10 October 1881, about 6 months before his death. In 1 month, sales reached 3500 copies, and 3 years later, 8500 copies, rivaling the sale of "On the origin of species", his scientific master-work. Thus, it was a major success at the time, a "best-seller", so to speak. However, despite its initial success, throughout the 20th century this book never enjoyed the popularity of Darwin's many other books, falling somewhat into oblivion. Nowadays, most people who are approached and asked if they know that Darwin wrote a book on earthworms, will react with surprise (and often a smile, etc.). Today's familiarity with Darwin's last scientific book is generally limited to the fields of biology and ecology (especially of soils). Even many soil scientists, to whom the book is most suited for, are not familiar with the work. In fact, until recently, relatively few papers and books dealt directly with Darwin's "Formation of vegetable mould" (compared with some of Darwin's other successes), and most of them from the scientific view-point (e.g., Satchell, 1983; Boulaine, 1989; Lee, 1992).

However, the tides are changing, and the interest for Darwin's book may be going through a new revival. The easiness with which information can now be obtained, such as over the Internet, combined with a resurgence of interest in the science and practice of sustainability, vermiculture[1] and more organic matter based techniques of farming and gardening, has heightened public awareness of the role of soil organisms such as earthworms in renewing soil fertility, bringing Darwin's book back into the limelight. Darwin's "Formation of vegetable mould" is now out of copyright and can even be read and printed over the Internet, in its very first edition (John Murray, London, 1881[2]) and in a mid-20th century version with an introduction by Sir Albert Howard (Faber and Faber, London, 1945[3]). A French edition was recently published (Darwin, 2001) with an interesting preface by P. Tort.

Yet, despite the abundance of information that can now be gathered on Darwin and earthworms,[4] this information is scattered over many different sources, and it is up to the searcher to sieve through it and discover the main lessons. In fact, we believe that there are many as-of-yet uncovered lessons still to be learned from Darwin's book that must be revealed. Therefore, in the present paper we have sought out to highlight the main teachings of Darwin's 'Worms' and his role as precursor and developer of a variety of important scientific fields: soil ecology, ethology, pedology, agronomy, geology and archaeology. We begin our paper by providing a brief history of the book and its edition, followed by a review of its major original teachings and the status of knowledge acquired after Darwin, in the various fields dealt with in his book.

2. The book and its edition

Although the book was actually published only in 1881, Darwin's interest in earthworms and their influence on soils began over 40 years earlier, in the mid-1830s. His first publication on the subject was "On the formation of mould", a speech made on 1 November 1837, before the Geological Society of London (Darwin, 1838b). His geologist colleagues did not share Darwin's enthusiasm on the subject, expecting something more grandiose than a speech on worms (Desmond and Moore, 1992). This was followed by three fairly similar papers (Darwin, 1840, 1844a, 1869). In these communications Darwin refers to his observations on the role of earthworms in the formation of the vegetable mould.[5] These observations are illustrated in his 1837 publication (Fig. 1), which also reveals a first attempt at soil profile differentiation and the stone-line formation process. He demonstrates convincingly that earthworms have an exceptional ability to displace large amounts of soil and that they play a major role in soil formation.

The book was published on 10 October 1881. The history of publication is given by Feller et al. (2000).

[1] Earthworm culture in composted organic wastes for fish-bait, biomass production (e.g., protein-rich worm flour) or organic fertiliser production.

[2] http://www.gruts.demon.co.uk/darwin/docs/vegetable-mould/index.htm.

[3] http://www.ibiblio.org/soilandhealth/01aglibrary/010115darwin/fvmc.html.

[4] A combined-word search over the Internet using these two key words will reveal close to 1500 references.

[5] Vegetable mould, or 'plant earth' is the term used at the time to refer to what today is called topsoil or A horizon.

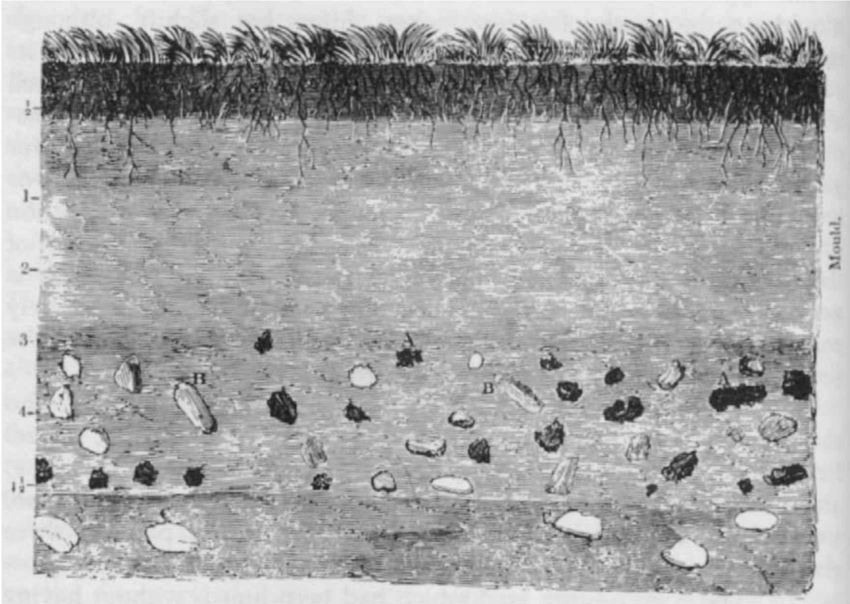

Fig. 1. Diagrammatic drawing showing a vertical soil section dug to about 5 in. (∼12.7 cm) depth, performed in October 1837 by Charles Darwin, in a field near Maer Hall (Josiah Wedgwood, Darwin's uncle's house in Maer, Staffordshire) which had been drained, ploughed, harrowed, and covered extensively with burnt marl and cinders 15 years earlier (1822). Drawing from Darwin (1838b). A: cinders; B: burnt marl; C: quartz pebbles.

At printing, the 2000 copies were sold immediately. On 5 November 1881, Robert Cooke, clerk of the publisher John Murray wrote to Darwin—"We have now sold 3500 worms!!!" (Graff, 1983). Between November 1881 and February 1884, 8500 copies of the English edition were sold, rivaling the sale of "On the origin of species". Beginning in 1882, numerous editions in foreign languages quickly followed: German (translated by Carus), French (translated by Levêque), Italian (translated by Lessona) and Russian (two simultaneous and different editions, translated by Menzbier and Lindeman). The famous re-printing of 1945, with an introduction by Sir Albert Howard, was even more successful than the original first edition.

Today, 120 years later, his book is once again gaining popularity and, inspired by Darwin's writings, since the book's 100th anniversary in 1981 (Satchell, 1983), earthworm scientists from all over the world meet at the International Symposium on Earthworm Ecology,[6] held every 4 years. Their proceedings have been published as books (Bonvicini-Pagliai and Omodeo, 1987; Edwards, 1998; Satchell, 1983) and special editions of scientific journals (Kretzschmar, 1992; Hoerschelmann and Andres, 1994; Edwards, 1997; Diaz-Cosin et al., 1999). Several other symposia and books have also been dedicated to this theme (Lee, 1959, 1985; Bouché, 1972; Minnich, 1977; Appelhoff, 1981; Wallwork, 1983; Tomati and Grappelli, 1983; Dash et al., 1986; Edwards and Neuhauser, 1988; Hendrix, 1995; Temple-Smith and Pinkard, 1995; Edwards and Bohlen, 1996; Lavelle et al., 1999). There is even a journal (Megadrilogica) which deals mostly with worm-taxonomic issues and several specialized newsletters (both on-line and on paper[7]), generally published by private organizations, which are dedicated mostly to promoting vermicul-

[6] The most recent (seventh) International Symposium on Earthworm Ecology took place in Cardiff, Wales, in 2002.

[7] For example, Jornal da minhoca online (http://www.minhobox.com.br); Australian Worm Growers Association (http://www.dragnet.com.au/∼lindah/awga/newslet.html); Worm Digest (http://www.wormdigest.org); Flower-field Enterprises (http://www.wormwoman.com); Wastebusters (http://wastebusters.orcon.net.nz/worm.htm); Casting Call (http://vermico.com/news.html); Impact Worm Farm Helpline (http://www.impactworm.com.au).

ture. In fact, over 200 articles are published every year on the various topics addressed by Darwin's worm book, and the trend is for continued increase in worm publications over the following decades (Satchell, 1992).

But, despite Darwin's book being welcomed and supported by many readers, its contents were also questioned and even rejected by contemporaneous scientists. For example, Wollny (1882a,b) doubted Darwin's (as well as Hensen's (1882)) statements on the potential benefits of earthworms for soil fertility (see later). Dokuchayev (1883) and Kostychev (1886) considered some of Darwin's conclusions (especially relating to burial activities) as hyperbolical (see later). Darwin himself had already mentioned the criticisms of d'Archiac (1847) (see footnote 15) who only considered Darwin's (1838b) theory on vegetable mould formation valid for "low-lying and humid prairies . . . but not arable lands, forests and upland prairies". Fish (1869) (see footnote 15) had also rejected Darwin's earlier papers because "considering their (the worms) weakness and their size, the work they are represented to have accomplished is stupendous". Both criticisms were dealt with by Darwin in his book (Darwin, 1881; pp. 20–21), and most latter criticisms were either addressed by Darwin's many letters after the book's publication, or by further research on the topic (e.g., Wollny, 1890; see later).

3. The main teachings of the book

To most people, especially in Darwin's day (and even to many people today), earthworms were merely unpleasantly slimy, ugly, blind, deaf and senseless animals, of little use except for fish-bait, and a general nuisance, particularly because of their 'unsightly' surface castings (Graff, 1983; White, 1789). Darwin restored a noble and useful character to earthworms, attributing them intelligence and benevolence. According to his book, their activities were responsible for large-scale land-surface changes, including substantial erosion, burial of surface-deposited matter (organic and inorganic), conservation of archaeological remains, formation of topsoil and its enrichment with mineral nutrients. In the following pages we 'dig deeper' into the main themes of Darwin's book, letting it speak for itself, and complementing it with more recent information, when and where available.

Throughout his book, Darwin addresses topics in various disciplines including: animal physiology and ethology, soil science (especially pedology), agronomy, geology and archaeology. These are each further developed in the sections below.

3.1. Darwin the pedologist

Darwin showed that earthworms are important players in soil formation (pedogenesis), by affecting the rate of weathering of rocks, humus formation and differentiation of the soil profile. This places Darwin as author of the first scientific publication on biological functioning of soils, formally introducing the concept of pedoturbation and bioturbation.

3.1.1. Earthworms and the weathering of rocks

According to Darwin, the role of worms in rock weathering processes was physical and chemical in nature. Physical weathering was achieved primarily by the grinding action of their gizzards. Darwin observed the gizzards of many earthworms and found that they generally had several small stones or grains of sand, sometimes combined with the hard calcareous concretions formed by the calciferous glands (p. 122[8]). Earthworms swallowed these coarser particles to help 'triturate' (grind) the ingested soil, organic matter and leaves, and to facilitate digestion (pp. 26, 40, 120, 123). Thus, by particle attrition, passage through the gizzard and the gut broke up the larger particles (pp. 122+), contributing to the physical weathering of soils. The role of calciferous glands is not yet clear as Darwin (1881) said that the calcite produced represents a true excretory product while recent studies showed that these glands might play a role in the water balance of earthworms (Morgan et al., 2002).

Today, more than 120 years later, studies on the intestinal contents of more than 30 earthworm species (e.g., see papers of Heymons (1923), Ponomaryova (1950), Kurcheva (1971), Lavelle (1971, 1973, 1978), Bouché and Kretzschmar (1974), Piearce (1978),

[8] All page numbers refer to the most recent (Darwin, 1976) edition of Darwin's book (based on the 1945 reprinting, with Sir Albert Howard's introduction). This very affordable edition can still be purchased easily in specialized book shops and over the internet.

Ferrière (1980), Németh (1981), Striganova (1982, 1984), Ka Kayondo (1984), James and Cuningham (1988), Reddell and Spain (1991), Judas (1992), Blakemore (1994), Rozen et al. (1995), Bernier (1998) and Mariani et al. (2001)) have shown that the amount of soil particles is highly variable depending on the feeding habits and ecological category of the earthworm. Litter-feeding and litter dwelling worms (epigeics, sensu Bouché, 1977), ingest little soil although they probably continue to use coarse particles and the 'trituration' process that Darwin mentioned, to help grind organic particles in the gut (Zragevskii, 1954; Schulmann and Tiunov, 1999). Soil-dwelling geophagous (endogeics) and litter-feeding (anecics) earthworms may have a large proportion of soil in their intestines, reaching 90 to almost 100% of the weight of ingested matter (Lavelle and Spain, 2001). It has been shown that these earthworms grind and intimately mix the soil and organic materials in their gizzards and intestines, totally re-working and re-organizing its structure (Barois et al., 1993), changing even the amount and orientation of the clay particles, compared with the uningested soil.

The importance of earthworms in chemical weathering was demonstrated in an experiment (p. 119), in which Darwin kept some earthworms in a pot filled with red-oxide sand. After some time, he noticed that the red sand in the worm casts, formed of the sand plus their intestinal secretions and digested leaves, had lost its coloration after passage through earthworm intestines. He attributed the dissolution of the oxide to acidic enzymes in the worm's digestive tube, with an effect equivalent to that of humus acids (pp. 119–120). Thus Darwin reached the conclusion that the process of ingestion, passing through, mixing, grinding and digestion in the earthworm intestines, of the whole superficial layer of mould (topsoil) of every field, continually exposed rock particles to chemical alteration, increasing the amount of soil (p. 121). However, the similarity of earthworm digestive enzymes with humus acids are still a matter of debate. Hayes (1983) doubted that the acidic enzymes of the worm guts were similar to humic acids, due to their polyelectrolytic nature, that could not be produced by the worms themselves. But, microorganisms, probably the main agents responsible for humus formation, are known to be stimulated in earthworm guts and their castings (reviewed in Brown (1995)), and this may speed the humification process. It has been recently shown that the stimulation of microorganisms (both in biomass and activity) in tropical endogeic earthworm gut and casts was due to the addition of intestinal mucus, which initiates a "priming effect" on the microflora (Barois and Lavelle, 1986). Thus, several authors (dell'Agnola and Nardi, 1987; Muscolo et al., 1993, 1999; Nardi et al., 1994) have proposed that microorganisms induce the production of humus substances (many with an auxin-like character) found in earthworm castings.

After Darwin, throughout the latter half of the 20th century, many studies on earthworm digestive enzymes were undertaken, mostly to determine whether earthworms are able to digest ingested food by themselves, or whether they require a mutualistic digestion system, i.e., digestion with the help of microorganisms (Martin et al., 1987; Lavelle et al., 1995; Lattaud et al., 1998). These studies and others (e.g., Tracy, 1951; Urbásek and Pizl, 1991; Zhang et al., 1993; Lattaud et al., 1997) have shown that earthworms can release a whole host of enzymes in their guts, some with acidic and others with basic pH, that help them digest their food. However, as with the ingested food, the spectrum of enzymes released is highly variable depending on the species and their ecological category, and some species are more dependent than others on microorganisms to help them digest their food (Lattaud et al., 1998; Trigo et al., 1999; Brown et al., 2000).

Darwin noted that vegetable mould (topsoil, soil surface horizon), consisting mostly of earthworm castings, always contained few coarse particles whose size surpassed those that could pass through the earthworm's intestine (pp. 78, 112), as opposed to deeper soil layers (figures on pp. 103–105, 121). It is well known that earthworm casts are generally of a different texture than the surrounding soil in bulk, i.e., that worms select soil particles of different sizes, generally ingesting smaller particles, richer in C and N (Dimo, 1938; Zragevskii, 1954; Sokolov, 1956; Barois et al., 1999). Nevertheless, there is still little evidence (beyond Darwin's claims) that earthworm activities can accelerate the alteration of parent materials or larger soil particles, as this has not yet been adequately assessed (Edwards and Bohlen, 1996). Some results of work performed with large *Octodrilus* earthworm species in the Romanian Carpathians by Pop and colleagues (Pop, 1998), has suggested that these worms are able to affect the clay mineralogy and the formation of illite in the soils they live in, a process that normally takes hundreds of thousands of years. Further experiments are needed to corroborate this phenomenon and Darwin's claims.

3.1.2. Earthworms and humus formation

Darwin believed that earthworms were responsible for both the destruction and addition of organic matter from mould. The disappearance was "probably much aided by its being brought again and again to the surface in the castings of worms" (p. 118), while the addition was achieved largely through the "astonishing number of half-decayed leaves which they draw into their burrows to a depth of 2 or 3 in." (p. 119). He also thought that the consumption and partial digestion of leaves and their intimate mingling with soil by earthworms, gave the topsoil its uniform dark tint (p. 119[9]). Although it is true that earthworms do play a very important role in the decomposition process, we know today that the darkening of the mould is a much slower process, that involves primarily chemical reactions and microbial activity (Hayes, 1983). This process, nonetheless, may be speeded by the earthworms, that prepare the soil and litter mixtures composed of fragmented, macerated and dilacerated leaves and fine soil particles, for microbial attack. For example, at the very end of his book, Darwin quoted Hensen's (1877) experiment (p. 147) in which two earthworms were placed in an earthen vase with sand and leaves, and in which the formation of a humus layer 1 cm thick was observed after a 6-week period. In fact, dell'Agnola and Nardi (1987) have proposed that one of the most important roles of earthworms in soils may be their ability to control humification rates through feeding, burrowing and casting activities and interactions with microorganisms.

In various parts of his book (e.g., p. 43), Darwin described (unknowingly) what are known today as earthworm 'middens',[10] created by *anecic* earthworms as they bury surface litter into vertically oriented burrows open to the soil surface (Nielsen and Hole, 1964). He makes multiple mentions of the large amount of leaves buried by worms (e.g., pp. 33, 39, 42–54, 61, 119). In fact, a few years later, Henry (1900) (see footnote 15; cited by Glinka (1931)) estimated that earthworms consumed in 10 months about 25% of the surface litter in a French forest. Today, we now know that the contribution of earthworms to the burial of surface litter (leaves, twigs, etc.) at some locations may reach 90–100% of the litter deposited annually on the soil surface by the aboveground vegetation (trees, crops, etc.) (Raw, 1962; Knollenberg et al., 1985), representing up to several tons per hectare per year of organic material.

Darwin's observations and experiments on leaf burial into the soil (see later), combined with surface cast production (which also buries surface-deposited materials), place him among the first to describe a phenomenon that leads to the formation of mull soils (e.g., Langmaid, 1964) and coprogenous (consisting basically of fecal materials) A horizons (Nielsen and Hole, 1964). Darwin thus concluded that the topsoil over the whole of UK "had passed many times through, and would pass again many times through, the intestinal canal of worms" (pp. 20, 145, 148) and proposed (p. 20) that the term "vegetable mould" should rather be changed to "animal mould", considering its animal origin.[11] Since Darwin's days, there have been few further developments on this semantic issue. Perhaps most scientists implicitly agree with Dokuchayev's (1883) view that vegetable mould should be called a 'plant–animal layer' (vegetable–animal mould), and not only animal or vegetable mould.

Unfortunately, Darwin had not had the chance to read the work of the Danish forester, Müller (1879, 1884) (see footnote 15) (for French edition, see Müller (1889)), before publishing his 'Worm' book, although his attention was called to Müller's work in a letter from Victor Hensen, dated 25 May 1881 (Graff, 1983). Müller was one of the brilliant precursors of modern pedology and one of the first scientists to study humus formation in soils, to grant a major role to soil biological phenomena and perform very rigorous in situ observations on soil fauna (Bal,

[9] "The leaves which they consume are moistened, torn into small shreds, partially digested, and intimately commingles with earth; and it is this process which gives to vegetable mould its uniform dark tint" . . . "The dark colour of ordinary mould is obviously due to the presence of decaying organic matter . . . " (pp. 118–119).

[10] "Where fallen leaves are abundant, many more are sometimes collected over the mouth of a burrow than can be used, so that a small pile of unused leaves is left like a roof over those which have been partly dragged in" (p. 43).

[11] The effect of earthworms on the humification process has been synthesised by Bachelier (1972).

1982). For example, he described the role of fungal mycelium and earthworms in humus formation and distinguished two phases of the humification process in which earthworms played a major role: (1) the plant residue fragmentation phase; (2) the phase of mixture with the mineral soil. Müller, on the other hand, did cite Darwin's earlier work (as well as Key's (1877)) (see footnote 15) and recalled Darwin's 1837 statements on the term "animal mould".[12] He proposed the terms (in Danish) of Muld and Mor (for mull and mor) and gave a very detailed description of these horizons according to their morphology, properties and biofunctioning: the mull characterized by the large presence of mycelia and earthworms and the mor by the lack of earthworms. Many works were later published on humus classifications including characterization of soil fauna (see Feller (1997) and Jabiol et al. (2000)).

Following Müller's and Darwin's footsteps, Wollny wrote his famous book "Organic matter decomposition and humus forms in relation to agriculture" (Wollny, 1902, French edition), addressing in detail the role of earthworms in the decomposition process. He noted that the dilaceration of leaves by earthworms had only a minor effect on the final mineralization of carbon. On the other hand, for soil, a large and positive effect on C mineralization and nutrient solubilization was observed after passage through earthworm intestines; for nitrogen, however, the effect was more variable.[13]

More recent studies (e.g., Toutain, 1987a,b; Ponge, 1990, 1991; Bernier, 1998) confirm, for the most part, the fore-mentioned importance of earthworms in the humification process. This appears to be mainly through controlling C inputs into the soil through litter burial and enhancing its decomposition rate, in regulating microbial activities in the drilosphere and protecting C in stable aggregates, i.e., their castings (see reviews in Lavelle et al. (1998) and Brown et al. (2000)). However, despite the rapidly growing knowledge in this area, much more work is still warranted, not only in temperate regions, but particularly in the tropics, where biological processes are much faster, and the conservation of organic matter in soils a much more pressing and important issue.

3.1.3. Earthworms and the differentiation of soil horizons

Darwin was the first scientist to recognize that earthworms, by their small, localized, yet repeated digging and surface casting action, could have a major impact on the differentiation of soil horizons. The burial of various materials (e.g., seeds, pebbles, etc., pp. 63–65) reached up to 2 m, depending on the depth of the burrows. Darwin's measurements on the rate of burial of different materials deposited on the soil surface (ashes, marl, red sand, stones) were followed from 3 up to 30 years (pp. 71–91), in variable conditions of soil and land management. His calculated rates of topsoil deposition ranged from 0.20 to 0.56 cm per year. He thus estimated that, on average, the amount of soil brought upwards by the worms ranged from 17 to 40 $t\,ha^{-1}$ per year (Table 1).

The rate of surface cast deposition depended on the number of earthworms present and their burrowing depth, the climate, vegetation and soil type, and the depth of the accumulated mould (pp. 76–77, 139, 140–141). Deeper mould layers or more superficially active worms led to lower mould accumulation rates (p. 77). Casts deposited on the soil surface, even on fairly level land, would be washed away by surface runoff during large rainfall events (see later) and soil compaction and plowing would increase this flow. Thus, formation of vegetable mould to an infinite thickness was impossible, and mould depth measurements cited in his book did not exceed 102 cm (p. 111). According to Darwin, the vegetable mould would only attain, ultimately, the depth to which worms ever burrow (p. 90), if all opposing agencies were neutralized. Hence, according to Darwin, the great depth of the mould in some Mollisols, for instance, the Russian chernozems, or prairie soils in the USA and grassland soils of the UK, would be, in part, due to the deeper activity of earthworms in these soils.

Darwin also noted that the vegetable mould was highly aerated (p. 88), consisting mostly of earthworm castings, and these, of aggregated fine earth ('terra tenuissima' or 'pâte excessivement fine', p. 126), created by the preferential selection of smaller particles by earthworms, and the grinding of larger particles in

[12] Müller also made a link between the size of soil aggregates and the species of earthworms present in the soil.

[13] He also studied their role in soil physical properties and observed lower water imbibition rates, but greater porosity (to water) and permeability (to air).

Table 1
Estimates of the thickness of the mould (topsoil) and the amounts of soil brought up to the surface by earthworms annually as castings, and the equivalent amount of soil or mould deposited on the soil surface (depth) in various meadows, lawns, pastures, prairies and grasslands under temperate climate conditions in Europe (ND: not determined)

Location (land use)	Author	Thickness of mould (cm)	Surface casts ($t\,ha^{-1}$ per year)	Equivalent depth of soil (mould) (cm per year)
England				
Down (lawn, "stony field")	Darwin (1881)	6.4	40.6	0.2
Down (pasture)	Darwin (1881)	16.5–22.9	ND	0.5–0.6
Maer Hall (grass field)	Darwin (1881)	6.4–8.3	ND	0.6
Maer Hall (coarse pasture)	Darwin (1881)	6.4–10.2	ND	0.5
Maer Hall (poor pasture)	Darwin (1881)	1.9–3.8	ND	0.5
Leith Hill (grass terrace)	Darwin (1881)	ND	16.9	0.2
Leith Hill (short turf, poor soil)	Darwin (1881)	ND	36.1	0.4
Rothamsted (1–300 year pastures)	Evans (1948)	10.2–12.7	2.2–55.1	0.05–0.6
Rothamsted (permanent pasture)	Evans and Guild (1947)	ND	24.6	0.25
North Wyke (pasture)	Knight et al. (1992)	ND	9.9–21.5	ND
Switzerland				
Zürich (permanent meadow)	Stöckli (1928)	ND	30.1	0.3
Zürich (golf course)	Stöckli (1928)	ND	80.1	0.7
Germany				
(Grassland)	Graff (1969)	ND	45	ND
Breslau (grassland)	Dreidax (1931)	ND	91.6	ND
Jura (permanent meadow)	Glasstetter (1991)	ND	45	0.6
Jura (pasture)	Glasstetter (1991)	ND	23	0.3
France				
Cîteaux (prairie)	Bouché (1982)	ND	74.5	0.6
Nice (lawn)	Darwin (1881)	ND	32.7	ND

their gizzards.[14] In support of these notions, Vysotskii (1900, 1930), for instance, measured castings and galleries of earthworms in Russian chernozems up to an 8 m depth, and attributed the high stability of the granular structure units of these soils to be largely due to earthworm activity.

Some recent estimates of surface cast production in grass-dominated vegetation with temperate climate conditions both in the UK and in various sites in France, Switzerland and Germany report values very similar to those in Darwin's book (Table 1). However, we now know that the amount of casts deposited on the surface may be only a small fraction of the total amount of soil moved by worms, ranging from a few percent up to almost 100%, depending on the earthworm species, its ecological category, soil properties (especially compaction and water content) and the time of the year (Lavelle and Spain, 2001). Furthermore, the land use system, climate and soil properties are also important in regulating the amount of surface or belowground casts produced. In fact, it is likely that most of the world's earthworm species (excepting the *epigeic* species) deposit their casts primarily belowground. These casts, deposited beneath the soil surface contribute largely to pedogenesis and soil structural properties (especially aggregation), while those deposited on the surface are important in soil profile differentiation, porosity and erosional and hydrological processes, especially rainfall runoff and infiltration (Lee, 1985). A general rule of thumb that can be used is that a similar amount of pores will be opened in the soil as the volume of casts deposited on the soil surface.

In his 1837 speech Darwin (1838b) illustrated earthworm burying activities in a splendid figure

[14] Darwin recognized that other agencies (organisms) could also be at work in producing vegetable mould, such as burrowing larvae and insects (especially ants), moles and aeolian dust deposition (p. 90).

(Fig. 1) representing a micro-soil profile 12.7 cm thick, where he distinguished the following horizons: “turf”, 1.3 cm thick; “vegetable mould”, 6.4 cm thick; “layer of fragments of burnt marl”, 3.8 cm thick. This last layer could be considered as a first step in formation of a stone line, as discussed by Johnson (1999) and Miklos (1992, 1996).

Darwin’s vision of soil, its formation and its differentiation into horizons, makes him one of the major precursors of modern pedology, although his role is seldom recognized, even in specialized books on the subject. As an expert naturalist, Darwin’s approach was both quantitative and dynamic (Boulaine, 1989).

Dokuchayev (1883), however, as the official founder of Pedology, minimized Darwin’s work, thinking that the numbers published in his book were either exaggerated or only applicable to his particular local situations (Ghilyarov, 1983). In fact, on the whole, one could probably characterize the taking into account of earthworms as a factor of soil formation by the early developers of pedology (Dokuchayev and his followers) as minimal (Johnson, 1990). Thus, following Darwin, few pedologists over the last 120 years have gathered data on the role of earthworms in pedogenesis, and only recently were vermic horizons and structures formally introduced in soil taxonomy (Buntley and Papendick, 1960; Pop and Postolache, 1987). It was not until the Seventh Approximation of the US Soil Taxonomy (Soil Survey Staff, 1960) that the term verm was introduced for vermiform soils or soils that had at least 50% or more of the A horizon and >25% of the B horizon volume, consisting of earthworm- or animal-derived structures (burrows and castings, fecal materials). Initially, the term was only applied to mollisols (e.g., vermaltoll, vermudoll, vermustoll), the US equivalent of chernozems. But in the last edition (Soil Survey Staff, 1998) the term was also extended to vermiboroll, vermic haploxeroll and other taxonomic classes as alfisol (vermaqualf) and inceptisol (vermaquept). There is still some debate as to the application of this concept, since micro-morphological evidence of soil fauna activity can be shown throughout the profile of most soil types (Pop, 1998), so perhaps the definition should include the premise ‘macro-morphologically stable aggregates, visible to the naked eye’. Obviously, there is still a lot of room to grow in the study of earthworm contributions to pedogenesis, and much more attention should be paid to properly defining and consolidating their role in current soil classification systems, and expanding the concept of bioturbation as a formative element in various other soil groups.

3.2. *Darwin the geologist*

Charles Darwin began his scientific career basically as a geologist, although he ended up becoming a naturalist with expertise in a variety of other disciplines. Under his initial training by Rev. Sedgwick at Cambridge and later by Charles Lyell (especially through his books; Lyell, 1930–1933), Darwin became an eminent geologist (Desmond and Moore, 1992), and published extensively on various geological topics (see, e.g., Darwin, 1838a, 1839, 1844b, 1846, 1849). Thus, it is not surprising that Darwin dedicates the last two chapters of his book (pp. 115–144) to describing the role of earthworms to geomorphology and landscape evolution. He recalls that worms play a major role in the erosion–sedimentation cycle through their action on the disintegration of rocks, combined with the surface casting of fine soil particles, which encourages their movement by wind and/or water. When slopes are steep and/or the rains violent, it is the whole castings that move with the rain-water (p. 127).

As mentioned earlier, the erosion of castings helps explain why, even though earthworms encourage the short-term formation of topsoil, it cannot accumulate over long periods to a great thickness.

To evaluate quantitatively the phenomenon, he performed various measurements of cast displacement due to rain and/or wind, taking into account factors such as the slope, rainfall intensity and soil cover. Using these data, Darwin attempted a mass balance of eroded matter. He calculated that about 0.5 cm per year equivalent of soil in castings were deposited annually on the soil surface by earthworms in grassland areas (Table 1). Thus, for a slope of 9°26′ at the Leith Hill short turf site (Table 1), Darwin calculated that 36 cm^3 per year m^{-2}, weighing 52.5 g were displaced (pp. 129–131) across a 1 yard line, values similar in order of magnitude for mass displacements in major river basins such as the Mississippi, with 0.07 cm per year, (p. 146). In this way, Darwin estimated that for every 100 yards (91 m) length in a valley with the above slope (9°26′), 7200 cm^3 of damp earth, weighing 10.4 kg would reach the bottom each year, and concluded that earthworms contributed to the building of alluvial soils or floodplains (p. 131).

Darwin's estimate of about 1140 kg ha^{-1} per year of sediment transport (runoff) from the Leith Hill turf (above) was very similar to that calculated by Sharpley et al. (1979) for a grazed pasture in New Zealand (1120 kg ha^{-1} per year). Over a period of a few years (decades), Darwin postulated that this 'denuding' (erosive) activity of worms was, in large part, responsible for the disappearance of furrows in abandoned sloping farmland (pp. 140–142) and the accumulation of soil on the edge of ledges, little embankments (pp. 134–136) and the bottom of sloping lands. Over longer geological time-scales (thousands to millions of years), this phenomenon could lead to vast amounts of sediment accumulation in river floodplains (see, e.g., p. 133; Nilgiri Mts, India). In fact, it has been suggested (Minnich, 1977), that the fertile floodplains of the Nile were created largely through the runoff and sediment deposition of eroded earthworm surface casts produced up-river, in the Ethiopian highlands. How much of this is actually true has yet to be determined but, undoubtedly, earthworms did play a role (in addition to termites and ants), not only up-river, but also down-river in the floodplains, where their activity was maintained high (Beaugé, 1912),[15] year-round, by the irrigation of cultivated fields.

Little has since been done on 'denudation' by earthworms. Their activities can influence many important soil properties that affect soil erodibility and erosion: particle size distribution, organic matter content and location, soil aggregation, aggregate stability and tensile strength, soil roughness, crusting and water infiltration into the soil (Blanchart et al., 1999). But there are few quantitative studies of the influence of earthworms on many of these parameters. Only a few cast runoff measurements have been made (e.g., Kirkby, 1967; Sharpley et al., 1979; Hazelhoff et al., 1981; van Hoof, 1983; Nooren et al., 1995; Binet and Le Bayon, 1999; Le Bayon and Binet, 2001), confirming Darwin's reports, and showing how earthworms contributed to soil creep and erosion under crops, pastures and forests through surface casting and the burial of surface-lying leaves that protect the soil surface from raindrop impact. The study of Nooren et al. (1995) even proposed that the washing away of clay-rich earthworm surface casts in a tropical forest of Ivory Coast was responsible for the build up of a sandy soil surface horizon.

On the other hand, Sharpley et al. (1979) and Hopp (1946, 1954) showed how earthworms improved soil structure, increasing water infiltration into the soil and thus reducing total soil runoff and erosion rates. Hence, in some cases, earthworms are said to increase soil losses while other studies emphasize their effects on soil structural stability and reduced erosion. Clearly, the ultimate effect of the activity of earthworm community in a particular site and ecosystem will be the balance between factors that enhance erodibility and erosion, and those that decrease these phenomena, factors that are highly dependent on the site's soil type, slope, land use and vegetation type and earthworm community.

3.3. Darwin the archaeologist

Darwin was intrigued by his uncle Josiah's comments to the extent that he began to ask himself—why were archaeological remains always underground and had to be dug up? In 1877, Sir Thomas Farrer discovered close to his garden (p. 94), the ruins of a villa from the Roman period, giving Darwin the perfect opportunity to see for himself (and measure) the effects of earthworms on archaeological remains (Fig. 2).

Most of the figures (10 of the 15) in Darwin's book are dedicated to explain the results of his work on the burial of ancient remains by earthworms. At some roman ruins Darwin noted that earthworms had managed to penetrate the concrete floors, walls and mortar. He believed that worms had lived beneath the floors of the ruins and began to penetrate them as soon as they became moist enough and pervious to rain. Their surface castings were "heaped on them during many centuries" (p. 97). In fact, Darwin saw little reason to doubt that earthworms had been doing what they do "since the period when the concrete was sufficiently decayed to allow them to penetrate it" (p. 97).

Darwin also attributed the sinking of floors "in chief part to the pavement having been undermined by worms, which we know are still at work" (p. 109).

[15] In this reference the original article was not consulted either because it was not accessible to the authors, was in a language not understood by the authors, or because it was cited by Darwin (1881) in the book itself.

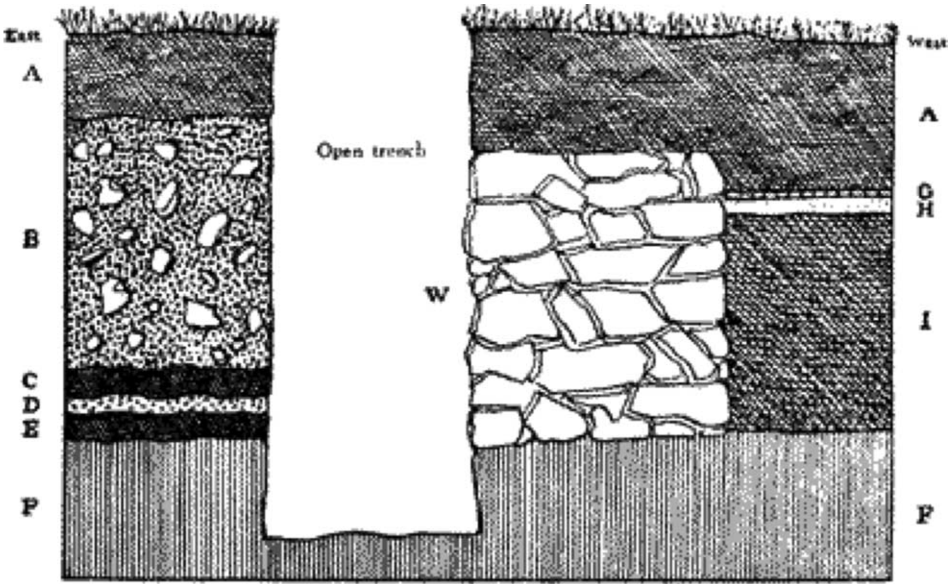

Fig. 2. Cross-section through the foundations of a buried Roman villa at Abinger, Surrey. The trench, about 1.2–1.5 m broad and up to 1.5 m deep, was dug through a buried wall and an adjoining room. A: fine vegetable mould, 27.9–40.6 cm thick over the wall and floor of the atrium (right-hand side of diagram), and 22.9–35.6 cm in the room, over a mass of thick blackish earth (B: left-hand side of diagram); B: dark earth full of large stones, 58.4 cm thick; C: thin bed of black vegetable mould, probably indicative of former land surface; D: layer of earth full of mortar fragments; E: thin layer, about 7.6 cm thick, of black vegetable mould, probably indicative of former land surface; F: undisturbed subsoil consisting of firm, yellowing argillaceous sand; G: Tesseræ (small red tiles), indicating the floor of the atrium (reception room); H: concrete layer; I: material of unknown nature; W: buried wall of the Roman villa, 58.4 cm thick (Darwin, 1881, p. 93).

Finally Darwin's results led him to conclude that worms "protect and preserve for an indefinitely long period every object, not liable to decay, which is dropped on the surface of the land, by burying it beneath their castings", and that "archeologists ought to be grateful to worms" (p. 146).

Unfortunately, little more has been said or done over the years, since Darwin's work, on the role of earthworms in the burial of objects and its importance in 'protecting' them. As with the previously mentioned innovative ideas of Darwin, this area of research had been mostly neglected until recently. A few papers (e.g., Wood and Johnson, 1978; Stein, 1983; Armour-Chelu and Andrews, 1994; Texier, 2000), have called attention to the importance of earthworm activities in protecting archaeological remains. Most artifact burial estimates have been comparable to (0.35 cm per year; Wood and Johnson, 1978), or slightly higher (0.9–1 cm per year; Yeates and van der Meulen, 1995) than those in the 'Worm' book (Table 1), showing the accuracy of Darwin's estimates, despite the 'rudimentary' research conditions and tools available at his time.

3.4. Darwin the soil ecologist

Darwin's naturalist approach, and his long-term experience in observing the behavior of different animals helped him distinguish various possible 'functions' of earthworms. He briefly alluded to, but did not specifically define, different functional groups of worms: deep burrowing and shallow burrowing species (p. 60), large-compact and small-granular casters (p. 69) and litter and soil feeders (pp. 34, 61–62). These characteristics are among the most important currently used in various functional classifications of the soil fauna and earthworms. Perhaps the most widely used recent functional classifications are those of Bouché (1977), Lee (1959) (see also Lee (1985)) and Lavelle (1981). These generally include three main groups (*endogeic*, *anecic* and *epigeic*), although several subgroups have been proposed (e.g., for the *endogeics* and *epigeics*), and some earthworm species do not seem to fit into any particular category or, rather, fit in between proposed categories (e.g., *epi-endogeic*; *endo-anecic*).

Other earthworms classifications include those of Lavelle (1997) and Lavelle et al. (1997), into ecosystem engineers and litter transformers, and of Blanchart et al. (1997), into compacting and de-compacting species. These schemes attempt to integrate knowledge on feeding habits and functional significance of earthworms in the soil. Darwin's contributions in this area deal primarily with the influence of earthworms on soil physical processes (casting, erosion, sedimentation, burial) although he also touches upon the selection and processing of particular leaf litters (see below). In the conclusion to his book Darwin provides several statements concerning physical soil engineering by earthworms, e.g., "The plough is one of the most ancient and most valuable of man's inventions; but long before he existed the land was in fact regularly ploughed, and still continues to be thus ploughed by earthworms" and "It is a marvelous reflection that the whole of the superficial mould over any such expanse has passed, and will again pass every few years through the bodies of worms" (both p. 148).

However, there were some shortfalls in Darwin's methodological approach to soil ecology. The most important one is that he never identified the species of earthworms he was investigating, and those that were producing casts and 'middens' on the soil surface. We can deduce from his descriptions that most of his experiments with surface cast production, litter burial and 'midden' production involved *anecic* species. In Britain, these are mainly *Lumbricus terrestris* (widespread), *L. friendi* (rare), *Aporrectodea longa* (widespread) and *A. nocturna* (widespread; Sims and Gerard, 1985). It is very likely that endogeics (other *Apporectodea* and *Octolasion spp.*) were also contributing to the surface casts estimated by Darwin. Moreover concerning southern English grasslands, fields and pastures, we know from the works of Satchell (1955, 1967) and Evans and Guild (1947) that about 8–10 species of earthworms are commonly present.

Another major limitation of Darwin's work was that he never quantified the earthworm populations in his field observation sites. He relied solely on estimates provided by Hensen (1877) for a garden in Germany (p. 84). Later research by Evans and Guild (1947) and Satchell (1955), among other British scientists, has shown that Darwin's estimates (about 133,400 ha^{-1}) based on Hensen's work were low, and more likely represented abundance values to be expected in poor lands such as acid pastures, rough hill grazing, scrub moor, etc. (Guild, 1955). In most agricultural soils, during periods of peak activity, populations of earthworms commonly range between 617 to >1235 $\times 10^3$ individuals ha^{-1} (Guild, 1955).

3.5. Darwin the agronomist

Before Darwin, throughout much of the 19th century and even the beginning of the 20th century, most persons considered earthworms as a garden pest, an undesirable animal that should be removed or eliminated from the soil (Graff, 1983; Walton, 1928). For example, in the Complete Course of Agriculture by the abbot Rozier (1805, vol. 11, supplement, p. 53), representing the synthesis of knowledge on the subject at the time, under the category "worm", one finds a long article dealing mostly with the pest aspect of earthworms, and the means to eliminate these noxious animals.

Even today, some traditional societies still consider earthworms as a pest (Ortiz et al., 1999), and they are often chemically eliminated from golf courses, due to their game-disturbing surface castings. Darwin, on the other hand, just like his former countryman White (1789),[16] believed that earthworms, as factors in the formation of topsoil, "the dark-colored, rich humus", contributed positively to soil fertility. In support of this notion, Darwin quoted the work of Dr. Gilbert

[16] In "The Natural History of Selborne", White (1789) made the following statement in his 1777 letter to the Hon. Daines Barrington: "... worms seem to be the great promoters of vegetation, which would proceed but lamely without them, by boring, perforating, and loosening the soil and rendering it pervious to rains and the fibers of plants, by throwing up such infinite numbers of lumps of earth called worm-casts which, being their excrement, is a manure for grain and grass ... Gardeners and farmers express their detestation of worms; the former because they render their walks unsightly, and make them much work; and the latter because, as they think, worms eat their green corn. But these men would find that the earth without worms would soon become cold, hard-bound, and void of fermentation, and consequently sterile".

(p. 120) showing that earthworm casts had 2–3 times more N than the non-ingested control soil. Using a cast production rate of $22.4\,\mathrm{t\,ha^{-1}}$ Darwin calculated that the surface casts would concentrate $87\,\mathrm{kg\,ha^{-1}}$ of N, much more than the N in the annual hay yields at the time (p. 120). Darwin also quoted several times (p. 65, 118, 147) the work of Hensen (1877), who showed that earthworms (in particular the anecic *L. terrestris*), were very important for soil fertility.

Darwin also attributed an important role of earthworm activity and muscular power (p. 122) in tilling the earth and burying organic debris, preparing the soil for plants (p. 146). This burial, combined with the ideal physical state of the soil due to their castings and burrows, promotes moisture retention, absorption of soluble substances, nitrification and decomposition, bringing nutrients within reach of plant roots (p. 147). Despite the lack of any direct evidence (data) for the effects of earthworms on plant growth and crop production, Darwin mentions and speculates on their role several times in his book:

- Referring to some giant castings collected by Dr. King in the Nilgiris (India) Darwin noted that "their surfaces had suffered some disintegration and they were penetrated by many fine roots" (p. 70).
- "On poor pasture land, which has never been rolled and has not been much trampled on by animals, the whole surface is sometimes dotted with little pimples, through and on which grass grows; and these pimples consist of old worm-casings" (p. 137).
- "Worms prepare the ground in an excellent manner for the growth of fibrous-rooted plants and for seedlings of all kinds. ... They mingle the whole (topsoil) intimately together, like a gardener who prepares fine soil for his choicest plants" (pp. 146–147).
- "The bones of dead animals, the harder parts of insects, the shells of land-mollusks, leaves, twigs, etc., are before long all buried beneath the accumulated castings of worms, and are thus brought in a more or less decayed state within reach of the roots of plants" (p. 147).
- Earthworm burrows ... "also greatly facilitate the downward passage of roots of moderate size, and these will be nourished by the humus with which the burrows are lined" (p. 147).
- "Many seeds owe their germination to having been covered by castings, and others buried to a considerable depth beneath accumulated castings lie dormant, until at some future time they are accidentally uncovered and germinate" (p. 147).

Of all the disciplines and subjects dealt with in Darwin's book, agronomy and the effect of earthworms on plants, received the most immediate attention. The German Wollny, at the time one of the most important soil scientists (and one of the first soil physicists; Gardner, 1986), was quick to criticize Darwin's book, disagreeing with Darwin's (and Hensen's) conclusions on the importance of earthworms (Wollny, 1882a,b). However, after his experiments with earthworms in pots a few years later (Wollny, 1890), he recognized that earthworms were, in fact, important for soil fertility and plant growth. In these experiments, he tested the effect of earthworms on the growth of various plant species and found increases in biomass of up to 733% in presence of earthworms. He warned, nonetheless, of the dangers of generalizing such results to field situations.

The decades following Wollny's experiments up to the mid-20th century presented a growing list of publications confirming the important role of earthworms in soil fertility and plant production, both in the field and the greenhouse, beginning with European scientists: Djemil (1896), Dusserre (1902) (cited by Glinka (1931)), Stebler et al. (1904), Ribaudcourt and Combault (1907), Russell (1910), Kashnitz (1922), Archangel'skii (1929), Dreidax (1931), Shiperovich (1936) and Brodskii (1937). In other parts of the world, published work on the topic began to appear in the 1930s and 1940s in the United States (Powers and Bollen, 1935; Chadwick and Bradley, 1948; Hopp and Slater, 1948, 1949) and China (Puh, 1941) and in the 1950s in New Zealand (Waters, 1951; Nielson, 1951, 1953; Duff, 1958; Lee, 1959; Stockdill, 1959) and India (Joshi and Kelkar, 1952; Nijhawan and Kanwar, 1952).

With the development of the concept of "organic farming" or "biological agriculture", before and after World War II, earthworms began to be considered by a certain number of agronomists and farmers as an essential determinant of fertility. Howard (1945) mentions that in Britain, "Our most experienced gardeners invariably judge the condition of their plots by the earthworm content" (p. 18, Introduction to 1945 edition). This explains why Howard, one of the major defender of "organic farming", wrote the book's 1945 edition's introduction and why it was so successful. It also explains the most recent resurgence of interest in Darwin's book.

3.6. Darwin the ethologist

Darwin's eclectic approach to science led him to address another controversial issue in this book: are earthworms intelligent or do they act solely by instinct? According to Darwin's son Francis (Darwin, 1888, p. 564), this well developed part of the book contributed greatly to its popularity. In fact, Darwin himself stated that his results on this topic surprised him "more than anything else in regard to worms" (p. 33).

Darwin began this research by performing diverse observations and tests to elucidate earthworm behavior and responses to various physical, chemical and biological phenomena, by touching them, breathing on them, giving them various different types of food (from meat to onions and from starch to beads), shining various lights on them and subjecting them to various temperatures, odors and vibrations (including playing the piano to them!). Some of his conclusions were that: "they are much more easily excited at certain times than others", "they must enjoy the pleasure of eating", they have favorite foods, "their sexual passion is strong enough to overcome for a time their dread of light", "the perception of vibration, seems much the most highly developed", they "do not possess any sense of hearing", they have a selective sense of smell and "light affects worms by its intensity and duration" (pp. 28–33).

Darwin had extensive experience in studying animal behavior with numerous observations on different species, some of which were deemed as having some intelligence, but no mention was made of earthworms in his previous works (e.g., Darwin, 1872).

Darwin suspected that some degree of earthworm intelligence could be exhibited in the habit of plugging the mouth of the burrows with various objects (p. 33), but how to prove it? He considered how an intelligent man would introduce leaves, leafstalks or twigs into a cylindrical hole, depending on their size and shape. If the object was larger in certain parts than the diameter of the hole, then logic would dictate that it would be best introduced by the narrowest part. How would earthworms behave when facing this problem? Thus, he conducted diverse observations and experiments with leaves of various English and foreign plants including pine leaves, and even pieces of paper cut into triangles of different shapes (Table 2).

Therefore, he estimated that the manner by which leaves were buried was not guided by chance, but corresponded to a choice. His conclusions of all the experiments were: "We may therefore infer—improbable as is the inference—that worms are able by some means to judge which is the best end by which to

Table 2
Summary of the results of Darwin's experiments on the burial, by earthworms, of leaves, stalks and pieces of paper

Nature of object	Drawn into the burrows, by or near the apex	Drawn in, by or near the base	Drawn in, by or near the middle
Leaves of various kinds	80	9	11
Leaves of the lime, basal margin of blade broad, apex acuminated	79	4	17
Leaves of a Laburnum, basal part of blade as narrow as, or sometimes little narrower than the apical part	63	27	10
Leaves of the *Rhododendron*, basal part of blade often narrower than the apical part	34	66	
Leaves of pine-trees, consisting of two needles arising from a common base		100	
Petioles of a *Clematis*, somewhat pointed at the apex, and blunt at the base	76	24	
Petioles of the ash, the thick basal end often drawn in to serve as food	48.5	51.5	
Petioles of the *Robinia*, extremely thin, especially towards the apex, so as to be ill-fitted for plugging up the burrows	44	56	
Triangles of paper, of the two sizes	62	23	15
Triangles of paper, of the broad ones alone	59	16	25
Triangles of paper, of the narrow ones alone	65	21	14

draw triangles of paper into their burrows" (p. 55) . . . for they then act in nearly the same manner as would a man under similar circumstances" (p. 58). Thus, "worms, although standing low in the scale of organization, possess some degree of intelligence" (p. 58).

Darwin, as other great 19th century naturalists (he quotes Fabre (1879) on p. 56, with a footnote: "See his interesting work, *Souvenirs entomologiques*, pp. 168–177"), was one of the precursors of later disciplines devoted to the study of animal behavior: comparative psychology, ethology and behavioral ecology. The sum of meticulous and complementary experiments related in this book is amazing. The reference to Fabre is relevant: Darwin's work carries the same sense of acute naturalist observation and smart devising of cross-controlling experimental protocols. Nevertheless, this work seems to have been overlooked by later ethologists, despite its popular success. In fact the book's title focusing on worms and vegetable mould is not indicative of its behavioral content, and one has to pick out the subtitle "with observations on their habits", which does not even address explicitly the topics of "intelligence" or "mental qualities".

Of course, for a modern ethologist, the comments of Darwin are loaded with the anthropomorphic vision of his time, and loose definition of terms like 'intelligence' (supposed to be identified through adaptability of the behavioral performance) versus 'truly instinctive' behavior (synonymous of 'inflexible'). It ensues that variations in animal behavior are somewhat hastily attributed to intelligence, under the additional superficial argument that worms "act in nearly the same manner as would a man" (p. 148), which is no proof in itself. This approach seems to overlook alternative interpretations, involving mechanisms that could lead to the same 'as-would-a-man' behavior by other means. Also, the argument that the leaf-picking behavior cannot be instinctive because it applies to leaves of "foreign" plants is hazardous, overlooking the possibility that the shape of the object may be sufficient to focus a stereotyped behavior beyond any notion of plant taxonomic characters, as otherwise indicated by the experiment with paper triangles. But despite some bold general conclusions, the whole reasoning of Darwin about behavior in this book is nevertheless far from simplistic and over interpreting, He repeatedly underlines that the experiments are not that conclusive, e.g., p. 56, "we see how difficult it is to judge whether intelligence comes into play, for even plants might sometimes be thought to be thus directed" (an obvious allusion to his work on movements in plants; Darwin, 1875). The author is thus quite aware that mere physiological mechanisms may support performances that mimic the products of human thought.

4. Conclusions

Darwin's book shows elegantly how small, seemingly insignificant causes can, upon accumulation (in space and time) produce great effects, and seemingly banal observations can create major theories. Darwin was able, from the observation of simple earthworm castings in a garden, to become a precursor of and address major scientific fields such as: pedology, archaeology, geology, soil biology, agronomy and ethology. It is therefore not surprising that Russell (1927) considered Darwin's book as "the most interesting book ever written on the soil", and that one of the major Russian soil science historians, Yarilov (1936), considered Darwin one of founders of the modern soil science, while the Russian microbiologist Ghilyarov (1983) considered Darwin "the true founder of soil ecology" and Righi (1997) considered him the founder of the science of biopedology.

Thus, Darwin's book is an issue for today, not only because of the increasing importance now being given to the role of soil fauna in the earth's biogeochemical cycles, but also because of the research method he presented us with. This is none other than a functional ecological and quantitative approach. Almost 120 years ago, Darwin did not use the same terms we use today, but the concepts were already present in his writings. Without a language to accompany the natural phenomena he was writing about, Darwin's work had a much smaller impact than it should have had on the various disciplines it covered. Reasons for this are complex, but reveal one of the fundamental aspects of how science progresses: innovative concepts and field work must be accompanied by a language that describes them (Johnson, 1999). Words such as bioturbation, stone-lines, ecosystem engineers, topsoil, all convey a message, a visual connotation of their meaning. Had Darwin been more of a 'jargonist', coining names and creating disciplines for the various processes he was describing and scientific fields he was addressing, perhaps his message would have fallen into more fertile ground and traveled farther in space and time, receiving the attention it deserves.

Other reasons for the failure of Darwin's book to influence agricultural teaching and research in the late 19th and the 20th centuries were ventured by Sir Albert Howard in his introduction to the 1945 edition of 'Worms'. According to Howard, it failed to have a larger impact because of the manner in which research on farming was developed, beginning with Liebig's (1840) book on "Chemistry and its applications to agriculture and physiology". Darwin's book appeared at the time when agriculture was still a part of chemistry, and Liebig's influence was at its zenith. "Thus, it occurred to no one that earthworm activities could be of profound significance for crop production. The attention of all concerned was directed solely to the chemistry of soil water, i.e., to a single factory only of a vast biological complex" (Howard, 1945).

We have entered the 21st century, and soil ecology is now an important part of soil science. In the previous pages we have highlighted much of what is known and many of the remaining incognita regarding the role and importance of macrofauna in various soil and land-forming properties and processes. To adequately address these complex issues and respond to the presently unanswerable, we must approach them with the same enthusiasm, fearlessness, ingenuity and dedication that Darwin used to write his 'Worm' book in little less than 10 years. In following Darwin's footsteps we may thus finally help to remove all doubts "that there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures" (Darwin, 1881, p. 148).

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