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With Darwin, earthworms turn intelligent and become human friends[a,b]

George G. Brown[1]*, Christian Feller[2], Eric Blanchart[2], Pierre Deleporte[3] and Sergey S. Chernyanskii[4]

[1] Embrapa Soja, C.P. 231, Londrina, PR, 86001-970, Brazil
[2] IRD (Institut de Recherche pour le Développement), Laboratoire MOST, BP 64501, 34394 Montpellier cedex 5, France
[3] UMR6552 CNRS - Université Rennes I, Station Biologique, 35380 Paimpont, France
[4] Department of Landscape Geochemistry and Soil Geography, Faculty of Geography, Lomonosov Moscow State University, Moscow, 119899, Russia

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Summary

In 1838 Darwin published his first paper on earthworms, showing their importance for bioturbation and the burial of surface-lying objects, and placing him as a pioneer of soil science. In October 1881, nearly 44 years after writing his first paper, and about 6 months before his death, Darwin published his last book, "The Formation of Vegetable Mould through the Action of Worms with Observations on their Habits." The book was a best seller at the time and can be considered a historical turning point in the perception of the importance of earthworms by humans, especially farmers, gardeners and scientists. Despite its great popularity, however, there were (and still are) criticisms regarding Darwin's broad statements and conclusions, and the book did not reach, throughout the 20th century, the popularity of his other masterworks. Nonetheless, 'Worms' dealt masterfully with topics such as earthworm intelligence (responsible in a great part for the book's popularity) and importance in the biogeospheric cycles. Darwin's book attributed intelligence and benevolence to earthworms, changing the notion that earthworms were only dumb, undesirable pests and a general nuisance. Although later research showed that Darwin's statements regarding intelligence were exaggerated and his experiments inaccurately attributed intelligence where instincts predominated, today, more than 120 years later, Darwin's conclusions continue to challenge scientists following in his footsteps, seeking to prove or disprove his ideas.

Key words: Charles Darwin, earthworms, behavior, soil ecology, perceptions on worms

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*E-mail corresponding author: browng@cnpso.embrapa.br

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Introduction

"The Formation of Vegetable Mould through the Action of Worms with Observations on their Habits", was Charles Darwin's (1809–1882) last book, published in 1881, shortly before his death. The book covered the importance of earthworm activities in soil and humus formation, the role of earthworm burrowing and casting (bioturbation[3]) in soil fertility, geological processes (especially the erosion-sedimentation cycle), and the burial of archaeological remains. Darwin's book also dealt with earthworm "intelligence", a topic highly appreciated by the readers and which contributed greatly to its success (Darwin 1888).

This book could be considered a "best-seller." In one month, 3500 copies were sold, and three years later, 8500 copies, similar to his other literary success, "On the Origin of Species" (Feller et al. 2003). A journalist even said that with Darwin, "earthworms turned friends of man" (Darwin 1888). However, despite its initial success, throughout the 20th century this book never enjoyed the popularity of Darwin's many other books, and was mostly ignored by both scientists and the general public. Some of the reasons for this disdain are presented in this paper, which focuses primarily on the topics of earthworm "intelligence" and the perception of earthworms by humans before and after Darwin. For further information on other topics, including pedology, soil ecology, geology, agronomy, ethology and archaeology, please refer to the recent review papers of Feller et al. (2003), Crist (2003) and Johnson (2002).

Darwin begins and ends his career with 'worms'

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 1837. One year after returning from his voyage on the Beagle, on one of his many visits to his maternal uncle (and later father-in-law) Josiah Wedgewood, Darwin had his first 'scientific' worm experience. His uncle took him to see several fields where lime, burnt marl and cinders had been placed on the soil surface a few years earlier (Darwin 1838). These materials were buried several inches below the soil surface and his uncle believed that worms were the culprits. Although his uncle thought that Darwin would not take so seriously such 'trivial gardening matters' (Desmond & Moore 1992), Darwin did not hesitate presenting a speech "On the Formation of Mould" a few weeks later (on November 1st 1837) at the Royal Geological Society in London.

The paper was his first publication on the topic, and appeared in the Geological Society's Proceedings (Darwin 1838). In the paper, Darwin discussed how burnt marl fragments, cinder, ash and other debris deposited on the surface of a lawn were recovered, some years later, evenly disposed in a layer at a measurable depth of several inches beneath the soil surface. These observations were the first attempt at soil profile differentiation and the stone-line formation process, placing Darwin as one of the pioneers of soil science and pedology (Feller et al. 2003). He demonstrated convincingly that earthworms had an exceptional ability to displace large amounts of soil and that they played a major role in (top)soil formation (Johnson 2002).

However, his geologist colleagues in London did not share Darwin's enthusiasm on the subject, expecting something more grandiose than a speech 'on worms' (Desmond & Moore 1992). Abashed, but not undaunted, Darwin somewhat abandoned the subject for the following 30 years, publishing only two other papers on the matter (Darwin 1840, 1844). It was not until 1869 that Darwin once again published a paper on earthworms (Darwin 1869), and, from 1871–80, "Worms" once again took priority (Graff 1983). Correspondence exchanges began to flow between Darwin and colleagues in Britain and abroad, and several experiments and field observations were performed over an almost 10 year period, with the help of several family members (especially three of his sons), to gather the information necessary to complete his 'worm book' (Graff 1983; Desmond & Moore 1992).

"Worms" was published on October 10th 1881, about six months before his death. Thus, Darwin practically began and ended his long scientific career with 'worms.' But, what did Darwin himself have to say about the book? In his letters there are various references to earthworms (Darwin 1888), where Darwin reveals some of his opinions regarding the 'worm book' before and after it was published.

Before publication:

- 21st September 1880. Letter to Victor Carus - "... I'm writing a very little book... Its title will be 'The Formation of Vegetable Mould through the Action of

[3] Soil disturbance and movement by biological means

Worms.' As far as I can judge, it will be a curious little book."
- April 1881. Letter to Victor Carus - "The subject has been to me a hobby-horse, and I have perhaps treated it in foolish detail."
- 1st May 1881. "I have now sent to the printers the MS. of a little book on *The Formation of Vegetable through the Action of Worms*. This is a subject of but small importance; and I know not whether it will interest any readers, but it has interested me."

After publication:

- 8th November 1881. Letter to Mellard Reade - "It has been a complete surprise to me how many persons have cared for the subject."
- November 1881. Letter to Thiselton Dyer - "My book has been received with almost laughable enthusiasm, and 3500 copies have been sold!!!"
- 4th February 1882. Letter to Anthony Rich - "I have, however, been plagued with an endless stream of letters on the subject; most of them very foolish and enthusiastic, but some containing good facts, which I have used in correcting yesterday the 'sixth Thousand'."

It is obvious that Darwin's opinions on his book did not foresee the immense popularity of this "little book" of "small importance." The famous 'Punch Magazine' even dedicated its 1882 cover to his book (Fig. 1). His son Francis, however was not so surprised with the book's popularity. In a book on his father's life, Francis said that "It is not difficult to account for its success with the non-scientific public. Conclusions so wide and so novel, and so easily understood, drawn from the study of creatures so familiar, and treated with unabated vigour and freshness, may well have attracted many readers" (Darwin 1888).

But, before discussing earthworm 'intelligence' and human perceptions of worms, it is important to become familiar with the work itself. The book is organized in seven chapters. Each chapter contains several subheadings that Darwin uses as a brief summary of its contents. The general structure of the book is presented in Table 1. The following sections deal primarily with the first two and the last chapter: earthworm habits and intelligence, and the perception of the role of earthworms in the biogeosphere.

Earthworm behaviour and intelligence

Darwin's book touched on a question that continues to fascinate many people when they study general zoology and must dissect an earthworm: they have a 'brain' (cerebral ganglion), but are they intelligent animals[4] (or do they behave only by instinct)? As mentioned earlier, this well developed part of the book contributed greatly to its general popularity. Darwin himself stated that his results on this topic surprised him "more than anything else in regard to worms" (p. 33)[5].

Various behavioural tests were performed on the worms[6], including response to touch and vibrations (including shouting at them or playing the piano to them), light or strong breath and odors (e.g., smoking tobacco), a wide range of foods (e.g., fat, raw meat, onions, starch, beads, paper, leaves of various plants, including lettuce), soft to bright lights and cold-to-warmer temperatures. Darwin found (p. 28–33) that they were quite sensitive to touch and vibrations but not so to sounds. They appeared to be sensitive to odors, having a 'selective sense of smell', and 'favorite foods', which they 'enjoyed eating'. Furthermore, he observed that they were also sensitive to light, preferring darkness or very soft light, but that "their sexual passion is strong enough to overcome for a time their dread of light."

Although Darwin had studied the behaviour of various animals before, and had published a book entitled "The Expression of Emotions in Man and Animals" (Darwin 1872), these were the first experiments he performed with earthworms, and were probably the first ever published on the topic. Furthermore, Darwin was the first person to describe in detail what are today

[4] Not to mention the comments made when they find out that earthworms have five pairs of hearts...

[5] Page numbers refer to a reprinting of the famous 1945 edition of Darwin's book (with introduction by Sir Albert Howard) (Darwin 1976).

[6] Although Darwin never identified the species in his studies, they probably included mostly earthworms of the *Lumbricus* and/or *Aporrectodea* genera. However, about 8–10 species of earthworms are commonly found in English grasslands (Evans & Guild 1947, Satchell 1955, 1967), so we cannot be certain which species were used/present in each of his trials. In cases where middens were studied these were most likely of *L. terrestris* and/or *A. longa.*

[7] "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. ... They often or generally fill up the interstices between the drawn-in leaves with moist viscid earth ejected from their bodies, and thus the mouths of the burrows are securely plugged" (p. 43).

called 'middens' (Nielsen & Hole 1964), created by *anecic* earthworms as they bury surface litter into vertically-oriented burrows open to the soil surface[7]. Darwin believed that "worms very much dislike leaving the mouths of their burrows open", and proposed several reasons for the formation of middens and leaf burial by the earthworms into their burrows: the leaves served as a food supply; the leaves provided temperature and air-humidity regulation within the burrows, reducing extremes; the cover prevented water from entering the burrows and provided a protective cover (concealment) against predators.

Fig. 1. Cover of Punch Magazine, December 6, 1881, about 2 months after publication of Darwin's book. The figure is an analogy to the evolutionary concepts detailed in Darwin's "On the Origin of Species"

Table 1. Chapters of Darwin's 'worm' book and brief description of their contents

Chapters	Abbreviated description from Darwin (1881)
Introduction	
1 and 2. Habits of worms	The nature of their habitats, their sensory capacities (visual, tactile, olfactory and mental qualities), morphological and physiological descriptions of worms, their nutrition, their intelligence in the burying of leaves, the construction of their burrows, the distribution of worms in the world.
3. The amount of fine earth brought up by worms to the surface	Speed of burial of various objects, number of worms in a given area, thickness of soil accumulated during a given time, weight of castings on the soil surface.
4. The part which worms have played in the burial of ancient buildings	Burial and covering of roman villas, subsidence of pavement and floors, thickness of mould.
5 and 6. The action of worms in the denudation of the land	Importance of worms in the denudation (erosion) process, dust deposits, the texture and colour of the vegetable mould, disintegration of rocks by acids similar to those of humus, the trituration of stones in the intestine of worms and its geological significance, quantities of earth annually brought up, the effect of tropical rainfall on castings, the accumulation of disintegrated castings, the formation and the quantity of soil above geological chalk layers.
7. Conclusion	The role of worms in the history of the world, their involvement in rock weathering (decay), soil erosion, preservation of archaeological remains, the preparation of soil for plant growth, the mental power of worms.

Table 2. Summary of the results of Darwin's observations and experiments on earthworm burial of leaves and petioles of various tree species and paper triangles of different dimensional proportions (sizes).

Nature of Object	Drawn into the burrows, by or near the tip	Drawn in, by or near the base	Drawn in, by or near the middle
1. Leaves of various kinds	80	9	11
2. Lime-tree leaves (foreign species), with broad base and acuminated tip	79	4	17
3. Laburnum leaves (foreign species), with base as narrow as, or sometimes little narrower than the tip	63	27	10
4. *Rhododendron* leaves, with base often narrower than the tip	34	66	
5. Pine-tree leaves, consisting of two needles arising from a common base		100	
6. *Clematis* leaf petioles, somewhat pointed at the tip, and blunt at the base	76	24	
7. Ash-tree leaf petioles, with thick basal ends often drawn in to serve as food	48.5	51.5	
8. Robinia leaf petioles, extremely thin, especially towards the tip, not well suited for plugging up the burrows	44	56	
9. Paper triangles of two different sizes	62	23	15
10. Broad-based paper triangles	59	16	25
11. Narrow-based paper triangles	65	21	14

Darwin's experiments on leaf selection, burial and midden formation

After many observations on earthworm behaviour, especially their habit of plugging the mouth of the burrows with various objects (p. 33), Darwin devised a series of interesting experiments to test the notion of whether the worms could 'learn' about the objects they buried and plugged their burrows with. With these experiments, Darwin had set out not so much to define intelligence, but to determine whether or not learning and experience could be applied to earthworms.

To test these ideas, he considered the use of logic to determine the best way to bury an object into a cylindrical hole, depending on its size and shape. Logic dictated that the best solution would be to insert the object by its narrowest part. Now, would earthworms follow this 'human logic'? His observations led him to believe that "if worms try to drag objects into their burrows first in one way and then in another, until they at last succeed, they profit, at least in each particular instance, by experience" (p. 57)[8]. In the following lines we briefly describe some of the main observations and experiments Darwin and his sons devised to answer the above question (pp. 45 to 55). The results they found are summarized in Table 2.

Dry leaves of mostly English plants were removed from hundreds of earthworm burrows and checked for their shape and position. Irrespective of the leaf species, they were shown to be incorporated into worm burrows preferentially by their narrower tip (80 % of the total), especially when not very flexible (Table 2, line 1). Arguing for the impossibility of "previous experience" of English earthworms to leaves of exotic plant species, and to exclude any possible conditioning to native English plants, leaves of foreign plants (lime-tree and laburnum) buried by the earthworms were studied separately. Most of the lime-tree leaves were buried by the tip (79 %) and only a slightly lower proportion of laburnum leaves were introduced by their tip (63 %), not appreciably narrower at the base (basal portion of the leaf) in this plant species. *Rhododendron* leaves, on the other hand, normally narrower near the base, were preferentially (66 %) dragged in by their basal ends. Pine leaves composed of two needles were pulled down by their base, and when bases were clipped and needles glued by their apex the worms continued to pull them by the base, which led Darwin to conclude that factors other than shape alone played a role in guiding the earthworms' preference. *Clematis* petioles were buried preferentially by their narrow tip, while the contrary occurred with those of the ash-tree, as these were frequently gnawed (used for food) and then pulled down (Table 2, line 6). Finally, in an attempt to distinguish the effect of shape from that of other attractive factors, pieces of paper cut into triangles of different sizes (dimensional proportions) were given to the earthworms, revealing the importance of the general shape of the object, especially the presence of narrower tips, in guiding earthworm burial behaviour.

Therefore, the manner by which leaves were buried was not guided by chance, but involved choice. Now, was this choice spontaneous or learned through experience? Would the initial seizure of the paper triangles be random (or not) and, given a greater difficulty in burying the apical parts, would they be seized by their base? This question was dealt with by observing the stains and creases left by earthworm on the paper triangles, although perhaps a better method would have been their direct observation under low-light conditions.

Darwin's conclusions from the above 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 draw triangles of paper into their burrows" (p. 55). Furthermore, "evidence has been advanced showing that worms do not habitually try to draw objects into their burrows in many different ways. … If worms are able to judge, either before drawing or after having drawn an object close to the mouths of their burrows, how best to drag it in, they must acquire some notion of its general shape. … If worms have the power of acquiring some notion, however rude, of the shape of an object and of their burrows, as seems to be the case, they deserve to be called intelligent; 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).

Are worms 'intelligent' animals?

In a letter to Nature, shortly after the book's publication, Romanes (1881) suggested that "although these observations are most interesting, it would seem worthwhile to try whether, by a series of lessons with similar triangles of paper, an individual worm could be taught to lay hold of the apex in a greater and greater proportional number of cases; if so, there could no longer be any question as to the intelligent nature of the action." This principle was later used by other researchers to test the learning abilities of earthworms, mostly using T or Y 'choice' mazes and a selection of various positive (reward), negative (punishment) and discriminatory stimuli (e.g., light, electrical shocks, sandpaper; Howell 1974). Unfortunately the lack of standardized methodologies, experimental deficiencies (with inappropriate designs, unchecked variables and lack of controls in some cases), and the presence of worm (mucus or pheromone) trails as well as anthropomorphic influences have led to considerable variation in results and hindered proper interpretation

[8] Darwin stated that "Mr. Romanes, who has specially studied the minds of animals, believes that we can safely infer intelligence, only when we see an individual profiting by its own experience" (p. 57).

(and comparisons) of the learning abilities of the earthworm species (slightly more than 10) studied (Rosenkoetter & Boice 1973; Howell 1974; Edwards & Bohlen 1996; Crist 2002). Therefore, much more work is needed before a clear picture emerges as to earthworm learning capacities and species differences, although the available evidence appears to suggest that at least some of the behaviour of some earthworm species can be accounted for by learning processes (Edwards & Bohlen 1996).

On reading Darwin's book, a modern ethologist will clearly see the weight of anthropomorphism, and loose definitions of terms like 'intelligence' (supposed to be identified through adaptability of the behavioural performance) versus 'truly instinctive' behaviour (synonymous with 'inflexible') (Feller et al. 2003). Intelligence was attributed to the worms because they "act in nearly the same manner as would a man" (p. 148), which is no proof in itself. Furthermore, the leaf-picking behaviour implies the presence of certain instincts of earthworms, rather than intelligence, when confronted with objects of different shapes, as indicated by the experiment with paper triangles. But despite his bold conclusions, Darwin's reasoning is far from simplistic and over-interpretive, and he mentioned several times the difficulties in judging whether intelligence is present or not. He also claimed that his experiments were not conclusive (as if trying to excuse himself of any possible misinterpretations of his work; p. 56).

Interestingly, Darwin makes little allusion to his previous works on natural selection and the evolution of behaviour in the 'worm' book. A superficial reading gives the overall impression that behaviour is treated as simple descriptions of performances, while the author cogitates over the "intelligence" problem in itself. Nothing here sounds like the large scale comparative survey of sexual behaviour and reasoning on the theory of sexual selection like in "The Descent of Man" (Darwin 1871), precursor of modern evolutionary behavioural ecology. Nevertheless, the very topic of studying "worm intelligence" is provocative, and resolutely stands in the Darwinian evolutionary perspective of filling the gap between human and animal biology. Moreover, as if connecting his long-lasting 'little hobby-work on worms' with the theory of evolution, two interpretations of behavioural evolution are given on p. 56. The statement "With animals, actions appearing due to intelligence may be performed through inherited habit without any intelligence, although aboriginally thus acquired," can be understood as the inheritance of acquired characters (initially performed through intelligent behaviour). But the following sentence proposes an alternative interpretation: "Or the habit may have been acquired through the preservation and inheritance of beneficial variations of some other habit; and in this case the new habit will have been acquired independently of intelligence throughout the whole course of its development." Obviously, the "whole course of development" stands here for evolution, "variations of some other habit" for modification of inheritable characters, and "preservation and inheritance of beneficial variations" for natural selection; that is no less than a striking summary of 'the essential Darwin'.

Popularity of earthworms before and after Darwin

The importance of earthworms for soils and society has undergone various phases, from profound recognition to utter ignorance and disdain. In fact, the perception of earthworms by modern humans was completely modified by Darwin's study and, historically, three periods can be distinguished regarding the popularity of earthworms: Antiquity, before Darwin, and after Darwin.

In classical Greek times, the mode of life and use of earthworms were well recognized and Aristotle called them the "earth's entrails" (or intestines), probably because they lived in and moved inside the soil, churning it up (Minnich 1977; Kevan 1985). In Babylonian times, they were used in medicines against lumbago (lower back pains) (Michaelsen 1928), and in the Egyptian Empire, they served as meteorological indicators (to predict weather phenomena) (Righi 1997). Furthermore, the importance of earthworms in the Nilotic valley soil was recognized to such an extent that Cleopatra (69–30 BC) decreed the earthworm a sacred animal, to be revered and protected by all her subjects (Minnich 1977). Egyptians were forbidden to remove it from the land, and farmers were not to trouble the worms for fear of stunting the renowned fertility of the Nilotic valley's soil. It is also believed that certain Egyptian priests were devoted full-time to the study of earthworms and their activities. Unfortunately, the results of their efforts have not survived, or have not so far been uncovered by archaeologists (Minnich 1977).

From Antiquity to Darwin's time, not much information is available on earthworms (see excellent review by Kevan 1985), excepting a few anecdotal descriptions of uses, activity, and taxonomic aspects (Kevan 1985; Righi 1997). Throughout much of the 19th century and even the beginning of the 20th century, most persons considered earthworms garden pests, undesirable animals that needed elimination from the soil (White 1789; Graff 1983; Walton 1928). For instance, in Rozier's (1805) Complete Course of Agriculture (Vol. 11, supplement, p. 53), representing the synthesis of knowledge on the subject at the time, the category

"worm" presents a long article dealing mostly with the pest aspect of earthworms, and the means to eliminate these noxious animals (Feller et al. 2000, 2003): "Every cultivator … knows the damage that worms do to seeds … it is thus advantageous to know the means to destroy them." And he thus provides a list of ways in which earthworms can be removed from the soil (and destroyed), including for example: collecting them in silence at night with the aid of a lantern; driving a stake into the ground and shaking it till the worms come out; striking the soil continuously with a mallet till they come out; pouring an infusion prepared with leaves of various kinds onto the soil, to drive out the worms. In the same article, however, Rozier also mentions some beneficial uses of earthworms, such as for certain medicines, food for certain Indian peoples and, of course, their role as fish-bait. In fact, Paoletti et al. (2002) recently showed the high nutritional value of earthworm flesh and their importance in the diet of Amerindians of the Alto Orinoco River Basin in Venezuela. However, even today, some traditional societies (e.g., some indigenous groups in Mexico) still consider earthworms as pests (Ortiz et al. 1999), and they are often chemically eliminated from golf courses, due to their game-disturbing surface casts (Walton 1928; Potter 1991).

Darwin himself mentioned the criticisms of d'Archiac (1847), who only considered Darwin's (1838) theory on vegetable mould formation valid for "low-lying and humid prairies ... but not arable lands, forests and upland prairies." Fish (1869) had also rejected Darwin's earlier papers because "considering their (the worm's) weakness and their size, the work they are represented to have accomplished is stupendous." Both criticisms were dealt with by Darwin in his book (1881, pg. 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 below).

Before Darwin, the importance of earthworms in soil fertility was thus not considered, except by very few naturalists. One of them was Gilbert White (1789) who, over thirty years before Darwin's birth, wrote in a letter to the Honorable Daines Barrington (May 20, 1777):

> „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".

But this passage seems to have been overlooked by Darwin, who did not mention it in his book, although he was probably called attention to the letter after the book's publication by his enthusiastic audience. Nevertheless, Darwin's book confirmed White's statements, and must be considered a turning point in history regarding work on earthworms and the perceptions on their importance (at least by most gardeners and the scientific community). His many letters written after the book's publication also attest to the work's great popularity at the time.

Although familiar with the work of his contemporary colleague the German V. Hensen (1877), which he quotes several times in his book, Darwin did not know of the work by P. E. Müller (1878), which also attributed earthworm's importance for soil fertility and humus formation. Nonetheless, following the publication of 'Worms', several scientists such as the famous soil physicist and editor of the journal *Forschungen Geb. Agricultur Physik*, the German E. Wollny, were quick to criticize Darwin's book (Wollny 1882) and promptly began research to disprove Darwin's statements. However (fortunately) Wollny's results proved Darwin was correct, showing positive effects of earthworms on yields of various plant species grown in pots (Wollny 1890). Research on earthworms by other European scientists closely followed that of Wollny, although the topic only began to be considered by scientists in other parts of the world after the 1930's and 40's (USA and China) and 50's (New Zealand and India) (see Feller et al. 2003).

Since then, thousands of papers have been published on the topic, and the number continues to increase exponentially (Satchell 1992). These papers confirm many of Darwin's statements, although in a few cases they also show some of the shortcomings of his work (Feller et al. 2003). For the most part, Darwin's ideas on the value of earthworms for soils and the biogeosphere have been widely accepted, but many of the topics raised in the book have still not been adequately addressed (Feller et al. 2003; Crist 2003).

Today it is well recognized that earthworms are important agents for the maintenance of 'healthy soils', and that they act as indicators of environmental quality (Paoletti 1999; Spurgeon et al. 2003). The resurgence of interest in organic farming and 'biological agriculture' (in which earthworms play a more important role influencing soil fertility) in recent years has brought Darwin's book and earthworms back into the limelight. The ideas expressed in Darwin's book, such as "Worms

have played a more important part in the history of the world than most persons would at first suppose" (p. 145), have even been used in popular comic strips (see e.g., Far Side cartoons and the book by Larson 1998) and in science fiction. One of the best fictional description of earthworms is given in the famous ecological novel "Dune," by Frank Herbert (1965), set in a world of giant sandworms. In this novel, the giant sandworms fulfill many of the same functions as earthworms. Furthermore, without sandworms, there is no life on Dune. As major regulators of the global ecological integrity of the planet Dune, they create the animal sand, just as earthworms create the animal mould on planet Earth. They are old friends of the Freemen and are treated as gods. Sandworms produce fertility both in the agricultural and human point of view (life water and the basis for family planning of the Freemen). They yield a wealth-creating commodity (i.e., the "Spice"), negotiable in all the Empire, somewhat analogous to the vermicompost that is now considered a valuable product of earthworm activity. Furthermore, the death of sandworms leads to life ("Tau Orgy") just as earthworms, through their life (activities) and death lead to the formation of humus and the fertile soil that constitute the basis of plant and animal productivity on Earth.

Conclusions

To most people, especially in Darwin's day (and even to many people today), earthworms were merely unpleasant, 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 (Feller et al. 2003). Darwin restored a noble and useful character to earthworms, attributing to them intelligence and benevolence.

However, despite the wealth of knowledge accumulated on earthworms since Darwin's days, and their formal recognition as important animals for both the soil and society, there are still many novel and important discoveries awaiting earthworm biologists. Behavioural and physiological aspects of earthworms continue to mystify modern scientists, and simple questions such as "what do they eat?", "how much do they cast?", "where do they live?" and "what is their effect on soils and plants?", still remain unanswered for many earthworm species (Brown et al. 2000). Considering that probably less than 50 % of the world's earthworm species have been identified so far (Reynolds 1994; Fragoso et al. 1997), and that only a few dozen have been relatively extensively studied, there is certainly much more to be learned from Darwin-like persistent, detailed, long-term, audacious and innovative work on earthworms. Let us over a century later pick up the gauntlet of the academic challenge, and follow in his footsteps...

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