Hindawi Publishing Corporation
Applied and Environmental Soil Science
Volume 2010, Article ID 823047, 11 pages
doi:10.1155/2010/823047

*Review Article*

# Charles Darwin's Observations on the Behaviour of Earthworms and the Evolutionary History of a Giant Endemic Species from Germany, *Lumbricus badensis* (Oligochaeta: Lumbricidae)

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Received 3 June 2009; Accepted 1 December 2009

Academic Editor: Martín Gerardo Rodríguez



The British naturalist Charles Darwin (1809–1882) began and ended his almost 45-year-long career with observations, experiments, and theories related to earthworms. About six months before his death, Darwin published his book on *The Formation of Vegetable Mould*, *through the Actions of Worms*, *With Observations on their Habits* (1881). Here we describe the origin, content, and impact of Darwin's last publication on earthworms (subclass Oligochaeta, family Lumbricidae) and the role of these annelids as global "ecosystem reworkers" (concept of bioturbation). In addition, we summarize our current knowledge on the reproductive behaviour of the common European species *Lumbricus terrestris*. In the second part of our account we describe the biology and evolution of the giant endemic species *L. badensis* from south western Germany with reference to the principle of niche construction. Biogeographic studies have shown that the last common ancestor of *L. badensis*, and the much smaller sister-taxon, the Atlantic-Mediterranean *L. friendi*, lived less than 10 000 years ago. Allopatric speciation occurred via geographically isolated founder populations that were separated by the river Rhine so that today two earthworm species exist in different areas.

## 1. Introduction

In his *Autobiography*, Charles Darwin (1809–1882) briefly commented on his last major publication in the following words: "I have now (May 1, 1881) sent to the printers the MS. of a little book on *The Formation of Vegetable Mould through the Actions 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. It is the completion of a short paper read before the Geological Society more than forty years ago, and has revived old geological thoughts" [1, page 136]. In a foot-note on the same page, Darwin's son Francis (1848–1925), who edited the letters as well as other documents after his father's death, remarked that "between November 1881 and February 1884, 8,500 copies were sold." Charles Darwin's "little book" [2] later gave rise to the scientific concept of "bioturbation", which can be defined as "the biological reworking of soils and sediments by all kinds of organisms, including microbes, rooting plants and burrowing animals" [3]. These ongoing activities of different soil (or sediment) organisms, which leads to a modification of geochemical gradients and the redistribution of organic substances, can be viewed as a kind of "ecosystem engineering." Moreover, it is obvious that soil texture is modified and different soil particles are dispersed [3].

In this article, we review the history and current status of Darwin's "earthworm research-agenda" (Figures 1 and 2), summarize the significance of his classical monograph [2] with respect to modern soil biology, and describe the ecology and biogeography of a rare, endemic species, *Lumbricus badensis*. The last section of our account is in part based on unpublished observations on this enigmatic annelid.


Figure 1: Charles Darwin as an earthworm scientist: caricature from the journal *Punch*, published in the year 1882.

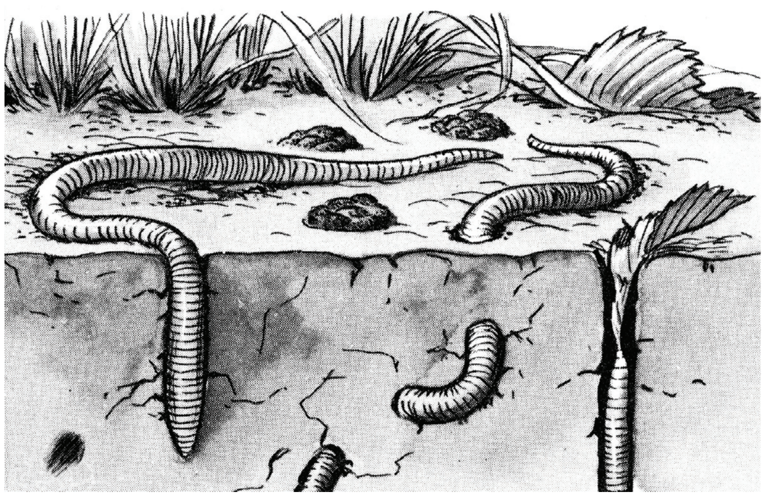

Figure 2: Schematic drawing of common European earthworms (*Lumbricus terrestris*) in their natural habitat. The annelids live in self-made burrows and forage by night on rotten leaves.

## 2. A Trivial Gardening Matter and Darwin's Speech to the Geological Society of London

Darwin first indicated the importance of earthworms in a lecture "On the formation of mould" to the Geological Society of London on 1 November 1837. This was published in the following year [4] and does not appear to have had a great impact on his colleagues [5]. Darwin probably realised this because he repeated his ideas in three following publications (published in 1840, 1844, 1869) [6–8], the last two being aimed at gardeners. The terms "vegetable mould" or "plant earth" were used by the Victorians to refer to what is called today "humus-rich topsoil" or the "A horizon" (Figure 3) or "mollic epipedon". It was his 1881 book [2] that had the greatest impact on those who had often regarded earthworms as pests that disfigured well-manicured Victorian lawns with their casts. They were thought to be useful only as fish bait or food for hens, but Darwin gave them a noble and useful character and even, more controversially, considered that they had intelligence.

Although the book was a great success at the time and was verified by many studies soon after its publication, it has become neglected in some areas of biology, especially soil science. A detailed review by Johnson [9] shows how biomechanical processes were largely ignored in models of landscape evolution, and how soil science became dominated by chemical and hydrological processes. However, this review also demonstrates how more recent models of dynamic denudation incorporate bioturbation on equal terms with other major archaeogenic, geomorphogenic, and pedogenic processes. Finally, it should be noted that although Darwin's book on earthworms became neglected by the earth sciences, it has continued to be quoted in zoological texts [10–12].

## 3. Earthworms as Living Ploughs: Darwin's Major Conclusions

As there are already some lengthy reviews of the scientific findings in Darwin's book on earthworms (e.g., [10, 13]), only the more important conclusions are summarised here. Darwin was probably the first scientist to examine a soil profile and suggest factors responsible for the structure of the various layers (Figures 2 and 3). This vertical soil section with a depth of about 13 cm was taken in October 1837 from a field near the family home of Darwin's uncle, the famous English potter, Josiah Wedgewood. The field had been drained, ploughed, harrowed, and covered extensively with burnt marl and cinders 15 years earlier. Darwin observed that this layer (Figure 3(c)) was now well below the surface and concluded that this was due to the actions of earthworms, a process described as bioturbation [3]. He was the first naturalist to point out the importance of earthworms in the formation of the layer of humus-rich topsoil that covers the land surface in every moderately humid country of the Earth.

Darwin first recognised this importance of earthworms in soil formation (pedogenesis) by them acting as agents of physical and chemical decomposition (weathering of rocks), by promoting humus formation, and by improving soil texture. More recent work has shown that they also influence soil pH and enrich the soil [11]. The processes of physical and chemical decomposition occur in the earthworm gut, chiefly in the gizzard and crop. Darwin concluded that the ingestion of the topsoil, and its mixing, grinding, and digestion in the gut, continually exposed rock particles to chemical alteration, increasing the amount of soil. This process, and the addition of faecal casts from the worms, builds up the humus-rich topsoil (Figure 3(a)) and buries various materials originally on the surface (e.g., seeds, pebbles, archaeological artifacts) down to depths of 2 m, depending upon the depth of the earthworm burrows. Darwin estimated rates of topsoil deposition in the range of 0.20–0.56 cm per year, and the mean amount of soil brought upwards by the worms as 17–40 t per ha per year. More recent studies in Britain, France, Switzerland, and Germany have produced similar values for grass-dominated vegetation in a temperate climate [13].

Earthworms are predominately saprophages and feed chiefly on organic detritus, usually the decomposing leaves and stems of plants together with smaller amounts of roots, seeds, algae, fungi, and testate Protozoa. They prefer materials rich in nitrogen and sugar, but low in polyphenols [14]. Variable amounts of mineral soil can be ingested together with organic material, and the mineral fraction reflects that of the external medium. Darwin observed that an "astonishing number of half-decayed leaves" were drawn down by the worms into their burrows (Figure 2). Here they were stored until they were sufficiently decomposed to be eaten. He thought that the mixture of partially digested leaves and mineral soil in the faecal casts was responsible for the characteristic dark colour of humus-rich topsoil (Figure 3(a)). It is now known that the darkening is a much slower process, involving primarily chemical reactions and microbial activity [15]. However, the earlier processing of the material in the earthworm gut may facilitate this process.

Darwin was also the first scientist to state that earthworms improved the quality of soil by improving soil texture. Earthworm activity facilitates the physical comminution of organic particles, the amelioration of soil pH, the enhancement of microbial activity, and the mixing of soil from different strata in the profile. They promote the formation of organomineral complexes and, by delivering faecal casts at the surface, they bring organo-mineral crumbs from the deeper parts of the profile to the surface. Earthworms also facilitate the transport of certain elements to the soil surface so that their faecal casts have concentrations of calcium, sodium, potassium, magnesium, available phosphorus, and molybdenum that are higher than in the surrounding soil. Therefore, earthworms not only improve the soil texture but also enrich the soil [3, 9, 10, 15].

Darwin suggested that earthworms may change the chemical composition of materials that pass through their gut. However, there is still little evidence that they can accelerate the alteration of parent materials or the breakdown of larger soil particles [11]. Some work with the large *Octodrilus* sp. in the Romanian Carpathians suggests that these worms are able to affect the clay mineralogy and the formation of illite in their habitat, a process that usually

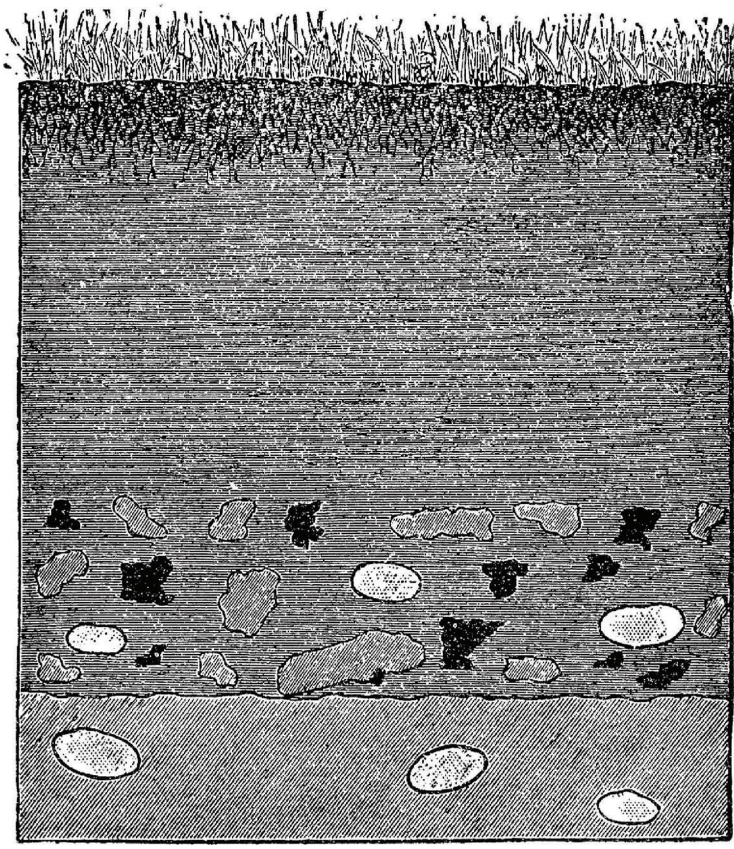


Figure 3: Cross section of the vegetable mould in a field, drained and reclaimed fifteen years previously. (a) Vegetable mould, without stones, (b) Mould with fragments of burnt marl, coal-cinders and quartz pebbles, (c) Subsoil of black, peaty sand with quartz pebbles (adapted from Darwin 1881 [2]).

takes many years [16]. If other earthworms are able to do this, then it is an important finding because sorption of radiocaesium on illitic-type clay minerals served to reduce the amount of radiocaesium entering terrestrial and freshwater food chains after the Chernobyl accident of 26 April 1986 [17]. Most of the radiocaesium became fixed in the interlayers between the platelets of the illite minerals. Thus, when the Chernobyl plume passed over Northwest England and it rained, the effects of the radiocaesium fallout varied considerably among lakes in the area and fish in the lakes [18–21]. In lakes with illitic minerals in their catchment, levels of radiocaesium decreased rapidly in the water, sediments, and fish, presumably because most of the radiocaesium was trapped in the catchment. In contrast, levels remained high in the water, sediments, and fish of lakes surrounded by acid moorland.

The most controversial section of Darwin's book dealt with earthworm behaviour and if they could be described as intelligent. This section was chiefly responsible for the popularity of the book. The poor worms were subjected to various tests, including response to touch and vibrations, strong breath and odours, a wide range of foods (e.g., fat, raw meat, onions, starch, beads, paper, leaves of various plants), and light and temperature gradients. He found that they were sensitive to touch and vibrations but not to sounds, also to odours with a "selective sense of smell", and to light, preferring darkness or very low irradiation, except when they were mating. He also concluded that they had favourite foods. Darwin observed that earthworms plug the mouth of their burrows with leaves, leaf stalks, or twigs and considered that an intelligent animal would draw such irregular-shaped objects into a cylindrical hole by their narrowest part (Figure 2). Therefore, he placed around the burrow entrance leaves of various native and foreign plants and triangular pieces of paper of various sizes. In the majority of trials, these objects were drawn into the burrows by or near their narrow apex. The only exception was pine needles that were drawn in, by, or near their base. He concluded that worms, although standing low in the scale of organisation, possess "some degree of intelligence instead of a mere blind instinctive impulse" [2, page 312].

Before considering this conclusion further, it is useful to compare earthworms with their cousins, the leeches. Both belong to the phylum Annelida and both are hermaphrodite with some segments near the middle of the body modified in mature animals to form a clitellum that secretes a cocoon for the eggs (see Figure 4). Hence, they are regarded as subclasses Oligochaeta and Hirudinea of the class Clitellata [11, 22]. Unlike earthworms, leeches are active predators [22–25]. Some species suck the blood of their prey whilst other species

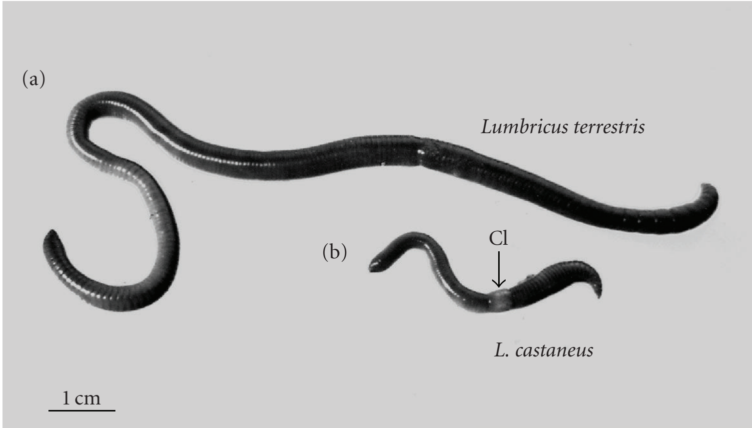


Figure 4: Photograph of two German earthworm species that inhabit grasslands, but occupy different ecological niches. *Lumbricus terrestris* (a), a burrowing (anecic) species, and *L. castaneus* (b), an epigeic earthworm. The swollen clitellum (Cl) of the sexually mature *L. castaneus* is indicated.

suck in their whole prey or devour pieces of moribund or dead animals. They have fewer segments than earthworms and a more compact, muscular, body with anterior and posterior suckers. Leeches are good swimmers but also travel by looping, using their suckers. Their sense organs are well developed so that they can detect movements of potential prey and chemicals released by injured prey. Most species have more than two pairs of eyes that can detect changes in light intensity and direction. The medicinal leech can also detect the warmest parts of its mammalian prey where it sucks its blood meal [26]. With such a range of senses, it is not surprising that leeches have a well-developed brain consisting of a fusion of ganglia in the anterior segments of the body. Leeches can therefore react rapidly to a wide range of stimuli but it would be wrong to regard them as intelligent; their behaviour is instinctive [23, 24]. Leeches can be regarded as "worms with character". The so-called "brain" in earthworms is much smaller than that of leeches, which is not surprising in an animal that is adapted to a subterranean life and is usually nocturnal. There are no definite eyes, but light-sensitive cells occur on the dorsal surface, especially at the anterior and posterior ends of the body, the regions most frequently exposed to light [11]. As noted above, they must have sense organs that are sensitive to chemicals, changes in temperature, and especially touch and vibration transmitted through solid objects. Like leeches, their behaviour is instinctive and it is wrong to describe them as intelligent animals.

## 4. Darwin and the Humble Earthworms: The Immediate Impact of His Book

Darwin's last monograph was published in October 1881 [2]. This book was distributed one year later in the United States of America via the publisher *D. Appleton and Company*, New York. The US-company advertised this last publication of the famous British naturalist, using a selection of sentences from book reviews that were published during the previous year (November/December 1881). We will quote here from some of these articles in order to document the immediate impact of Darwin's little "earthworm book".

In the journal *The Academy, London*, it was pointed out that "Mr. Darwin's powers of work are inexhaustible, and not less remarkable than his genius. Here is another delightful book from his pen, … One of the charms of the present work is, that it is extremely easy to read … it will delight everyone, every page being full of interest". In the *Sunday Review* we read that "Mr. Darwin's little volume on the habits and instincts of earth-worms is no less marked than the earlier or more elaborate efforts of his genius by freshness of observation, unfailing power of interpreting and correlating facts, and logical vigor in generalizing upon them. … All lovers of nature will unite in thanking Mr. Darwin for the new and interesting light he has thrown upon a subject so long overlooked, yet so full of interest and instruction, as the structure and the labors of the earth-worm".

In the *New York Graphic*, a similar, very positive evaluation was published: "The result of the author's observations is the production of proof that the small and apparently insignificant earth-worm is the cause of mighty changes in the surface of the earth, seeing that each of them, on the average, passes about twenty ounces of earth through its body every year, which earth it brings often from a depth of eight or ten feet below the surface to deposit it on the mould at the top, thus doing the work of a plow. What the result of this must be will be evident when it is known that an average of 30,000 such plows are at work in every acre of common arable land, and the worms must, therefore, work over about ten tons of earth per acre every year".

The review published in the *Brooklyn Times* emphasized the novelty of Darwin's observations and conclusions: "Darwin confers upon the despised and humble earth-worm an interest it never possessed before, and introduces it as a factor of, perhaps, unsuspected importance in agriculture. Portions of his book read almost like a romance, for there is much in his revelations of surprising strangeness and novelty. So much is seen that might be patent of the dullest eye that it seems remarkable that so little should have been known of earth-worms before".

In the *New York World*, it was pointed out that Darwin's book is "Curious and interesting throughout". Finally, in the *Boston Adviser*, the role earthworms that have played over thousands of years are described in the following words: "Respecting worms as among the most useful portions of animate nature, Dr. Darwin relates, in this remarkable book, their structure and habits, the part they have played in the burial of ancient buildings and the denudation of the land, in the disintegration of rocks, the preparation of soil for the growth of plants, and in the natural history of the world".

These statements on Darwin's last publication and his general conclusions concerning soil biology and so forth. document that the "little book on a subject of small importance" had a large, immediate impact (Figure 1). The monograph sold so well that on 5 November 1881, less than four weeks after the book became available, a clerk of the British publisher John Murray (London) wrote to Darwin: "We have now sold 3500 worms !!!" [13]. Only five months later, on 19 April 1882, Charles Darwin died. In the following years, his "worm book" was translated into several foreign languages, but this monograph never became so well known as his work on the species problem published in 1859 [27, 28].

## 5. Biodiversity and Reproductive Behaviour of European Earthworms

In his most famous book *On the Origin of Species* [27], Charles Darwin (1859) did not define what species are and how they can be distinguished from varieties [29]. Decades later, Theodosius Dobzhansky (1900–1975) and Ernst Mayr (1904–2005), two of the "architects" of the synthetic theory of biological evolution of the 1950s, introduced the biological species concept that defines species as "populations of interbreeding organisms that are reproductively isolated from other such groups" [30]. Darwin's relaxed opinion concerning species definitions may have been the reason why he did not identify the species of earthworms he was investigating [28]. It is likely that Darwin (1881) [2] studied the most abundant burrowing (anecic) earthworms of Britain, *Lumbricus terrestris* (widespread), *L. friendi* (rare), *Aporrectodea longa*, and *A. nocturna* (both widespread) [11, 15, 29]. However, it is well known that in southern English grasslands, 8 to 10 earthworm species occur [29]. Hence, more than the four taxa listed above may have contributed to the "physical soil engineering" or "bioturbation" described by Darwin [2].

The common earthworm *L. terrestris* lives solitarily in vertical, aerated burrows that are 1 to 2 m deep. The oligochaetes forage and mate on the surface at night (Figure 2). After heavy rainfall and inundation of the soil, the oxygen-dependent (aerobic) invertebrates escape from their anoxic burrows and creep over the moist soil. During these forced excursions, most of the free-living earthworms are eaten by predators (birds, etc.) or die as a result of intense radiation and heat caused by the reemerging sun. These well-known, dramatic "mass destructions" of earthworms after the submergence of their burrows were not mentioned by Darwin [2]. Representative specimens of two common earthworm species that were captured after a heavy rainfall in Germany (*L. terrestris* and *L. castaneus*) are depicted in Figure 4.

As summarized above, Darwin [2] analyzed the behaviour of earthworms with reference to their sensory capacities, the construction of their burrows, nutrition, and their supposed "intelligence" in burying of leaves. However, he only briefly mentioned the reproductive biology of these terrestrial oligochaetes.

Four decades later, a detailed description of the reproductive biology of the common species *L. terrestris* was published by Grove (1925) [31]. Oligochaetes (earthworms) and hirudineans (leeches) (class Clitellata) are simultaneous (or protandrous) hermaphrodites with reciprocal insemination [23, 24]. In other words, in contrast to gonochorists, hermaphrodites function as males and as females. The mating process of *L. terrestris*, as described by Grove [31] and supplemented by more recent studies [32, 33], is depicted in Figure 5. During these nocturnal episodes, which last from one to 3 hours, the partners remain anchored in their home burrow with their tail end, which permits a rapid retreat in case of an attack of a predator. During copulation, both worms establish a contact to the clitellar region of the partner (see Figure 4). Thereafter, both earthworms bend their anterior segments away from the partner's body, which results in an "s-like" position. During this tight body contact, both partners exchange sperm and hence function as males. After reciprocal insemination is finished, the worms separate from each other, a mechanical process that can cause severe body damage due to the partner's sharp copulatory bristles (setae).

According to Michiels et al. [33], the lunar cycle affects mating activity, since the relatively high copulation frequency during dark nights (once every 7 to 11 days) is very low during the full moon. Moreover, the authors have discovered that sometimes smaller individuals are pulled out of their burrows by the larger partner after a "tug-of-war" that ends a mating episode. As pointed out by Nuutinen and Butt [32], *L. terrestris* is the only earthworm species for which mating on the soil surface has been documented. In general, the mating process in *L. terrestris* (Figure 5) is reminiscent to that of aquatic leeches of the genus *Erpobdella* and that of the European land leech *Xerobdella lecomtei* [24, 25]. Several days after copulation, the earthworms act as females and produce lemon-shaped capsules (cocoons) that contain 5 to 8 fertilized eggs via their clitellum, a process that resembles that of worm-leeches of the genus *Erpobdella* [23, 24].

## 6. The Discovery of the Giant Endemic Earthworm *Lumbricus badensis*

In contrast to his son Francis, who supported his father in his researches on the movements of plants, as well as the earthworm studies described here, and later became a professional plant physiologist, the geologist/biologist Charles Darwin never visited Germany. The older Darwin would have been

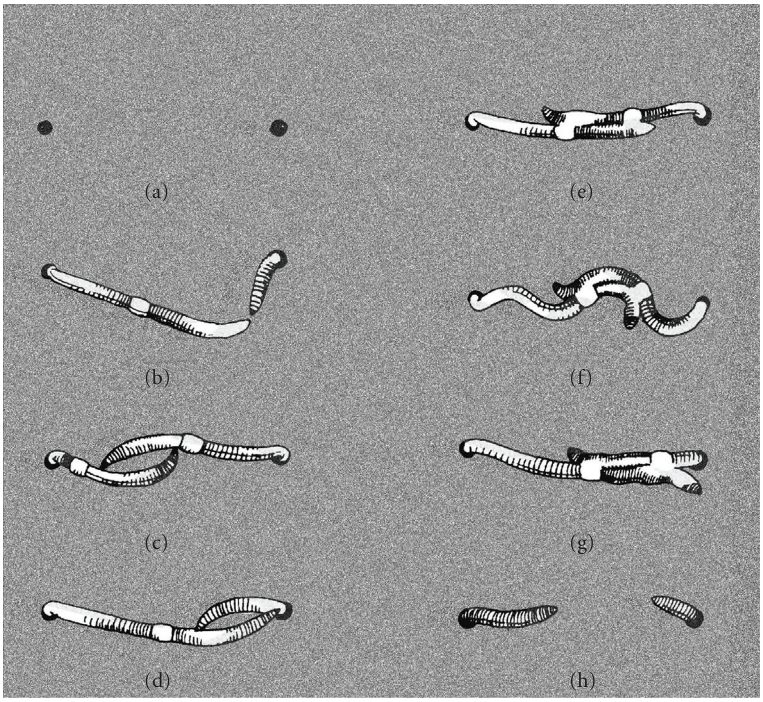


Figure 5: Precopulatory behaviour and mating in the common earthworm (*Lumbricus terrestris*), observed during dark summer nights with special equipment. Both partners remain anchored in their burrows (distance of the holes ca. 7 to 8 cm) (a) and evaluate each other in an extensive courtship process (b), (c), (d). Copulation occurs via the reciprocal attachment of the clitella (see Figure 4) and results in the exchange of sperm (e), (f), (g). After 1 to 3 hours the worms separate and retreat into their burrows (h) (adapted from [32]).

pleased to study the geology and biology (fauna, flora) of the Black Forest (Schwarzwald), a wooded mountain range in southwest Germany (Federal State Baden-Württemberg) that consists of a cover of sandstone on top of a core of gneiss. During the Würm glaciation, which ended ca. 10 000 years ago, the Black Forest was covered with glaciers. The six highest mountains are the Feldberg (1493 m), Herzogenhorn (1415 m), Belchen (1414 m), Spieshorn (1349 m), Schauinsland (1248 m), and the Kandel (1241 m above sea level). The dense forests consist mostly of pines (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which are grown in many places as commercial monocultures. In addition, beech (*Fagus sylvaticus*) forests form integral parts of the lower regions of this unique landscape in Southern Germany.

More than a century ago, the German annelid specialist W. Michaelsen investigated the soil of the southern part of the Black Forest, but no common earthworms (*L. terrestris*) were found in this habitat. However, he discovered a single individual of an unidentifiable earthworm that he later described as *L. papillosus* (Syn. *fiendi*) var. *badensis* [34]. Hence, Michaelsen interpreted his giant earthworm from the Federal State Baden-Württemberg as a local (geographic) variety of the common Atlantic-Mediterranean taxon *L. friendi*. Later, it was discovered that this large earthworm (Figure 6) represents a separate biospecies that is not closely related to the widespread *L. terrestris* but is a sister taxon of *L. friendi* [35], a relatively small species (length ca. 12 cm) that Darwin [2] may have studied in Great Britain [10, 13, 29].

In contrast to the common earthworm (*L. terrestris*), which can reach a body length of 15 cm (diameter at rest ca. 0.6 cm) (Figure 4) and does not cooccur with *L. badensis*, adult Black Forest-worms (Figure 6) are up to 34 cm long with diameters of 1.2 to 1.6 cm (body mass: 25 to 40 g). When fully extended, adult *L. badensis* individuals can reach a length of up to 60 cm [35] and hence are on average as large as the common limbless burrowing reptile *Anguis fragilis*. This vertebrate is also known under the name “slow worm” and has been confused with *Lumbricus badensis*. In Figure 7, an adult *L. badensis* that was isolated from its burrow and an *A. fragilis* of average length are juxtaposed. Both animals were collected in the same habitat. The enormous body size of the giant Black Forest earthworm becomes apparent [35].

In forests with large litter layers, the usually deep-digging (anecic) species *L. terrestris* can live epigeic, without the construction of a burrow [37]. Darwin [2] would have been surprised to hear that one of his “common worms” has, in certain European habitats, adapted to such an alternative way of life. Detailed studies have shown that the Black Forest earthworm (Figures 6 and 7) displays a switch from an epigeic to an anecic (burrowing) way of life during its ontogeny. This aspect of the life cycle of *L. badensis* is described in the next section.

## 7. Biogeography, Evolutionary Origin, and Ecology of *Lumbricus badensis*

After decades of research it is now definitively clear that the giant earthworm *L. badensis* is a neoendemic species that inhabits exclusively the acid soils in a relatively restricted


Figure 6: Photograph of a giant Black Forest earthworm (adult individual of *Lumbricus badensis*) in its natural habitat. Note that the worm is anchored with its anterior body part in its burrow (adapted from [36]).

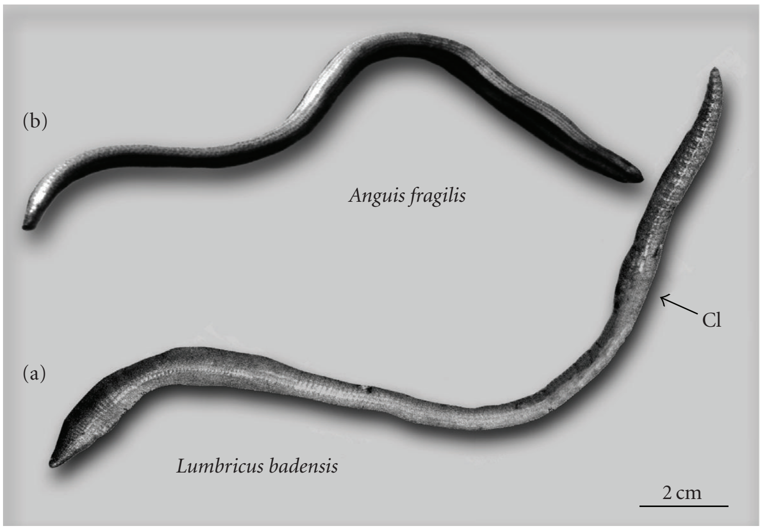


Figure 7: Photographs of adult individuals of the giant earthworm (*Lumbricus badensis*) (a) and a limbless reptile (*Anguis fragilis*), the "slow worm" (b), collected in the same habitat in the Black Forest (Schauinsland, Southern Germany, ca. 1200 m above sea level). Note that the worm and the reptile are about the same size. The heads of both animals point to the right side. Cl=Clitellum.

area of the Black Forest, a region where no other *Lumbricus*-species occur [36, 37, 39]. Detailed biogeographic studies on the occurrence and habitats of the sister taxa *L. friendi* (length ca. 12 cm) and *L. badensis* (length up to 34 cm) revealed that, after the end of the last ice age (ca. 10 000 years ago) founder populations of the smaller and more widespread ancestor (a species closely related to extant *L. friendi*), were separated via the river Rhine and hence became geographically isolated [37]. The young founder populations of ancient *L. friendi*, which may have originated during a time period between 8000 and 6000 years ago, rapidly occupied the new habitat in the Black Forest in regions from 300 to 1400 m above sea level, where presumably no other competing earthworm species lived. As mentioned above, the common species *L. terrestris* does not cooccor with *L. badensis,* possibly due to the high acid content of the soil that the Black Forest worms inhabit. In this specific habitat, which represented a vacant ecological niche at that time, the geographically separated Atlantic earthworms established a new, reproductively isolated biospecies. Due to the large difference in body size and hence the dimension of the corresponding clitellum, no copulations are possible between extant *L. friendi* and *L. badensis*. Zoogeographic studies along the narrow regions in Southwest Germany, where both species co-occur, have never found hybrids [35, 39]. It follows that Ernst Mayr's model of allopatric speciation accounts for the evolutionary origin of the endemic Black Forest-earthworm *L. badensis* [30, 40]. However, the question why *L. badensis* evolved such an enormous body size within only a few thousand years is not yet answered. It is likely that these neoendemic earthworms rapidly adapted to the new habitat where predators were abundant and hence larger individuals in the variable founder populations had a better change of survival, but more work is required to further corroborate this hypothesis. As an alternative, it has been postulated that specific environmental conditions, such as the composition and structure of the soil, were factors that caused the selection and survival of larger individuals

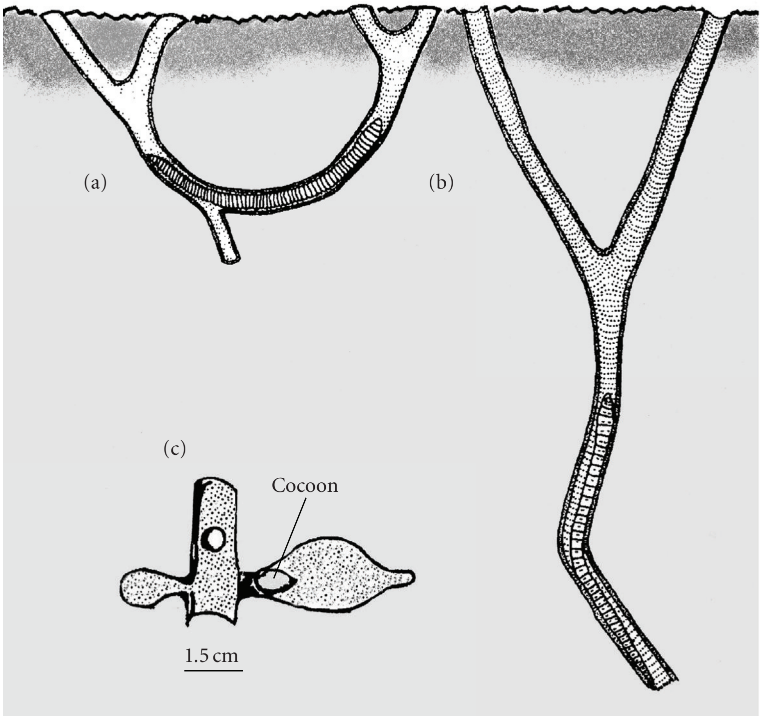


Figure 8: Schematic drawings of the burrows of juvenile (a) and adult (b) individuals of *Lumbricus badensis*. At depths of 40 to 150 cm below the soil surface, along burrows of adult *L. badensis* individuals, cocoon chambers with egg-capsules have been observed and documented (c). This indicates that parental investment is part of the reproductive strategy in this endemic earthworm species (adapted from [37]).

over thousands of subsequent generations [35], but no direct evidence supports this idea. It should be noted that, according to Wikelski [41], a number of hypotheses have been proposed to account for the evolution of body size in animals. Unfortunately, no consensus has yet emerged as to a general explanation for this phenomenon.

Twenty five years ago, the burrows of juvenile and adult *L. badensis* were investigated in fir-beech forests located in the southern part of the Black Forest about 1000 m above sea level [35, 37]. After hatching from the cocoons, which are deposited in chambers located 40 to 150 cm below the soil surface (Figure 8(c)), *L. badensis*-individuals are 5 to 7 cm long (body mass: 0.4 to 0.6 g). It should be noted that nothing is known about the mating behaviour in this earthworm species. The juvenile worms crawl upwards until they reach the soil surface. Most of the newly hatched individuals, which are found during the spring, build horizontal tubes with their casts, usually between the soil surface and pieces of bark, and so forth. One to 2-year-old earthworms (body mass: 1.5 to 2.5 g) construct U-shaped burrows (Figure 8(a)) that are similar to those of adult *L. terrestris* (see Figure 2) [42]. Older juveniles with body masses of more than 2.5 g construct deep, V-shaped burrows (depth ca. 2.5 m) that are indistinguishable from those of the adults. A characteristic feature of all of the *L. badensis* burrows investigated in the Black Forest is that the tube splits into several (2 to 6) outlets near the soil surface (Figure 8(b)). In the burrows of adult earthworms, several cocoon chambers along the main tube were found in the region at 40 to 150 cm below the soil surface (Figure 8(c)). As in semiaquatic leeches of the genera *Hirudo* and *Haemopis* [24, 25], the giant earthworm constructs brood chambers for the next generation. Hence, parental investment has evolved as a survival strategy of the populations in this endemic Black Forest earthworm. It is not known whether such a sophisticated mode of parental investment occurs in any other earthworm species.

At any rate, Charles Darwin, who explicitly pointed out that his metaphorical "struggle for life" does not only mean the competition for limited resources but also includes the care for young by adults, and hence nonselfish, cooperative behaviour [43], would have been pleased if he had known that one European "worm species" had evolved such an "intelligent" mode of reproduction. In addition, it is obvious that the earthworm burrows are a striking example for "niche construction", that is, the active modification of the habitat of organisms with positive consequences for survival and mode of reproduction [12, 44].

## 8. Conclusions

In 1837, one year after his return from the voyage of the *Beagle*, Charles Darwin started his career as an independent scientist with observations and a subsequent speech on earthworms that was published in 1838 [4]. Almost 45 years

Figure 9: Cartoon by E. L. Sambourne, published in the *Punch* in 1882 with the sentence "Man is but a worm". This parody of Charles Darwin's concepts on the origin of humanity has been corroborated by recent molecular data on the phylogenetic relationships of annelids and vertebrates (adapted from [38]).

later, he ended his life with the publication of a little book on "worms" [2]. This became so popular that a famous cartoon connected ancient annelids, via intermediate forms, with the human species, represented by Charles Darwin (Figure 9). It should be noted that Darwin's monograph rapidly modified the perception of earthworms by society. Up to then, earthworms were considered by gardeners, agriculturists, and so forth, as soil pests that have to be eliminated—Darwin's work changed this belief forever and finally led to the concept of bioturbation as well as the discipline of soil biology [3, 10, 13].

It is likely that Charles Darwin [2] was referring to the common species *L. terrestris* when he pointed out that earthworm burrows are "... not mere excavations, but may rather be compared with tunnels lined with cement" [2, page 112]. Hence, according to the British naturalist, earthworms actively construct their home according to their needs. This is one of the earliest examples for the concept of "niche construction" we could find in the scientific literature on the evolution of macro-organisms on Earth [12, 44].

We conclude that Darwin's monograph on the biology of earthworms was not simply a "curious little book of small importance" [1], but a significant work that is still cited today in a variety of scientific disciplines [3, 28]. Finally, we want to point out that modern "earthworm research", which originated with Darwin [2], yielded the insight that geographic separation of founder populations can result in the "creation" of new *Lumbricus* species within a time period of less than 10 000 years [35]. In his masterpiece *On the Origin of Species* [27], Charles Darwin argued that speciation events are too slow to be observed (or reconstructed) within the lifetime of one human being. He would have been pleased to read that, 150 years later, earthworm researchers have elucidated a rapid speciation event that occurred after the end of the last Ice Age in a restricted area of the south western part of Germany.

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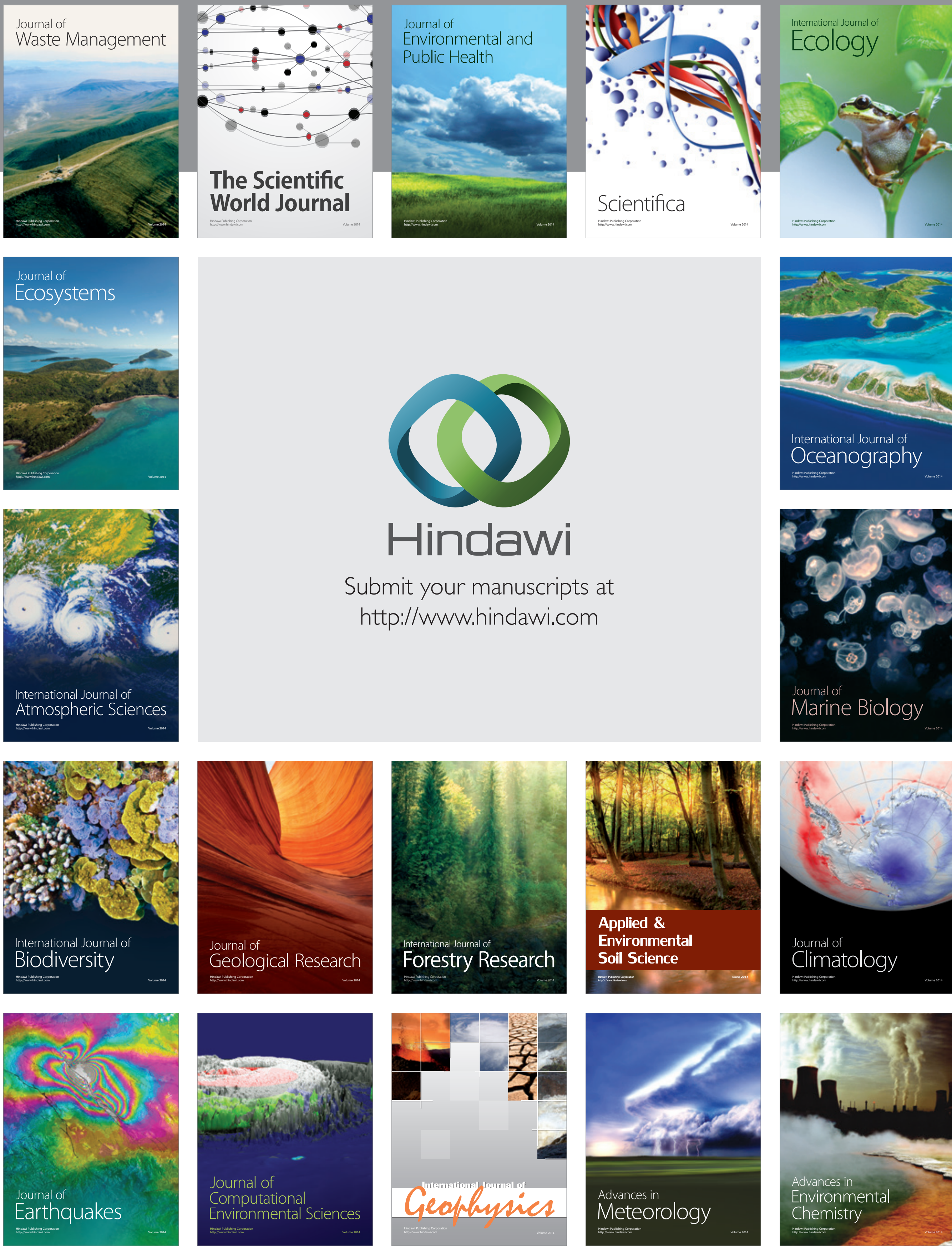
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