Biology of Earthworms

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Foreword to First Edition

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As the classroom type of the Annelida, 'the earthworm' is familiar to every student of biology. Dissection manuals neatly package its anatomical features and numerous texts admirably relate earthworm form and function. Beyond these frontiers, student and teacher alike are met by a bewildering mass of publications ranging in content from the military value of earthworms as survival food, to the species stored by moles. The volume of this literature is quite exceptional for an invertebrate group which is important neither as pest nor food. It stems from the inherent zoological interest of the earthworm as a terrestrial form retaining many of the characteristics of its aquatic ancestors; from its convenience as an experimental animal for behaviourists and physiologists; and from its effects on soil fertility.

This last aspect had already been perceived two centuries ago by Gilbert White of Selborne who, in 1770, wrote, 'Earthworms, though in appearance a small and despicable link in the chain of Nature, yet, if lost, would make a lamentable chasm ... worms seem to be the great promoters of vegetation, which would proceed but lamely without them, ...' In more recent times, such ideas have been critically examined and extended at Rothamsted Experimental Station in a programme of earthworm research pioneered by Sir John Russell and continued by a number of workers during the last twenty-five years. It is particularly appropriate that the task of surveying the earthworm literature and summarising it at readable length should have been undertaken by the current representatives of this Rothamsted tradition.

An important part of this book which will be particularly valuable to soil zoologists, is the bibliography of between five and

six hundred literature references. An analysis of their frequency distribution in time throws an interesting light on the development of earthworm studies. Divided into twenty-year periods they fall as follows: 1870–1889 6; 1890–1909 12; 1910–1929 68; 1930–1949 106; 1950–1969 361. Allowing for some selection in favour of more recent studies, it seems that, whereas around the turn of the century earthworm papers were published on average about one every other year, in the last two decades one was published on average about every three weeks. If publication continues at this exponential rate, a revision of this book in twenty years' time will involve the formidable task of reviewing another 640 papers.

In the face of this alarming publication explosion it is interesting to note how slowly concepts and attitudes change, even amongst contemporary ecologists. Charles Darwin's famous book, *The Formation of Vegetable Mould through the Action of Worms*, published in 1881, provides a good example. When Henry James described the requirements for a successful mid-Victorian genre painting as 'that it shall embody ... some comfortable incident of the daily life of our period, suggestive more especially of its ... familiar moralities', he might well have had in mind Darwin's analogies of earthworms as beneficent gardeners and industrious ploughmen. It is significant to find this anthropocentric approach epitomised almost a century later in this present book in the chapter title 'Earthworms as benefactors'. Indeed, as the authors show, some of our ideas about earthworms can be traced back to Aristotle.

Despite the voluminous literature of the intervening period, E. W. Russell, summarizing our knowledge of the importance of earthworms in agriculture, wrote in 1950, 'They may play an important role in the conversion of plant into humus..., but this has not yet been rigorously proved'. Twenty-two years later this is still substantially true for we now know that earthworm activity is primarily important through its effects on soil microflora and these effects are extremely difficult to measure outside the artificial conditions of laboratory cultures. Advances in this field await developments in the techniques of microbiology.

The prospective student of earthworm ecology should not be inhibited by the weight of past research for much remains to be done. Important land-use changes may be expected in Europe in

the coming decades with the restoration of former industrial sites and the withdrawal of five million hectares from agricultural use under the Mansholt plan. It is in this marginal and restored land, rather than in the agricultural lowlands, that earthworm research is likely to be most relevant and fruitful for it is under the less intensively managed land on base rich sites that soil processes generally become dominated by earthworm activity. Outside the temperate zone and particularly in the tropics, much progress has been made in recent years in the basic taxonomy of indigenous earthworm species, but knowledge of their functional role as components of ecosystems is, at the best, fragmentary. Dr Edwards' and Mr Lofty's review of the current state of earthworm knowledge will prepare the way for another generation of research in these diverse and important fields.

J. E. Satchell

Preface to Second Edition

Earthworms can be defined as invertebrates, belonging to the Phylum Annelida, Order Oligochaeta, Class Clitellata, which live in soil. They range in size from a fraction of a centimetre to two or more metres long.

Oligochaetes can be aquatic or terrestrial; members of seven families that are aquatic and rather small are termed microdiles (Microdili), whereas worms in the other ten families are mostly terrestrial, much larger and are usually called megadriles (Megadrili).

It is worms in the latter group that we normally call earthworms. There are about 1800 species of earthworms distributed all over the world. The commonest worms in Europe, Western Asia and most of North America belong to the family Lumbricidae (the twenty-eight species belonging to eight genera reported from the British Isles to date all belong to this family). Other regions of the world are dominated by species from different families, thus, members of the Glossoscolecidae are most numerous in Central and South America, and the megascolecid group is most important in southern and eastern Asia and Australasia. Nevertheless, some lumbricids that are found commonly in North America, India, Ceylon, New Zealand and South Africa have probably been introduced from Europe, because their distribution often follows European colonization, and they are most numerous close to populated areas. Where these species are introduced they often multiply rapidly and supplant the native species.

Earthworms make a large contribution to the total weight or biomass of invertebrates in soil, particularly in temperate regions. Aristotle first drew attention to their role in turning over the soil

and called them 'intestines of the earth'. However, it was Charles Darwin (1881) who concentrated attention on the role of earthworms in breakdown of dead plant and animal material in soil and forest litter, and in maintenance of soil structure, aeration and fertility. His famous book *The Formation of Vegetable Mould through the Action of Worms* summarized the conclusions he had reached during the preceding forty years of experimental work and led him to express the opinion that 'earthworms have played a most important part in the history of the world'. Other scientists contemporary with Darwin (Hensen, 1877; Müller, 1884; Urquhart, 1887) also believed that earthworms played a beneficial part in soil formation, and some stated that they were essential for soil fertility.

Many of the conclusions and hypotheses reached by Darwin have been repeated so many times in the literature, that they are taken as almost unassailable fact, and have been little tested either in field or laboratory. One of the difficulties of interpreting Darwin's conclusions is that he did not identify the species of worms in his experiments, and different species of worms behave very differently; for instance, only a few species have permanent burrows and produce casts.

Nevertheless, the importance of his contribution to our knowledge of earthworms cannot be stressed enough, and his work led to the great upsurge of interest in earthworms during the late nineteenth and early twentieth century. Unfortunately, much of this work was concentrated on morphology and detailed histology, rather than on basic biology and ecology, although it included elegant experiments on the functioning of the nervous, digestive and excretory systems. However, workers such as Russell (1910) and Salisbury (1925) confirmed the importance of earthworms in soil fertility.

There have been few books or reviews on earthworm biology. The standard work of reference on oligochaetes is still the extensive and painstaking work of Stephenson (1930), which not only reviewed their taxonomy and morphology, but contained much information on their biology, some on physiology and other aspects. Reviews have been published by Avel (1959), Satchell (1958, 1967), Tembe and Dubash (1961) and Stolte (1962); and

Laverack (1963) effectively reviewed the physiology of earthworms; there is also considerable scattered information in various chapters in books on soil zoology by Kühnelt (1961); Kevan (1955, 1962); Bachelier (1963); Müller (1965); Doeksen and van der Drift (1963); and Graff and Satchell (1967). There have been excellent taxonomic reviews by Graff (1953) for Germany, Bouché (1972) for France, Gerard (1964) for Great Britain, Gates (1972) for Burma and Lee (1959) for New Zealand. A useful compilation of papers was published by Rodale (1961) and there have been two books on breeding earthworms, Barrett (1949) and Gaddie and Douglas (1975). A valuable series of papers on the ecology of earthworms in the U.S.S.R. was published in 1975 by Atlavinyte. We have made extensive use of the review by Satchell (1967) for chapters 6, 7 and 8 and the many publications by Bouché, Doeksen, Evans, Gates, Graff, Ghilarov, Guild, Ljungström, Murchie, Reynolds, van Rhee, Satchell, Sims, Zajonc and Zicsi in the rest of the book.

The authors would like to express their gratitude to those of their colleagues at Rothamsted who provided valuable assistance in many different ways. In particular, we should like to thank Dr C. G. Johnson for encouraging the project, Mrs Doreen Fisher for typing much of the manuscript, Mr I. H. Haines and Mr D. J. Holdaway for critically reading the manuscript, Mr Roger Turner for assistance with the stereoscan photographs, and Mr A. E. Whiting, Mr J. E. Bater and Miss B. A. Jones for preparing the diagrams and their help with the index.

Most of the diagrams were redrawn from various sources, and acknowledgements are given below the figures. In particular Figs 4, 5, 7, 11a and b, 12, 14 and 16 were redrawn from Grove and Newell's textbook, *Animal Biology*, Figs 3, 6, 10, 15 and 17 from Stephenson's monograph, *The Oligochaeta*, and Figs 21, 29, 33, 45 and 49 from Satchell's review (1967). Dr D. S. Madge kindly provided the photograph for Plate 7a and Dr J. M. Hirst those for plates 6a and 6b.

No previous book has attempted the almost impossible task of reviewing all the aspects of the biology, morphology, physiology, taxonomy and ecology of earthworms fully in a single volume. In particular, earthworm taxonomy is still in a very fluid state with

considerable discussion and controversy. We have attempted to cover these topics and present the available data on biology and morphology in a straightforward manner emphasizing most, the ecology of earthworms and their important contributions to soil formation, structure and fertility. We hope it will serve to interest a wide audience, and even if its only contribution is to emphasize the paucity of current knowledge in respect of some fundamental aspects of the biology and ecology of earthworms, we feel it will still have made a useful contribution. We are encouraged by the fact that the first and second printings of the book have sold out, and in this, the second edition, we have attempted to bring the book up to date on developments in the three and a half years since the first edition and fill several omissions.

Rothamsted Experimental Station, C.A.E.
Harpenden J.R.L.
July, 1976

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1. Morphology

The principal systematic features of earthworms are that they are externally segmented, with a corresponding internal segmentation. They have no skeleton and a thin pigmented cuticle bearing setae on all segments except the first two. They are hermaphrodite with relatively few gonads that are situated in definite segmental positions. When mature, a precisely located swollen area of the epidermis called a clitellum secretes a cocoon in which the eggs or ova are deposited. These are usually fertilized and there is development within the egg without a free larval stage, the newly-hatched worms resembling the adults.

Structurally, earthworms have large coelomic cavities containing coelomocytes, a closed vascular system with at least a dorsal and a ventral trunk and a ventral nerve cord. The alimentary canal is basically an anterior – posterior tube with excretion through the anus or specialized organs called nephridia; respiration is mainly cuticular.

1.1 Segmentation: external

Earthworms are divided externally into bands or segments along the length of the body by furrows or intersegmental grooves, which coincide with the positions of the septa dividing the body internally. The segments vary in width, usually being widest in the anterior and clitellar regions. Segments are arbitrarily numbered from the front to the rear, and the grooves are designated by the numbers of the segments on either side, e.g. 3/4, 10/11, etc. Often, the external segments are subdivided by one or two secondary grooves, particularly in the anterior part, but these are superficial divisions which are not reflected in the internal

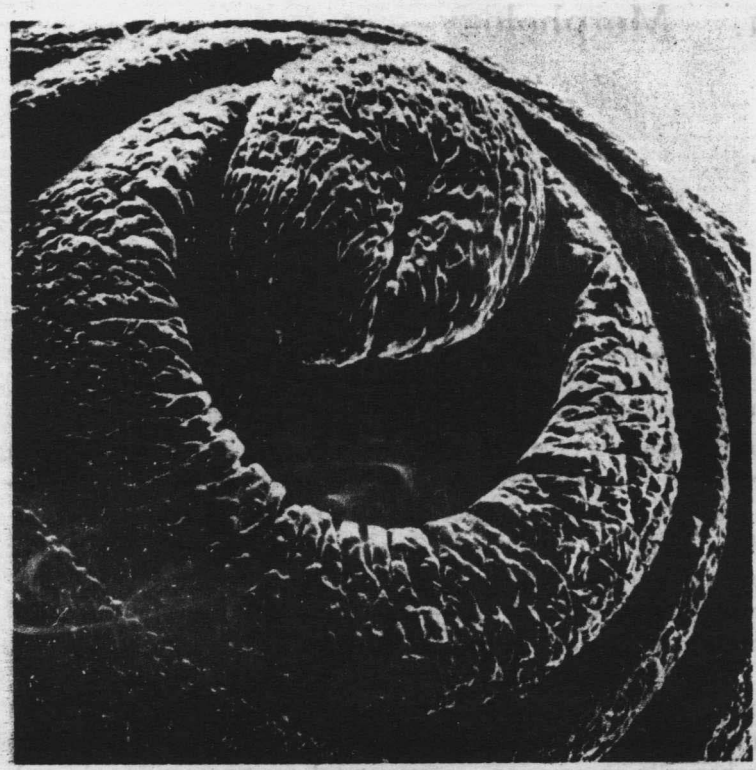

Plate 1 Prostomium of *A. caliginosa*

anatomy. The mouth opens on the first segment, or peristomium, which bears on its dorsal surface the prostomium, a lobe overhanging the mouth (plates 1, 2a and b). The prostomium varies in size, and in some worms it may be so small that it cannot be distinguished. The way the peristomium and the prostomium are joined differs between species and is a useful systemic character. The connection is termed zygolobous, prolobous, epilobous or tanylobous, depending on the demarcation of the prostomium (Fig. 1). Some of the aquatic worms (Naididae and Lumbriculidae) have the prostomium extended forward into a proboscis.

Plate 2a Epilobous prostomium of *A. chlorotica*
Plate 2b Epilobous prostomium of *A. caliginosa*