# SOIL ZOOLOGY, THEN AND NOW - MOSTLY THEN

*D. Keith McE. Kevan*
*Department of Entomology and*
*Lyman Entomological Museum and Research Laboratory*
*Macdonald College Campus, McGill University*
*21, 111 Lakeshore Road*
*Ste-Anne de Bellevue, Que. H9X 1C0*
*CANADA*

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## ABSTRACT

*Knowledge of the animals that inhabit soil remained fragmentary and virtually restricted to a few conspicuous species until the latter part of the 19th Century, despite the publication, in 1549, of the first attempt at a thesis on the subject by Georg Bauer (Agricola). Even the writings of far-seeing naturalists, like White in 1789, and Darwin in 1840, did not arouse interest in the field. It was probably P.E. Müller in 1879, who first drew particular attention to the importance of invertebrate animals generally in humus formation. Darwin's book on earthworms, and the "formation of vegetable mould", published in 1881, and Drummond's suggestions, in 1887, regarding an analgous role for termites were landmarks, but, with the exception of a few workers, like Berlese and Diem at the turn of the century, little attention was paid to other animals in the soil, save incidentally to other investigations. Russell's famous* Soil Conditions and Plant Growth *could say little about the soil fauna other than earthworms. Prior to the Second World War, Bornebusch, in 1930, and Jacot, in 1936, attempted to broaden the horizons of both zoologists and pedologists, but it was not until the end of the war years beginning with Forsslund's work in Sweden, published in 1945, that soil fauna studies really got under way. From the pedological, rather than the zoological point of view, a book by Kubiëna, published in 1948, set the stage. Then, in addition to research publications, several books on different aspects of soil fauna in general appeared from 1949 to 1951 by: Gilyarov, Franz, Kühnelt, and Delamare de Boutteville. The first international colloquium on soil fauna was held in 1955, since when there have been many, the latest before the present one in 1982. There has nevertheless (with a few notable exceptions) been a general lack of interest in the fauna on the part of pedologists, and reluctance to intrude into the realms of so-called "soil science" by soil zoologists, to mutual disadvantage. There is still an almost complete absence of appreciation, especially among those who determine the directions of soil research, that we are still without the means of proper identification of innumerable members of the soil fauna, and that the understanding of basic soil ecology and the pedological importance of the fauna is impossible without this.*

## RÉSUMÉ

*L'auteur passe en revue le développement des connaissance sur les animaux qui habitent dans le sol, depuis les débuts jusqu'à maintenant. Ces connaissances demeurèrent fragmentaires et pratiquement restreintes à quelques espèces frappantes jusque dans la deuxième moitié du XIXième siècle, et ce malgré la parution, en 1549, d'un premier essai de*

*thèse sur le sujet par Georg Bauer (Agricola). Même les écrits de naturalistes clairvoyants, tels que White (1789) et Darwin (1840), n'émulèrent que peu d'intérêt dans ce domaine. P.E. Müller (1879) fut probablement le premier à porter une attention particulière au rôle important des invertébrés dans la formation de l'humus. L'ouvrage de Darwin (1881) sur les vers de terre et «la formation des moisissures végétales» et les suggestions de Drummond (1887) concernant un rôle analogue chez les termites constituèrent des évènements marquants, mais, à l'exception de quelques chercheurs tels que Berlese et Diem à la fin du siècle, la plupart portèrent peu d'attention aux autres animaux vivant dans le sol, sauf accessoirement durant le cours de d'autres travaux. Le fameux ouvrage de Russell paru en 1912 et intitulé* Soil Conditions and Plant Growth *contient peu d'informations sur la faune des sols autre que les vers de terre. Avant la Deuxième Guerre Mondiale, Bornebusch (1930) et Jacot (1936) essayèrent d'élargir les horizons des zoologistes et des pédologues, mais ce ne fut qu'à la fin de la guerre que l'étude de la faune des sols prit vraiment son essor avec les travaux de Forsslund en Suède en 1945. Du point de vue pédologique plutôt que zoologique, l'ouvrage de Kubiëna (1948) établit le domaine. Par la suite, en plus d'articles scientifiques, plusieurs ouvrages traitant de différents aspects de la faune des sols en général parurent en succession rapide: Ghilarov (1949), Franz (1950), Kühnelt (1950) et Delamare de Boutteville (1951). Le premier colloque international sur la faune des sols eut lieu en 1955 (Kevan, 1955) et fut suivi par plusieurs autres, dont le dernier précédent celui-ci eut lieu en 1982 (Lebrun* et al., *1983). Néammoins, on remarque en général un manque d'intérêt dans la faune des sols chez les pédologues (mis à part quelques exceptions notables), de même qu'une hésitation de la part des zoologistes étudiant la faune des sols à s'ingérer dans le domaine des soi-disant «sciences des sols»; cette attitude constitue un désavantage mutuel. Il existe un manque quasi total d'appréciation, particulièrement chez ceux qui décident de l'orientation de la recherche sur les sols, du fait que nous ne disposons toujours pas d'outils adéquats pour identifier les innombrables membres de la faune des sols, et que notre compréhension des éléments de base de l'écologie des sols et de l'importance pédologique de la faune ne pourra s'améliorer sans cela.*

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## INTRODUCTION

Prehistoric man was well aware of other creatures that shared his environment, and he undoubtedly associated some of these, such as various "worms", ants and termites with the earth beneath his feet. Like his present-day counterparts among the Bushmen of southern Africa and the Aboriginals of Australia, too, he probably obtained an appreciable part of his food by digging for insect grubs. Nevertheless, the nearest thing, of which I am aware, to direct evidence for this acquaintance with such humble creatures is what seems to be a presumed amulet in the form of a possible *Necrophorus* burying-beetle of the Magdalenian culture of southern Germany, some 25,000–30,000 years ago (Peters & Töpfer, 1932; Schimitschek, 1977)(Fig. 1a). Another representation of a subterranean insect (though of a cave-, not a soil-inhabiting one) is also from the Magdalenian culture, but from southern France and

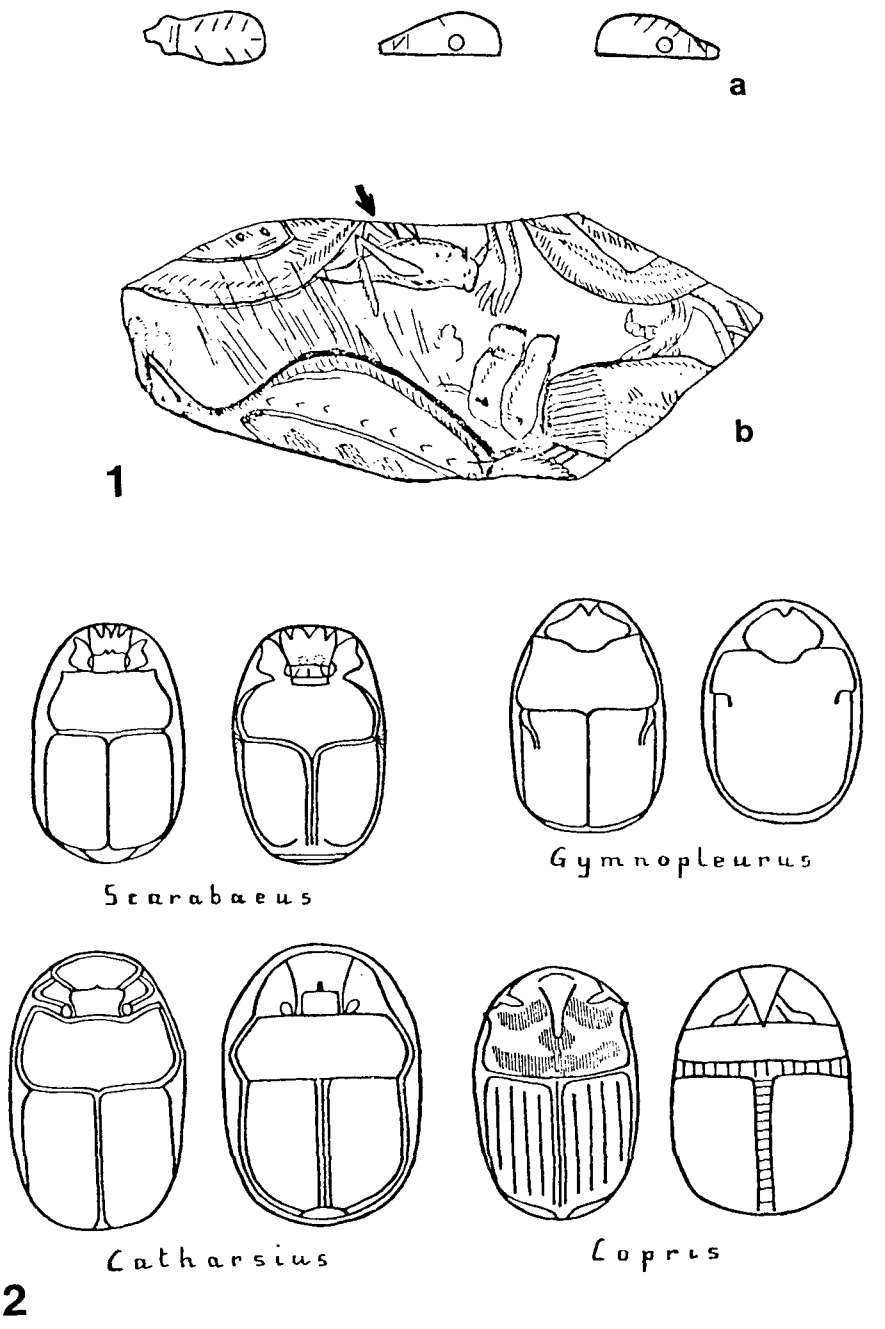


Fig. 1. Artifacts from the Magdalenian culture of Europe. (a) The oldest known representation of an insect. probably a *Necrophorus* burying-beetle; amulet made of Tertiary carbon from Hegau, Baden, Germany, 25,000 to 30,000 years old; after Peters and Toepfer (1932). (b) *Troglophilus* camel-cricket scratched on bison bone, Caverne des Trois Frères, Ariège, France, some 20,000 years old; after Bégouen and Bégouen (1928). Fig. 2. Ancient Egyptian stylized scarab seals (right member of each pair, various dates), compared with actual insect sketched on ovals (left member of each pair). After Petrie (1917).

apparently of considerably later date, though probably some 20,000 years old. This is in the form of a picture, scratched on a bison bone, clearly representing a species of the camel-cricket genus *Troglophilus*, which does not now occur in the region (Bégouen & Bégouen, 1928; Chopard, 1928; Schimitschek, 1977)(Fig. 1b). I know of little if anything else which antedates the ancient civilizations of Near, Middle and Far East that is relevant to our present theme.

## THE ANCIENT WORLD

From very early times (though there is little direct evidence from earlier than the 3rd Millennium B.C.E.), scarab beetles were revered, depicted and modelled in Egypt as symbols of Khēper (Fig. 2), a manifestation of the all-powerful Sun-god, Rā or Re (see, for example, Newberry, 1905; Petrie, 1917; Bodenheimer, 1928, 1949, 1960; Efflatoun, 1929; Schimitschek, 1968, 1977; Harpaz, 1973). It is thus unlikely that the priestly class was entirely unaware of the biology of such important creatures, parts of whose lives are intimately associated with soil. Nevertheless, so far as I can discover, and despite implications repeated by Harpaz (1973) to the contrary, there seems to be no written record of anything that may have been known at the time (with or without religious or philosophical association), other than what the adult beetles looked like and that they rolled dung-balls (Bodenheimer, 1928, 1949, 1960). Whether "worms" attacking ancient Egyptian crops were specifically cutworms (*e.g., Agrotis ypsilon*), as suggested by Efflatoun (1929), is a moot point.

We can infer from ancient sources, dating back to the 2nd Millennium B.C.E., that cicadas have been known from time immemorial to be part-time denizens of the soil, emerging in "ghostly" or "spiritual" form, as from the grave, symbolizing, notably in China, purity, immortality and/or resurrection after death (Brentjes, 1954, 1964; Schimitschek, 1968, 1977; Kevan, 1978; Riegel, 1981). They also had less lofty significance in "magic" and medicine and (as nymphs) as food (Chou, 1980; Riegel, 1981). The ancient Hellenes later, ultimately from the east (H. Kühn, 1935; Brentjes, 1954, referring also to two other publications by Kühn from 1943), acquired a reverence for cicadas. Especially among the people of Attica and Ionia, these insects came to symbolize an almost religious bond between man and his native soil. This sacred significance did not, however, preclude cicada nymphs from being dug up in large numbers by the ancient Greeks and used as food, as they were in China (*cf.* Kevan, 1978: 28, 29, 42, 45, 49). The oft-cited Athenian hair-ornaments called *têttiges* (i.e., cicadas) were probably based, if any actual insects were involved, upon soil-dwelling nymphs and not on winged adult cicadas (certainly not on grasshoppers as misguided western tradition has it!). This topic has been briefly discussed fairly recently by Kevan (1978: 435–436), but see also Hauser (1906–1908) and Brentjes (1954, 1958). Probably of similar antiquity to the Old World tradition, though without tangible evidence of this, are the Amerindian legends of both cicadas and ants being among the first creatures to emerge through the soil from the centre of the earth to populate its surface (see Kevan, 1983b). The soil fauna is thus something that has always been of interest to civilized as well as to primitive man.

Although legends and artifacts form a significant part of our source material relating to early knowledge and belief, we tend to place greater emphasis on the written word. In this regard, other than the earliest ancient Egyptian hieroglyphs for scarab beetles, and at least as old in written origin (though not in existing writing) as some of these, the earliest known references relating to our theme are those of the ancient Sumerians of present-day southern Iraq. Some 4,000 or more years ago, at the very latest, these enlightened people were certainly

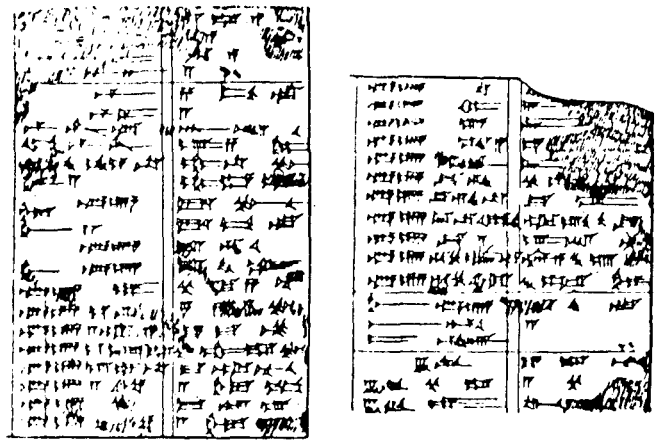

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Fig. 3. Fragments from the ancient Sumerian-Akkadian zoological lexicon, the *Ḫarra-Ḫubullu* - see below. After Bodenheimer (1949).

familiar enough with various members of the soil fauna to have applied different generic and specific (binominal) names to a number of them *and to have written these down.* Of such names we know a few from the *Ḫarra Ḫubullu*, a compendium prepared in the 9th Century B.C.E. by the successors and neighbours to the Sumerians, the Akkadians, giving equivalents in the two languages (Landsberger and Krumbiegel, 1934; Bodenheimer, 1949, 1960; Harpaz, 1973)(Fig. 3). The Sumerians of the early 18th Century B.C.E. (the time relevant to the later Akkadian text), and probably much earlier, distinguished between at least seven kinds of ants or *Kiši* (including *Kiši* ririga, or flying ants, and *Kiši* kurra, light-coloured and perhaps termites, not ants) and two kinds of earthworms of the annelid genus *Mar*, the *Mar gal* (or *Mar dib*) or *Mar tab* and *Mar* šāsur. They also had binomina for what seem to have been a mole cricket (*Gryllotalpa*), which they called *Ub pad*; for (field) crickets, known as *Buru zapâag(-tira)*) or *Buru balag(-gana)*) (*Buru* being the generic name for orthopteroid insects); and for a small, self-burying orthopteroid named *Buru saḫarra*, or "dust locust" (which, very tentatively, I have identified elsewhere as the pyrgomorphid *Tenuitarsus angustus* (Blanchard)).[1] What the Sumerians or Akkadians knew about these animals, however, we have no idea, though we can surmise that the former probably knew much more than history or archaeology will ever reveal. After all, in the fifth part of their most ancient of epics, the "Flood" legend of Gilgāmesh, they apparently associated adult dragonflies with the moulting of their aquatic nymphs (Sandars, 1959) thousands of years (so far as we are aware) before anyone else did so.[2]

Not quite so ancient as Sumerian sources are the early Sanskrit Vedic books of late in the 2nd Millenium B.C.E. These refer not infrequently to ants and/or termites, as indicated by various verse quotations given by Kevan (1978), though, apart from an association with subsurface moisture in two examples, the references are little related to soil.[3] Kevan (*op. cit.*) also gives later examples from early literature (including old Tamil, or Sangum, and later Sanskrit) relating to ants and termites, but mention of their role in the soil is again minimal.

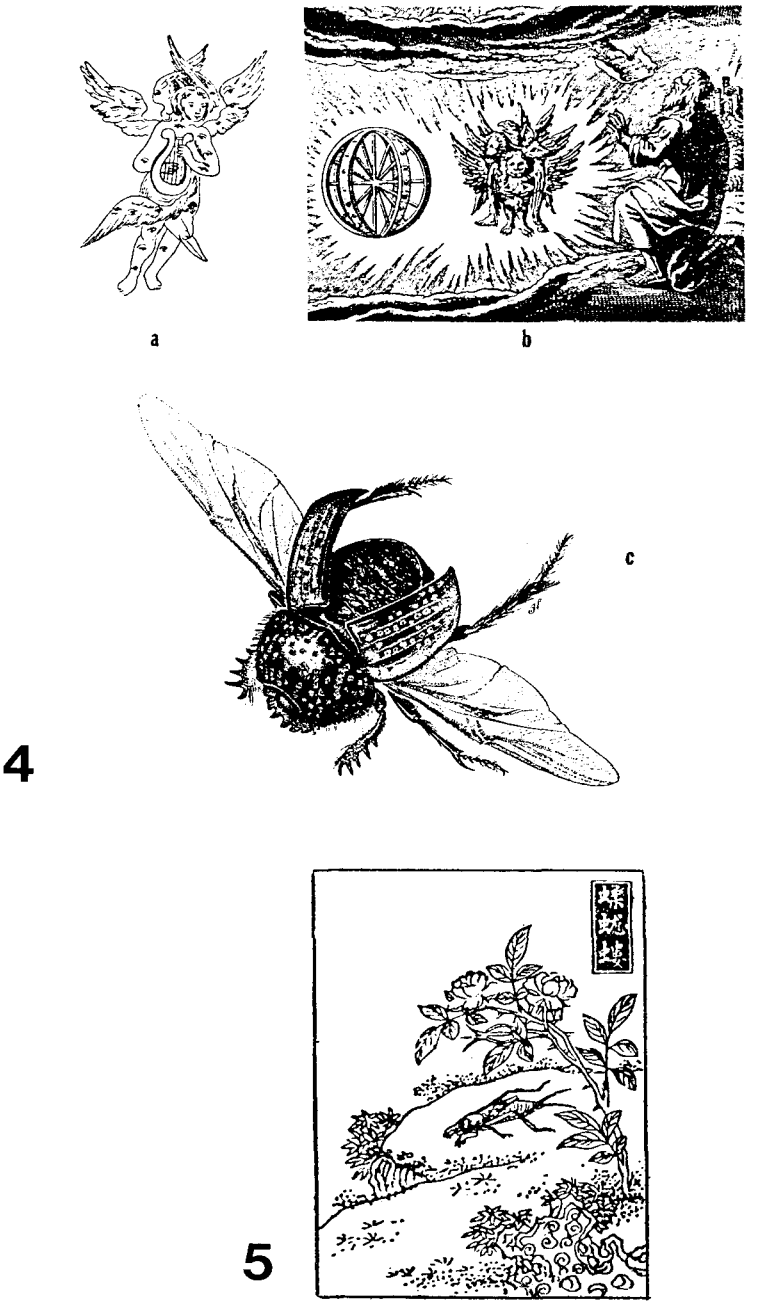


Fig. 4. "Ezekiel's wheels" (see text). (a), (b) Artists' fanciful interpretations of Ezekiel's cherubim; (a) after G. Eicke, 1964, in Schimitschek (1968); (b) after W. Merian, 1650; for reference, see Hogue (1983). (c) *Scarabaeus cicatricosus* in flight, showing salient features compatible with Ezekiel's account; after Hogue (1983). Fig. 5. Chinese mole cricket, *Gryllotalpa orientalis*, from the ancient illustrated encyclopaedia of Pu Shang, the *Erh-Ya*; from a late printed edition of about A.D. 1600. After Bodenheimer (1928).

The allusions to cicadas and ants in early Hellenic literature of the Homerian and immediately subsequent periods (9th-8th Century B.C.E.) are likewise mostly unrelated to the soil, and it is only in considerably later works that we come across surviving references to their "earthly" associations (see Bodenheimer, 1928, or, more briefly, Morge, 1973).

Although much Israelitic tradition is very ancient, most of the Hebrew scriptures as we know them, with some exceptions, were written down no earlier, and often much later, than the 6th Century B.C.E. These Scriptures, though referring quite frequently to insects, make virtually no unequivocal references to the soil fauna (the allusions to ants, in Proverbs VI, 6, and XXX, 24–25, being near exceptions).[4] Such references as there are to "worms" (*tola'ath*), where epigeic, plant-feeding insect larvae are not involved, are almost invariably to flesh-feeding dipterous maggots. Bodenheimer (1928, 1929, 1960) reviews briefly the insects referred to in the Hebrew Scriptures. There is, in addition, one brief reference, in the Book of Micah, VII, 17 ("King James", 1611 version: "... like crawling things of the earth they shall come trembling out of their close places ... ") that might conceivably refer to earthworms (indeed an alternative translation uses "worms ... move"). The principal interest of this uninformative passage lies in its possible antiquity. The book in question probably dates from about 720 B.C.E., though its later sections (including Chapter VII) could well be by a later author.[5]

Much more intriguing, on account of its controversial nature, is the somewhat later book of the prophet Ezekiel, originally dating from about 590 B.C.E. The Egyptian scarab cult, to which reference has already been made, eventually became widespread in the Near and Middle East, including Babylonia, where Ezekiel, like other Israelites of note, was captive. It is possible that, being a priest, he studied these religiously important insects out of interest, if not conviction. It has been concluded (Sajó, 1910; Schimitschek, 1968; Hogue, 1983) that he gave them the name *cherubim*, couching his description (made, probably, in the glaring sun) in allegorical, pseudoreligious terms (as would befit such venerable creatures) to the subsequent (possibly intentional) mystification of all and sundry (Fig. 4a, b). If an entomological interpretation of Ezekiel's *cherubim* be accepted, however, there is little in his account that goes much beyond the identification and description of the scarab beetles (Fig. 4c) and their dung-balls, though there is a hint of something more (Hogue, 1983).

In the 5th Century B.C.E., about a century after Ezekiel was allegedly peering myopically at scarabs by the Chebar canal in Babylonia, the Chinese illustrated encyclopaedia of Pu Shang, known as the *Erh-ya*, made its first known appearance (to be followed by numerous editions throughout the centuries). In it, soil fauna, including mole crickets (Fig. 5), scarabaeoid beetles (and their dung-balls and larvae), ants of several kinds, cicadas and centipedes were all included (Bodenheimer, 1928, 1929), though how many of these were in the "first edition", I do not know. So far as I can tell, little was included on the direct soil association of any but the mole crickets and cicada nymphs. Other ancient Chinese literature, e.g., in the form of early "herbals" or *pên-ts'ao*, is referred to by Chou (1957, 1980) and Konishi & Itô (1973), but the soil fauna is scarcely considered.

Although there were a number of early Hellenic literary references to insects and other terrestrial invertebrates (see, for example, Bodenheimer, 1928; Morge, 1973; Kevan, 1978), virtually none of the surviving writings mentioned soil-inhabiting animals, with the exception of brief allusions to gigantic, subterranean gold-digging "ants" in "India", which eventually became the mythical "ant-lions", and a hateful, biting creature known as the *amphisbaina* (amphisbaena). The latter, mentioned by Aiskhúlos (Aeschylus, 5th Century B.C.E.) in his

*Agamemnon* (see Druce, 1910), was traditionally (from later sources) a two-headed, poisonous burrowing serpent. Of both of these denizens of the earth, more will be said later, but it may be noted here that the giant ants are mentioned in the *Historíēs* Apódexis of Hēródotos Halikarnēsseos (Herodotus) of the mid 5th Century B.C.E. (Rawlinson, 1910). Quatrefages (1854) suggested that large termite mounds, rather than ant-hills, provided a basis for the legend. Hēródotos also mentions, in passing, the underground activities of Greek ants, but it was not until the time of Aristotēles Asklepiádos (Aristotle) that we have anything approaching scientific observation.

Of Aristotēles' five "notebooks" on zoology of about 320 B.C.E., four, now known by their Latin titles of *Historia Animalium*, *De Generatione Animalium*, *De Partibus Animalium* and *De Incessu Animalium*, the *original* Greek texts being long since lost, mention a few soil-dwelling creatures (see D'A.W. Thompson, 1910; Platt, 1910; Ogle, 1911; Farquharson, 1912). Though western scholars have, for centuries, been "brainwashed" into accepting Aristotēles as the founder of biology, he was really a late-comer, if an extremely important one, to the scene. His contributions to various aspects of the science were undoubtedly of immense significance, but he may well have transmitted many ideas from already ancient Middle Eastern (or even Oriental) sources of which we have no record. (One can scarcely imagine that the Sumerians, for example, did not bring about the dissemination of valuable zoological information). For all his great erudition and commendable powers of observation, Aristotēles contributed surprisingly little knowledge of the soil fauna (see the short entomological review by Bodenheimer 1928, 1929, and the even shorter one by Morge, 1973, based upon it). Indeed he had some very peculiar ideas on mould, decay and humification. With great originality (!) he observed (*Historia Animalium*, I, 1), that "some creatures dwell under ground, as the lizard and the snake. " (he had just mentioned that some provide themselves with homes, including mole and ant, so he did not immediately cite these again as examples); other versions of the text read: "some make themselves holes; others not so" (D'A.W. Thompson, 1910). He gave a reasonably good, succinct description of the life-history of cicadas, including the subterranean nymphal stage, or *tettigometra* (which he pronounced to be good to eat), and he also gave some notes on the biology of scarab beetles (*kântharoi*) and their dung-balls, and on the life of ants. Other soil fauna which he briefly described were myriapods, earthworms ("γēr emseqa or "earth's entrails") and moles. Both millipedes and centipedes were said to remain active after being cut into pieces (though there seems to be some confusion here with their marine, annelid-worm, counterparts). His two main references to earthworms were oddly confused with the origin of eels. Moles, he stated, cannot burrow if they are transported from one location to another. Aristotēles also mentioned certain "marginal" soil animals: woodlice, scorpions, pseudoscorpions, mites on insects (Oudemans, 1926), and digger wasps, burrowing bees and bumblebees. He did not mention the amphisbaena. His disciple Theophrastos, though making valuable contributions to entomology in the course of his botanical studies, did not refer to subterranean insects except for (cut)worms (?) that attack both roots and stems of wheat. Later, we have the opinion of Kleanthēs, about 270 B.C.E., that ants behave only instinctively - though Plutarch, about 100 A.D., believed later that they reacted intelligently (see Bodenheimer, 1928; Morge, 1973). Shortly before 200 B.C.E., the Roman playwright Titus Macchius Plautus (in *Mostellaria*, III, 2) refers to "*tarmes*" (some kind of wood-feeding insects, conceivably termites) boring from below ground (Kevan, 1978: 425).

The Macedonian physician Níkandros (Nicander) of Kolophōn, in his *Thêriakos* and *Alexipharmakos* of about the mid 2nd Century B.C.E., wrote extensively (in verse) on animals,

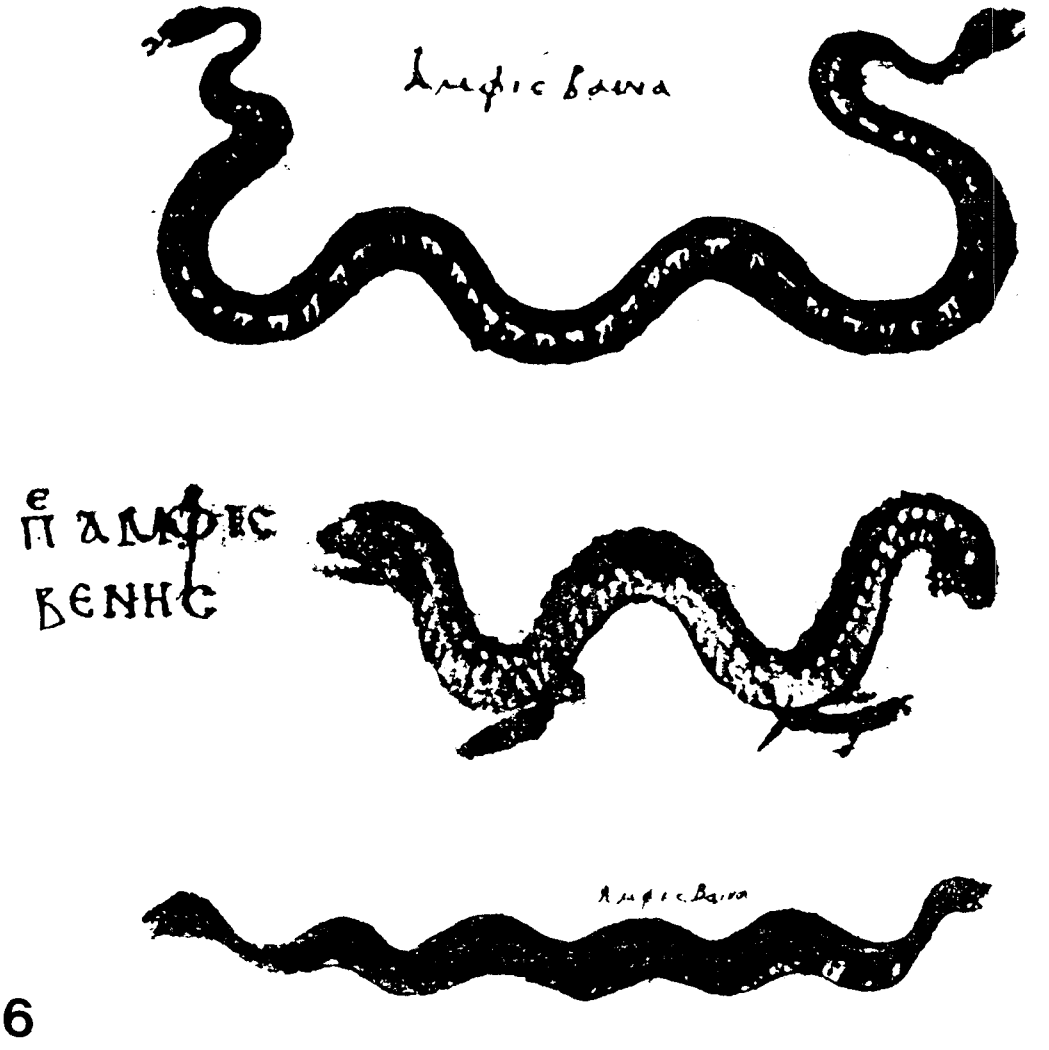


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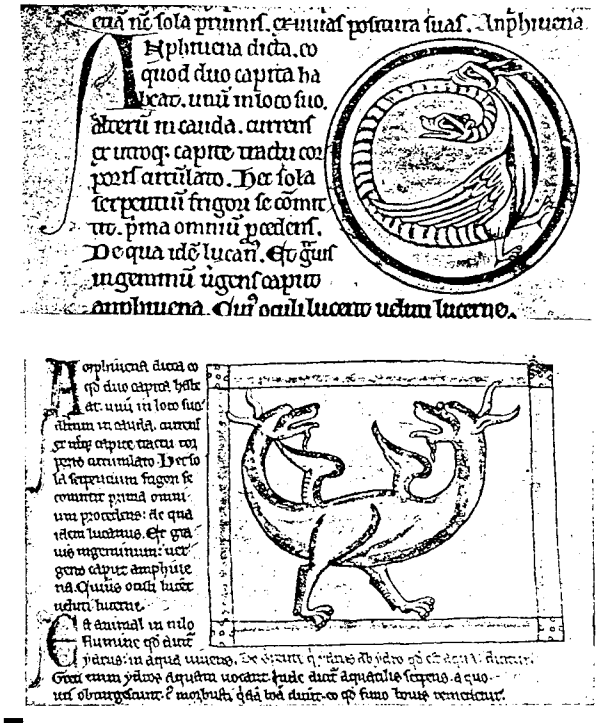
Fig. 6. The dreaded, two-headed, subterranean Amphisbaina (see p. 375): illustrations from Byzantine manuscripts descended from Níkandros' *Theriaka* of 2nd Century B.C.E., taken from Kádár (1978 : pl. 8, 55, 101). Top, from Cod. Paris. Suppl. Gr. 247, 10th Century; middle, from Cod. New York Pierpoint Morgan M. 652), 10th Century; bottom, from cod. Bonon. (Bologna) Bibl. Univ. Gr. 3632, early 15th Century.

without knowing very much about his subject. He had much to say about serpents and scorpions, and, with reference to the former, there is, in *Thē*riakos, a formula for utilizing the skin of the abhorrent amphisbaena against various maladies (*cf.* Druce, 1910; Kevan, 1978; 63, 444; the latter gives a fragment of the Greek original with a somewhat "unorthodox", inaccurate English translation from a Latin version). Much the same is given (in prose) by his approximate contemporary, Apollodōros of Athens, in his *Bibliothē*ka, and it would seem likely that this was Níkandros' immediate source. The rather small, poisonous, half blind underground serpent (Fig. 6), with a head at each end and the capacity to progress in opposing



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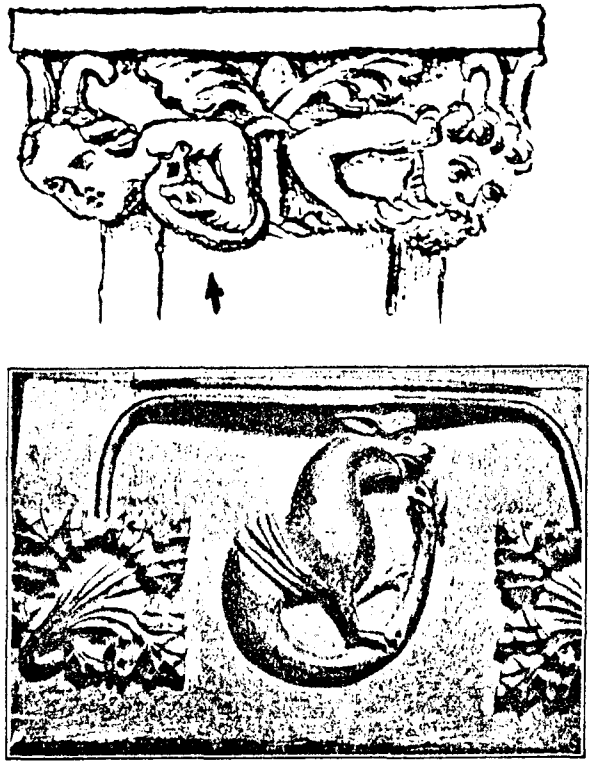

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Fig. 7. Mediaeval concepts of the "Ampisbena" or "Amphivena" (1). From Anglo-Latin "Bestiaries" in the British Museum Library, London (after Druce, 1910). Above, from MS Harley 4751, late 12th Century (there is a similar example, MS 764 fol. 97, in the Bodlean Library, Oxford); below, from MS Harley 3244, early 13th Century. Note: in both examples the creature has sprouted wings and two legs (in which it resembles a Basilisk or Cockatrice) and it is no longer soil-dwelling; the upper figure indicates one mode of progression adopted – by seizing the posterior neck in the anterior jaws and rolling like a hoop! Fig. 8. Mediaeval concepts of the "Amphisbena" or "Amphivena" (2). From ecclesiastical architecture and furniture (after Druce, 1910). Above, pillar capital, Freising Cathedral, Bavaria (? 13th Century), showing simple, wingless apodous, "Satanic" form of the beast biting the arm of Eve (?), left (from Cahier and Martin, *Mélanges d'Archéologie*); below, carved misericord, Limerick Cathedral, Ireland (? 14th Century), sophisticated form as in Fig. 7.

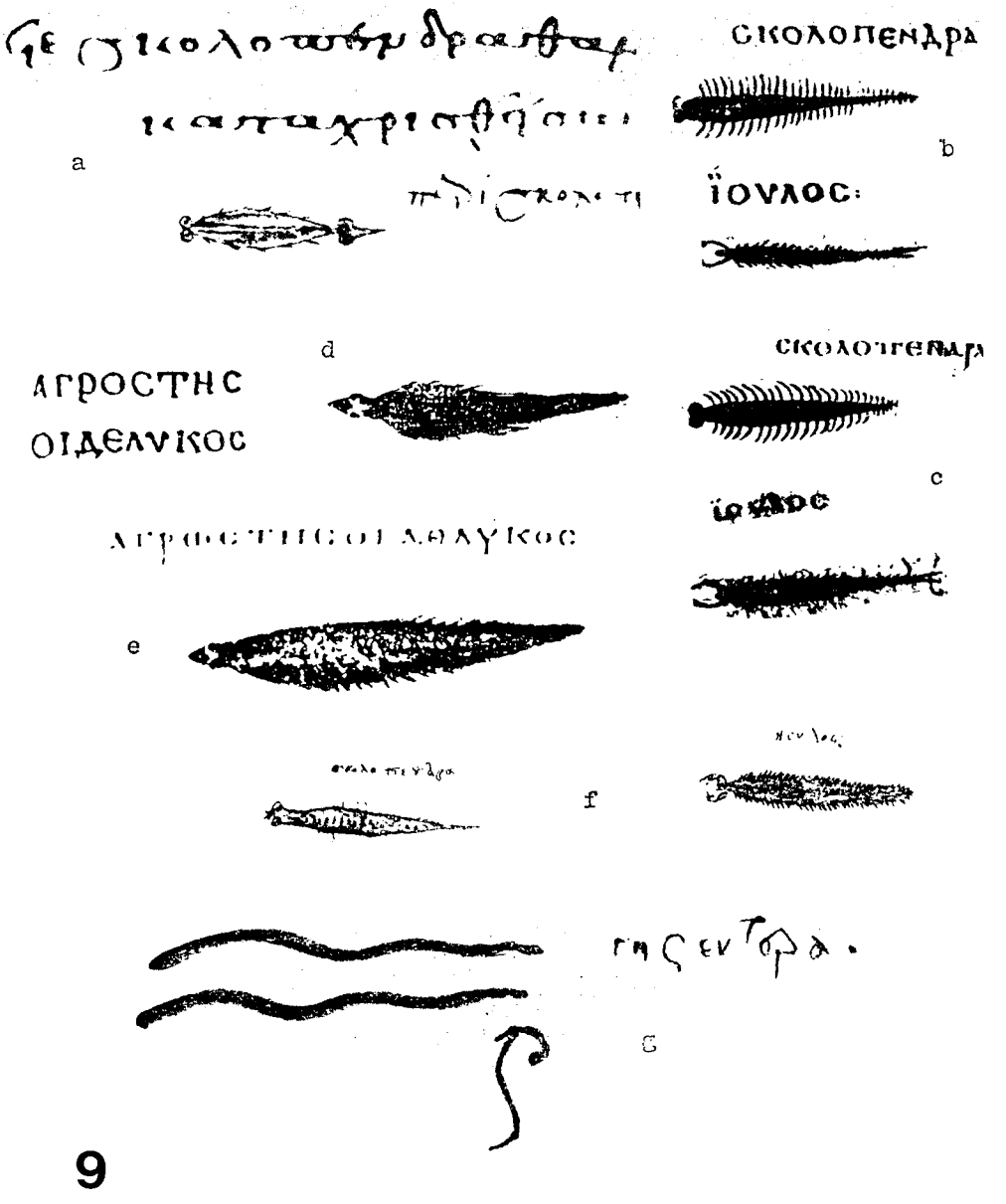


Fig. 9. Illustrations of myriapods and worms from Byzantine manuscripts descended from Níkandros' *Theriaka* and *Alexipharmakos* of 2nd Century B.C.E., and from Diascoridès' *Pharmaka* of 1st Century A.D., taken from Kádár (1978). (a) *Skolopendra* (centipede), from Cod. Vatican. Gr. 284, 10th Century; (b) *skolopendra* and ī̆oulos (? millipede, possibly marine polychaet worm), from Cod. New York, Pierpoint Morgan M. 652, 10th Century; (c) the same, from Cod. Vindobon. (Vienna) Med. Gr. 1, ? 10th Century; (d) *agrostēs* hoi de lukos (possibly a polydesmid millipede, but may be modelled on a marine polychaet worm), same source as (b); (e) the same, same source as (c); (f) *skolopendra* (centipede) and ĕoulos (millipede), from Cod. Bonon. (Bologna) Bibl. Univ. Gr. 3632, early 15th Century; (g) *gēs* entera (earth's entrails, earthworms), same source as (a), name transposed from above worms.

10

Theobaldus

De naturis animalium

Ex postq̃ p malam suggestionem deceptus fuit accessit eũ z momordit ipm p peccũ Sic diabolus antiqꝰ serpens hominẽ nudũ a peccatis z cmũdatũ a vitijs fugit. et vestitũ peccatis ledit inq̃rũ pr mortẽ eterna. Nã ꝓpterea ot auro: sicut radij solares fugant vmbrositates noctis. simili modo hõ mũdus a peccatis fugat a se demonẽ. attamen oportet ipm adhuc habere pugnas z diuersas tribulaciones per totam vitam suã. tanq̃ homo certans in agone. Vnde iob. Militia est vita hominis super terram. Et alibi. Qui legitime certauerit coronabit.

Item serpens totũ corpus suũ exponit lesioni vt caput obtineat illi lesum ad finem ne moriat: Simili mõ debet z vtiq̃ tenet vnusquisq̃ christianus totam vitã temporalem exponere pro capite. id est p christo. Vnde christus est omnium christianorꝫ caput. z christiani econtra sunt membra ipsius. Si ergo aliquis vellet impugnare fidem christiana. homo christianus deberet exponere totũ corpus pro ea. z potius mori q̃ christũ denegare. Multi em̃ sanctorum mortui sunt pro fide christiana. sed eternã receperũt retributionem Nota q̃ adhuc ssꝫ alie nature serpentis. q̃s phs in libris de aialib recitat Quarus vna est q̃ serpens habet linguã diuisam ad modũ duorꝫ digitorꝫ. Qd sic exponitur allegorice. Aliqui sunt homines duas linguas habentes. qui scz in ꝑsentia aliquorꝫ loquunt bona: z in absentia eorũdẽ de ipsis loquũtur mala detractorie. z isti bilingues veluti serpentes vitandi z fugiendi sunt. nec in aliquo credendi Item alia natura serpentis est. scz q̃ q̃n aliquis dormit in campo aperto ore. rũc serpens intrat os illius. Cuius ratio est. quia serpens frigide est nature: z anhelitus hominis est calidus. ergo q̃tum potest nititur appropinquare anhelitui hominis z sic os aptum inueniens ipsum intrat: Sic homines aliqui quando audiunt aliquem predicantem aut docentem. in verbis ipsius eius capiunt reprehendendo verba sua

De formica

Est modũ viuẽdi dat
Exemplum nobis prebet formica laboris
dum ꝓsuetũ genit
Quando suo solitum portat in ore cibum
gestis denotat
Inq̃ suis factis res monstrat spirituales
s^c res diligit ideo
Quas (quia iudeus non amat). inde reus

Vt valeat brume fieri secura furure
s^c est s^c formica
Dum calor in terra non requiescit ca

b i

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Fig. 10. Illustrations of (presumably) the isopod crustacean *Armadillidium vulgare (Onoi hoi hypo tàs hydrías)* from 10th-Century Byzantine manuscripts descended from Dioskoridēs' *Pharmaka* of 1st Century A.D., taken from Kádár (1978: pl. 72, 89). Above from Cod. New York, Pierpoint Morgan M. 652; below from Cod. Vatican. Gr. 284. Fig. 11. Part of the account of the Ant from a late metrical version of the *Physiologus* attributed to Bishop Theobald of Monte Cassino, early 11th Century. From the printed version, *Physiologus Theobaldi Episcopide naturis duo decim animalium*, Köln, 1492 (see Rendell, 1928).

directions (simultaneously ?!), seems to have been known and feared since before the time of Aiskhúlos and Hēródotos, though Níkandros did not mention its venom, or its mode of progression. It was probably based originally on the harmless burrowing, worm-like reptile we now call *Trogonophis* (the related modern genus *Amphisbaena* is tropical), rather than on the blind-snake, *Typhlops*, which was also known at the time.[6]

Níkandros also made various references to insects, though nothing definite was said about their relationships with the soil. Judging by Byzantine illustrations (Fig. 9), copied from generation to generation (see Kádár, 1978), he seems to have known, in the Aristotelean tradition, about centipedes (*skolopendra*) and possibly millipedes (*ī*oulos), though both may more usually have been (? marine) annelids. (With reference to the latter, see discussion of a Greek 2nd Century A.D. poem by Neumenios, in Kevan, 1978: 334). Kádár (1978) indicates that another, later and much better-known physician, active in the middle of the 1st Century A.D., Pedanios Dioskoridēs, also knew of some soil animals, such as earthworms and the others referred to by earlier authors, including Aristotēles and Níkandros (Fig. 9, 10). These he listed in his *Pharmaka* (*De Materia Medica*). Woodlice of the genus *Armadillidium* (presumably) were apparently known to him as *onoi hoy hypo tàs hydrías*. In the lst Century also, the poet Marcus Annaeus Lucanus (Lucan, 39–65 A.D.) emphasized the venomousness of the burrowing amphisbaena in his *Pharsalia* (see Druce, 1910).

The Aristotelean tradition, somewhat embellished, was carried on by the Roman Gaius Plinius Secundus, or Pliny the Elder (77 A.D.; see Rackham, 1940). Though a great compiler, he was unoriginal and often gullible. In his *Naturalis Historia*, he had little to say (and nothing new) about the soil fauna, though he did mention cicadas (including their subterranean *tettigometra* nymphs) and scarabaeoid beetles. He also seems to have been responsible (after Strabōn, or Strabo, in his *Geōgráphikos* of 23 A.D.) for "popularizing" the early myth of the fabulous, gigantic, dog-like, gold-digging "ants" of "India", to which reference has already been made (see above, and George, 1981). The "ant-lion" (*myrmēcoleōn*, later *mirmicoleon*, etc., sometimes also called "ant-dog") made its way into early versions of the symbolistic Christian *Physiologus* (below and *cf.* Fig. 12), to which the lost 2nd-Century Greek *Peri Zōōn* of the Syrian monk Tationos may also have contributed.

"*Physiologus*," or "The Naturalist," was presumably originally the pseudonym adopted by, or for, an unknown compiler of the book that bears the name. The latter originated in the eastern Mediterranean (Alexandria or Syria ?), probably towards the end of the 1st or in the early 2nd Century A.D., but the Christian *Physiologus* perhaps came a century or so later. Extant material goes back to about the 5th Century (James, 1928; Rendell, 1928; Bodenheimer, 1928; McCulloch, 1962; George, 1981). It was copied in several versions and eventually led to the Mediaeval "Bestiaries" (*Libri Bestiarum*). The earliest Greek versions included 63 chapters, of which 56 were devoted to different animals (C. Peters *in* Bodenheimer, 1928; Morge, 1973). Of these, only the ant, the "ant-lion" and the scarab concern us here. The second of these, though fabulous as presented, and having mythical attributes, had, like other strange animals in the *Physiologus*, a basis of factual existence.[7] As explained by George (1981), this was probably the badger-like ratel (*Mellivora capensis*), which burrows in sand and soil, though the pangolin (*Manis*) had been considered previously to be a likely candidate (Rawlinson, 1910, and others noted by George, 1981).

Before concluding our brief review of the so-called "classical" period of the Western World, we should perhaps note that there were various other works that had a bearing on applied entomology, from Cato, 235 B.C.E., to Palladius, *ca.* 380 A.D. (Bodenheimer, 1928; Morge,

1973). Although virtually none have any direct relation to the present context, we should perhaps mention the account of field crickets given by Publius Nigidius Figulus, mid 1st. Century B.C.E., in his *De Animalibus* (*cf.* Wotton, 1552; Bodenheimer, 1928), as this was distorted much later by Rhabanus Maurus (see p. 384?). Field crickets burrow backwards in the soil (and chirp at night); they may be hunted by inserting an ant on a hair, blowing away the dust the while; they can then be dragged forth together with the ant [which clings to it. Greek references to catching crickets in much the same way, by means of a strand, go back much further into antiquity.] Collumella, *ca.* 50 A.D., mentions ants, snails and miscellaneous caterpillars. Aelianus, about 200 A.D., dispensed numerous moral tales involving animals, including ants in particular, but also the "ant-lion" and amphisbaena, but these had not even a pseudoscientific signifance. Gaius Iulius Solinus, in his *Collectranea Rerum Memorabilium* (later *Polyhistor*) of the second half of the 3rd Century, transferred the ant-lion from India to Ethiopia. He also maintained that the amphisbaena had two heads.

In the Orient, this late classical period of the Occident was not particularly notable for known observations on soil-inhabiting animals, though, in China, there was, as in the West, a keen interest in "herbals", or *pên-ts'ao*, which included medically important insects. The earliest proper pharmacopoeia, the *Shen-nung Pên-Tsao Ching* was apparently compiled about the 2nd Century A.D. (Chou, 1957, 1980; Konishi & Itô, 1973). Scarabaeoid beetles and mole crickets were among the soil-inhabiting fauna mentioned.

## THE EARLY AND MIDDLE MEDIAEVAL PERIODS

By the second half of the 5th Century A.D., with the rise of barbarism and the demise of "classical" traditions, European culture was sinking to its lowest ebb. Give or take a century or so, this was also true, to a greater or lesser degree, of most other civilizations including that of China (and possibly also in the Americas). In about 500 A.D., however, another edition of the Chinese *Shen-nung Pên-Tsao Ching* pharmacopeoia by T'ao Hung-Ching was prooduced (Konishi & Itô, 1973), though it does not seem to have added much actual information to the 2nd Century version already noted.

For long after the decline of the Western Roman Empire there was no science in Europe, though some semblance of culture and scholarship eked out a rather precarious existence in Ireland (devoid of Greek) and in the Eastern (Byzantine) Empire. In zoology, apart from some tanscriptions of old Hellenic works in the latter region (*cf.* Kádár, 1978), only the *Physiologus* persisted, but even that was placed on the list of proscribed and heretical writings by the Roman Church in 496 A.D. The ban was not lifted for just over a century. The earliest Mediaeval Latin versions of the *Physiologus*, judging by the oldest surviving copies now available (8th and 9th Centuries) varied little in substance, accounting for some 43 animals (mainly mammals and birds, as noted by George, 1981) in 48 or 49 chapters (see also James, 1928; T.M. White, 1954; McCulloch, 1962). There was thus a slight reduction from the "late classical" 56 animals already mentioned for the Greek text by Bodenheimer (1928) and Morge (1973). The Latin versions, for example, did not refer to scarab beetles. Among soil inhabitants, these insects symbolized heresy and their dung-balls evil thoughts; and ants were symbols of provident virtue (encouragement of the "work ethic" - which some to-day might also regard as heresy! - among the peasantry being important politically to both religious and secular institutions). Ants were also noted for their wisdom, particularly, in the present context, for their astuteness in biting grains in two to prevent their germination when stored in the soil.

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Fig. 12. "Ant-lions" or "ant-dogs" (see text, p. 383) from an early 14th-Century Anglo-Latin "Bestiary," in the British Library, London (MS Royal, 2B, VII, fol. 96; *cf.* George, 1981).

(That ants do neither this, nor reject barley in preference to wheat, was immaterial). The "ant-lion" (or "ant-dog"), derived from the gold-digging ants of the ancients (*cf.* George, 1981), was hybrid - yes, between lion and ant! - that symbolized man's ambivalence: its carnivorous front part, dominated by its vegetarian rear part, and *vice versa*, meant that it could eat neither meat nor plant material and so, though paradoxically surviving, it perished due to starvation soon after birth! Unlike its later namesake it did not live in pits in sand or soil. At least one Mediaeval illustration later showed it as a dog-like mammal inhabiting mounds of earth (Fig. 12).

By the 7th Century, the great plague of the mid 6th Century in the Mediterranean region had come and gone, and the worst was over - "culturewise" at least -in both Occident and Orient. It was early in that century that the glimmerings of biological science began to revive when Isidoro de Sevilla (Isodorus Hispaniensis) produced his encyclopaedic *Origines sive Etymologiae*. This not only borrowed from, but was later to contribute additional material to, the *Physiologus*, resulting in the development of the second "family" of *Libri Bestiarum* or "Bestiaries". Amongst the animals considered by Isidoro were the amphisbaena, the mole, and a handful of invertebrates, including earthworms and one or two soil-dwelling beetles (Bodenheimer, 1928, 1929; Morge,1973). Isidoro's "cicadas", however, were Cercopidae (originating in the saliva of cuckoos, not in the soil like true cicadas). In passing we might also mention, in the 7th Century, Aldhelm (639–709 A.D.), England's first great scholar and senior contemporary of Northumbria's Baeda or "Venerable Bede". When prior of Malmesbury, Aldhelm composed, in Latin verse around 695 A.D.,[8] his famous 100 "Riddles" (*Aenigmata Aldhelmi*) as part of his *Epistola ad Acircium* (*Letter to Aldfrith* [King of Northumbria]; see

Pitman, 1925). The reason for referring to Aldhelm here is not that he really mentioned the soil fauna, but to draw attention to a general omission in histories of biology. Aldhelm, though not prolific in the field, was one of the few first-hand recorders of nature during the millennium since Aristotēles. His only riddle remotely associated with soil fauna uncharacteristically concerned the "*Myrmicoleon*" or "ant-lion" in the mythical, symbolistic tradition of the *Physiologus*.[9] Baeda (Bede, 673–735 A.D.) in his *Natura Rerum*, of about 725, did not, so far as I know, refer to the soil fauna at all.

Also, in passing, we might mention the anonymous Old English epic poem. *The Deeds of Beowulf*, probably the oldest surviving major poem in a western "modern" language. This deals, in part, with events of the early 6th Century, but was apparently composed in the late 7th, or more likely early 8th Century (the only known manuscript is late 10th Century). Beowulf, the mighty hero, was eventually wounded by a gigantic, fire-breathing, subterranean Wyrm or Worm (alternatively, Dragon - see Earle, 1892), which may be equated with The Mediaeval "*Daemon subterraneum truculentus*" (see footnote to Table I).

In the first part of the 9th Century, the German bishop Rhabanus Maurus completed his *De Universo*, which, though it drew heavily on Isidoro de Sevilla, was a much more erudite work than his. In it (Bodenheimer, 1928; Morge, 1973) he mentioned "*vermes*" of various sorts (including anything from fleas to clothes-moth larvae), some of which may have been true (annelid) earthworms or possibly terrestrial beetle larvae. He also referred to "*scarabaeus*" beetles (*Geotrupes*), to (field) crickets (*Gryllus, s. str.*, which burrow backwards into the soil and which are hunted by ants wielding hairs - a distortion from Nigidius, see p. 382), and to ants, with their various virtues. These last also included the fearsome, Indian giant gold-diggers of the ancients, formerly confused with "ant-lions", and transferred by him to "Aethiopia" (in accordance with Solinus, *antea*, and Isidoro). For apparently the first time, too, a *true* insect ant-lion (*Myrmeleon*)[10] was mentioned, under the latinized name of *formicaleon* (perhaps to distinguish it from the mythical *myrmēcoleōn*). It is described as a veritable lion amongst ants, burrowing in the dust and killing its victims as they carry along their loads. His "*cicadae*", however, like those of Isidoro, were Cercopidae and their nymphs not soil-dwelling.

By contrast, in the early 9th Century (and probably long before), the development of cicadas (*ts'ân*) from eggs laid in the soil was widely known in China, as exemplified by a poem by Po Chu-I, quoted by Kevan (1983a: 42–43). Kevan (*op. cit.*) also quotes other Chinese and Sanskrit poems of the period (late 8th to 9th Centuries) that refer to cicadas, mole crickets, termites and/or ants, though few are pedologically oriented.

A notable western scholar of the middle 9th Century was the Irishman, John (the) Scot (Johannes Scotus Erigena, *ca.* 810 - *ca.* 877; the Scots, *sensu stricto*, originally came from Ireland!). His *De Divisione Naturale*, written betwen 865 and 870, included much original thinking – presumably contributing to its subsequent condemnation by the Roman Church - but, as it drew mainly on "Pseudo-Dyonisius" and similar authors of antiquity, it again gives us nothing to note on soil fauna. The 9th Century was also notable for the rise of Saracen[11] scholarship. Early in this period, there were translations into Syriac and Arabic of old Hellenic writings, including those of Aristotēles, now lost in the original. In the middle of the century, however, at about the time that John Scot was most active, an independent zoological work, the *Kitabal-Ḥayawan* (*Books on Animals*), was compiled by Al-Gahiz (or Aljahid). Regrettably it too, included virtually nothing on soil animals, other than some generalities on beetles in Book 3, and on ants in Book 4 (Bodenheimer, 1928). The later, better-known author, Ibn-Sina ("Avicenna"), of the late 10th to early 11th Century, was, it seems, merely a translator, whose

most valuable contribution was to be among those who helped to preserve the writings of Aristotēles. He did, however, discuss the amphisbaena, whose Arabic name was given as *auksimem*. During the 10th Century, too, other old Hellenic texts were being transcribed under the influence of the Byzantine rulers of Constantinople (Kádár, 1978), but nothing original transpired. Thus it was that, by 1000 A.D., soil zoology, like most other scientific disciplines, had progressed little further than these early works - where they had not, in fact, retrogressed.

The 11th and 12th Centuries, pedobiologically, were no more fertile, though imagination and moralizing (e.g., in respect of ants) increased slightly in the shrunken *Physiologus* (see, for example, James, 1928; Rendell, 1928; McCulloch, 1962) and the appearance in church architecture of relatively uncomplicated forms of the amphisbaena (Druce, 1910). We may, however, mention a few works marginally associated with soil fauna, though the late 11th-Century comments by Shlomo Jizechaki (or Rashi), on insects mentioned in the Talmud, cited by Morge (1973), do not seem relevant. In China, there was a revived interest in pharmacopoeias and the old *pên-tsao's* were restructured along taxonomic lines in the form of the *Chêng-Lei Pên-tsao (Reorganized Pharmacopoeia)* by T'ang Shen-Wein in 1108 (Konishi & Itô, 1973). This discussed, amongst vermin and other lowly creatures, scarabaeoid beetles and mole crickets (Bodenheimer, 1928, 1929). Not long afterwards, in Germany, the Benedictine abbess, Hildegard ("St. Hildegardis")[12] began compiling her *Libris Physicis*, which may be said to date from about the middle of the century. Her work differed from earlier "herbals" as it was based on personal experience and local usage, not upon established "authority" and hearsay. Field crickets (which she called "cicadae") had certain medicinal properties; and she also mentioned ants.

Another mid-12th Century author, of great erudition (according to himself) and extreme verbosity, was Iōánnes Tzétzēs of Constantinople, whose enormous metrical (one cannot say poetical!) work, *Bíblos Histôrikē* (commonly called *Chilediades),* written about 1165–1170, included a fair amount of animal lore among his (un)natural history verses. However, he said nothing not already written by earlier authors. Examples of his writings (on cicadas, though not in soil) are given by Kevan (1983a). The mid 12th Century also produced the work of the Saracen scholar Ibn-Rashid (or "Averroes"), another major translator of Aristotēles, but not, a contributor. In this period, too, we should mention the credulous Anglo-Latin work of the Englishman Alexander Neckam, *De Naturis Rerum*, of 1170 (*cf.* Wright, 1863a; Raven, 1947), and of the even more credulous Norman-Welsh Silvester Gerald de Barri, or Giraldus Cambrensis, *Topographia Hibernicae*, of 1182 (*cf.* Wright, 1863b; Raven, 1947), if only in a negative sense. Though both works refer quite extensively to natural (and unnatural) history, including mention of insects, spiders and other invertebrates, the former refers, among soil-dwellers, only to the mythical amphisb(a)ena and the "seps" (probably based on a gecko, but which could mean almost anything from a poisonous serpent-lizard to a woodlouse or a myriapod), and the latter to the badger which is said to dig burrows in the earth.

The late 12th Century was the time when "Bestiaries" (*Libri Bestiarum*) not only started to become more elaborate, but when the numbers and complexity of "species" (real as well as "derived") mentioned therein increased (*cf.* James, 1928; T.M. White, 1954; McCulloch, 1962). In the early 12th Century, they had typically included relatively few (about 36) chapters, like the Latin *Physiologus*. By some curious turn of events (most likely due to inadvertent omission of a passage by some copyist, though I have not seen this theory advanced), the "*mermecolion*" later generally became confused with the *margarita*, or pearl, as was the case in the 12th-Century manuscript discussed by James (1928) and T.M. White

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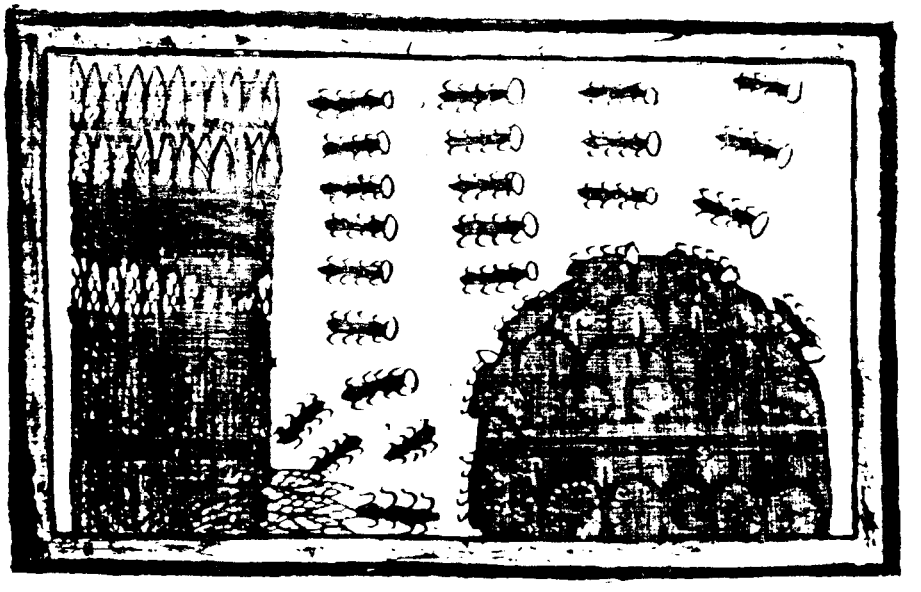

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Fig. 13. "Millipede" (resembling *Glomeris*; possibly an isopod crustacean *Armadillidium*) from 13th/14th-Century manuscript in the British Library, London (MS Harley 3244), apparently copied from an earlier (12th Century) Latin "Bestiary" (probably English). In the present manuscript, above this illustration is one of "*vermes*" ("life history" of earthworm) and another of spiders (with 7 pairs of legs!); below are mouse-like (or more probably shrew-like) "scorpions" (named in bottom line of text as shown); most of the above will be found (in white on black) in Davis (1958). Fig. 14. Industrious (8-legged!) ants carrying "grain" (pupal coccoons). From a Mediaeval "Bestiary" of (?) 13th Century (Pierpoint Morgan Library, New York, MS. 81, f. 311 - *cf.* Rowland, 1973).

(1954). Thereafter it tended to disappear altogether. The manuscript mentioned above included some chapters relevant to the present context: on mole, ant, "*amphivena*" (amphisbaena, but winged and no longer soil-inhabiting - *cf.* Fig. 7, 8) and "*vermis*". The last included earthworms, but also (in the tradition of Isidoro and Rhabanus Maurus) a wide range of arthropods, amongst which were scorpions, spiders, "millipedes" that rolled up into a ball (i.e., either *Glomeris* diplopods or *Armadillidium* isopods - *cf.* Fig. 13) and "termites" (by which seemed to be understood, almost any kind of wood-feeding insect *other* than true termites!).

In China, during this period, versions of the *Erh-ya* encyclopaedia and the *pên-tsao* pharmacopoeias with their occasional references to soil fauna continued to appear.

## THE LATER MEDIAEVAL PERIOD

We may continue the story in China with a single reference of marginal pedobiological interest. Ever since the later T'ang-dynasty period (8th Century), crickets had been admired and kept for their songs, but, by later centuries, cricket fighting had become an important part of Chinese culture. As large wagers were made on the outcomes of the encounters, much care was lavished on the contestants. This demanded a basic knowledge of cricket biology (particularly as regards their care and maintenance). As fighting crickets are all ground-dwelling species, a number of which burrow in soil, a fair amount was known of such species. An extensive manual on the subject was written by a member of the Sung-dynasty court, Kia Sê-Tao, at the beginning of the 13th Century. It was called *Tsu-chi King*, or *The Cricket Book* (see Chou, 1957, 1980; Petit & Théodoridès, 1962). Needless to say there were successors in Ming-dynasty and later times.

With reference to crickets, it is also interesting to note that these were mentioned in the longer, 71-chapter, version of *Bestiaire* written in northern France before 1218 by one Pierre (called "le Picard" or "de Beauvais"). The insects were called *cri(s)non* or *gresillon* and were said to sing so much that they lose their appetites, forget everything else, let themselves be hunted and die singing. (This is really a distorted cicada myth.) One 13th Century manuscript of this work illustrates the cricket in front of a hole in the soil, though a 14th-Century one shows crickets on a hearth (McCulloch, 1962).[13]

In 13th-Century Christian Europe, though the "Bestiaries" (Fig. 14) remained the main sources of zoological (mis)information, scholarship began slowly to emerge from the stagnant morass into which it had sunk. To some extent this resulted from, and in others it paralleled, the Saracen advances in knowledge and the rereading of classical authors. Three major encyclopaedias compiled by members of the Christian Dominican order, and one by a Franciscan, all written between 1230 and 1270, referred to a few members of the soil fauna. The works are briefly reviewed by Bodenheimer (1928, 1929) and, through him, by Morge (1973). They are those of Thomas de Cantimpré, or Catimpratornus (*Liber de Naturis Rerum*, 1233–1248), of his apparent mentor, Albert von Bollstädt, or Albertus Magnus (*De Animalibus*, in his *Opus Naturarum*), 1255–1270, of Vincent de Beauvais, or Vincentius Bellovacensis (*Speculum Maius Tripartitum [naturale, historiale et doctrinale]*, the relevant parts, I, Books 17–23, also *ca*, mid 13th Century), and of Bartholomew (Glanville? the) English, or Bartolomaeus Anglicus (*De Proprietatibus Rerum*, of roughly the same date - see Raven, 1947). These authors, between them, mentioned moles, earthworms, amphisbaenas, ants (including their larvae and pupae), true ant-lions, crickets (often confused with cicadas), various beetles (including ground-beetles) and their larvae, and so on, but, apart from Albertus'

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opimacus

Opimacus vermis corpore exiguus sed animo elatus. dicitur enim cum serpentibus habere certamen et plerunq; ingenio eos superare pugne exercitio

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Fig. 15. Scarabaeoid beetles (*khunfusa*) from the Arabic manuscript (Munich Codex) of H. Al-Qazwīnī's *Nuzhat-ul-Qulūb*, originally written in 1341. After Bodenheimer (1928), who says that the illustration probably originated during the lifetime of the author, and perhaps under his supervision. Fig. 16. The Bishop of Lausanne excommunicating cockchafers in the 15th Century. Copied from a contemporary illustration, after Bodenheimer (1928). Fig. 17. Mole-cricket, *Opimacus*, now *Gryllotalpa*; water-colour from Book IV of the *Codex Animalium* of Petrus Candidus Decembrus, *ca.* 1460. After Bodenheimer (1928).

denial that the amphisbaena had two heads, they still really had nothing to say on these animals that had not been said previously, mostly by the *Physiologus* and by Aristotēles.[14] In the very early 1300's (1304–1309), Pietro de Crescenzi (Petrus Crescentii), in his *Ruralium Commodorum Libri XII*, dealt with crop pests, though mostly on the basis of reports by classical authors. Once more, soil-inhabiting forms do not appear to have been considered, though he did recommend certain remedial measures for the control of ants (Bodenheimer, 1928; Morge, 1973).

Meanwhile, the Saracen scholars were gradually expanding knowledge in many fields (though scarcely in relation to soil fauna). The cosmography of Zakarīyā bin-Moḥammad bin-Maḥmud Al-Kummūnī Al-Qazwīnī (*cf.* Wiedemann, 1916; Bodenheimer, 1928), the *'Ajā'*kh al-Makhlūqāt (*Wonders of Creation*), completed in 1263, refers briefly to earthworms, ants, scarabaeoid beetles and crickets. This work was drawn upon and expanded by another Al-Qazwīnī (Ḥamdullāh Al-Mustaufā of that ilk) in his encyclopaeida, *Nuzhat-ul-Qulūb* (*Hearts' Delight*), of 1341 (*cf.* Stephenson, 1928). Soil animals mentioned included termites (*araḍat*; they eat earth and are attacked by ants), woodlice (*ḥimāru-l-qabban*), earthworms (*kharaṭin*; with medicinal and aphrodisiac properties), beetles (*khunfusa*; including small scarabaeoids, Fig. 15), various "worms" (*dūd*; including insect larvae of divers kinds, some subterranean), crickets (*ṣarṣari* in Persian; *tātūk* in Arabic; with medicinal properties) and ants (*naml*; various kinds enumerated).

A little prior to this work, in 1320, we have what is probably the first involvement of the Christian Church in the control of soil pests - though against the aerial adults - the excommunication of May-beetles (*Melolontha*) at Avignon. Similar exercises in exorcism (Fig. 16) continued for centuries, since pest outbreaks always diminished thereafter - eventually!

One of the landmarks of Mediaeval biological literature was undoubtedly the great zoological lexicon, the *Ḥaýāt* al-Ḥayawān (*Life of Animals*), completed in the late 14th Century, by the Egyptian scholar Kamal Ad-Din Ad-Damīrī (see Jayakar, 1906, 1908; Bodenheimer, 1928, 1929; Morge, 1973). Soil-inhabiting animals were mostly of the same kinds, with much the same information, as included by the Al-Qazwīnī's: Termites (*al-'arada*, *as-surfāh*), various insect larvae (*al-asāri'*, including some subterranean), field crickets (*al-gudgud*, *sharrār* al-lail), scarab beetles (*al-gu'āl*; dung-feeding by larvae noted); "worms" (*ad-dūd*; including earthworms and a range of insect larvae, but also termites and [parasitic] nematodes), a "worm" that rolls up in a ball (*ash-sha'hamat al ard*; either an *Armadillidium*-like isopod or a *Glomeris*-like millipede), woodlice (*himār*-kabbān), earwigs (*al-'ukubān*) and dung beetles (*qish'ibān*), as well as a whole range of ants (*naml*, generally; *al-gathlah*, black; *ad-dinnah*; *ad-dharr*, small, red; *as-simsimah*; *ash-shaisabān*, male; *at-thathrag*; *al-'ugrūf*, ? carpenter; *'aygabuf*; *hayzabūn*; *al-fazir*; *mūq*, winged; and *heigemāna*, very small). Although Ad-Damīrī was comprehensive, he was not particularly innovative or informative, especially in terms of soil-fauna relationships.

In these times, also, other writers of the Islamic world mention something of various agricultural insect pests, but, to all intents and purposes, relating only to those above ground. Several of the zoological and agricultural works, and copies later made from them, included illustrations of the animals. These were, however, seldom, if ever, drawn from nature - locusts were often bipedal and like birds, and (almost in the present context) crickets quadrupedal and like newts!

When considering the 14th Century, one should perhaps not be surprised at the lack of progress for, in the very middle of it, came the Black Death. This was by no means confined to

Europe, but it was most terrible there, especially from 1347 until 1350. This plague (followed by severe typhus epidemics) had dreadful and lasting consequences for human activities of all kinds, including scholarship. At least a quarter, and probably a third of the entire population of Europe died. Like Ad-Damīrī in Cairo, Cunrat von Megenberg, who translated Thomas de Cantimpré's *De Naturis Rerum* into German *(Das Püch [= Buch] der Natur)* about this time (see Note 14), survived in Regensburg, but many scholars did not. Then, a century later, came another major catastrophe for Christendom (though less so for scholarship); the Byzantine Empire fell to the Osmanli Turks in 1453.

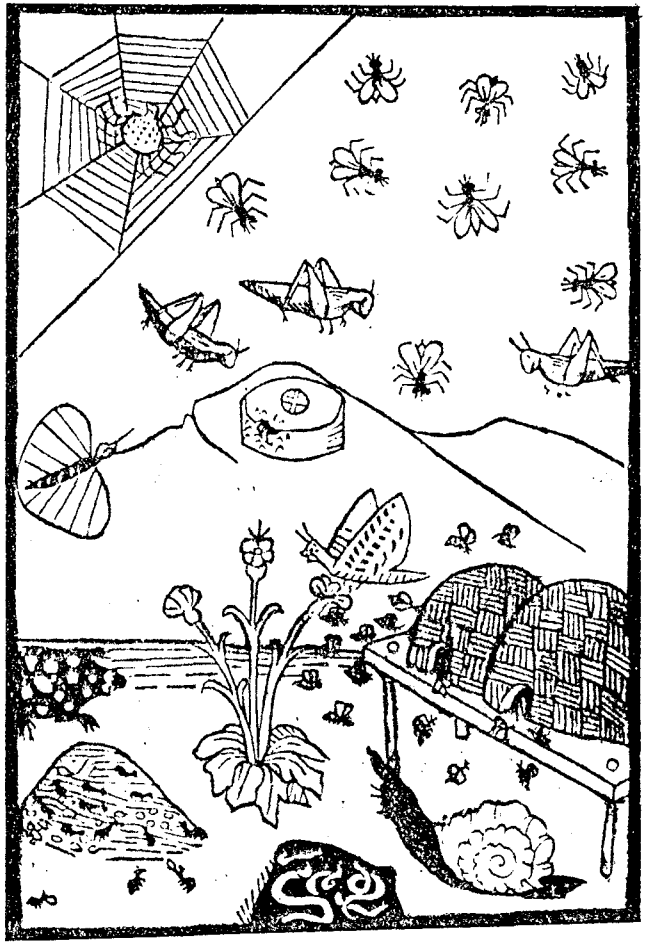
Scholastic recovery from this second disaster was not so slow as from the Black Death, for the Renaissance, spurred on by the resulting economic revolution in its wake, was already beginning. The Middle Ages had come and gone, and within less than half a century, both in the Far East (where it had long been known) and in the West, the era of the almost *universal* use of printing had arrived.

Belonging to the scientifically rather sterile transitional period of the early Renaissance, but Mediaeval in tradition, we may note in passing the beautifully illustrated *Codex Animalium* of Petrus Candidus Decembrus, about 1460 (*cf.* Bodenheimer, 1928, 1929; Morge, 1973). This drew heavily on the 13th-Century European encyclopaedias (and on old Plinius Secundus!). It contributed nothing new, but, in its fourth volume, it included references to various "worms" and insects, such as ants and "cicadas" (really crickets), and excellent watercolours of a mole cricket (called *Opimacus*, Fig. 17), and of a true (if 4-legged) ant-lion larva (see Bodenheimer, 1928). Here, too, it would seem appropriate to place what would appear to be the first definite evidence since the ancient Sumerians of discrimination between species of earthworms. *A Treatyse of Fysshynge wyth an Angle*, attributed (possibly erroneously) to Dame Julyana Barnes (born ? *ca.* 1388), Prioress of Sopwell Nunnery, Hertfordshire, England, recommends the "great angle Twytch" (probably *Lumbricus terrestris* or *Allolobophora longa* or both) for catching eels, but "red" worms for all other fish. A manuscript (perhaps of as late as 1479, and thus presumably posthumous to the alleged authoress) exists (T. Satchell, 1883); printed versions also exist, that under the name of Julyana Berners (1496) being the earliest.[15]

## THE RENAISSANCE

The European Renaissance was no sudden phenomenon, and it developed at different times in different places, but we can think of it as occupying much of the 15th through to the middle of the 17th Centuries. In the Orient, also, there were roughly coincident changes in Chinese philosophy, but these were not so marked nor did they so radically affect attitudes toward learning in general and science in particular. The European entomological and associated literature of this period is briefly reviewed by Beier (1973), though he makes virtually no reference to soil fauna. Some scattered information on the topic is, however, "buried" in Bodenheimer's "History of Entomology" (1928, 1929).

Immediately after the widespread adoption of printing, already mentioned, there was less immediate change in biological knowledge than might be anticipated, and the old works prevailed in printed, rather than manuscript form. Bartholomaeus Anglicus' mid-13th-Century *De Proprietatibus Rerum* appeared in a first printed edition in 1470, and Cunrat von Megenburg's mid-14th-Century *Das Püch [= Buch] der Natur* in 1475, became the first illustrated, printed natural history book (see above and Fig. 18). Not long afterwards appeared (*Fysshynge wyth an Angle*, see above) and the first edition (of many) of *Ortus* (or *Hortus)*



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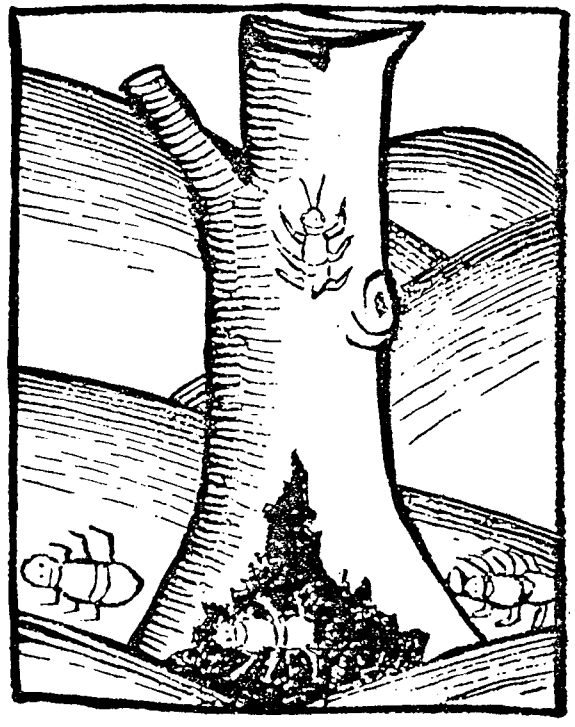

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Fig. 18. Folding woodblock "plate" including ants and earthworms, from Cunrat von Megenberg's (1475) *Das Püch der Natur* from Mss. of the middle of the previous century. Fig. 19. Ants emerging from the ground, illustrating the section "Formica" in an early printed version of *Ortus Sanitatis* (see p. 390), *ca.* 1500. After Bodenheimer (1928).

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Fig. 20. Mushrooms, earthworms, snail, etc., 16th Century. Above, woodcut from Lyons (French) edition, 1572, of Mattioli's (1548) *Commentario*. Below, embroidery (34x34cm) based on the same, by (or under the direction of) Elizabeth, Lady Shrewsbury ("Bess of Hardwick"), *ca.* 1580; one of a series now at Hardwick Hall, Derbyshire, England; note prominent isopods above the earthworm. [From a photograph.]

7

GEORGII AGRI=
COLAE DE ANIMANTIBVS
ſubterraneis Liber.

CORPVS ſubterraneum, ut res ipſa demonſtrat, in animatum diſtribuitur, & inanimatum. quod autem animi expers eſt, rurſus diuidi tur in id quod ſua ſponte erumpit ex terra, & in id quod ex eadem effoditur. De altero inanimi genere dixi in quatuor libris de natura eorum quæ effluũt ex terra inſcriptis, de altero in decem de natura foſſilium: nunc de ſubterraneis animantibus dicam. Cum uerò genus animantium omne conſtet ex quatuor elementis, & corpus humidum ac ſiccum, id eſt aqua & terra, ad accipiendum apta ſint, neceſſe eſt ea ipſa duo elementa animantium materiam eſſe. Ex quo rurſus illud quadam naturæ neceſſitate conſequitur, ut omne animal & in aqua uel terra gignatur, & in eis commoretur atque uita fruatur. Nam beſtiæ uolucres,

a 4 etſi

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Fig. 21. The first page of text from Georg Bauer's *De Animantibus Subterraneis* (Agricola, 1549; Preface dated 1548). [Facsimile now in Macdonald College Library.]

*Sanitatis*, a sort of herbal-cum-pharmacopoeia based upon the various Mediaeval encyclopaedias already mentioned. It has been attributed to Johann Wonnecke (or Dronnecke) van C'aub (Johannes de Cube or John Cuba), though some consider him to have been merely the translator of the work into German (*cf.* Wonnecke van C'aub, 1480, 1485). Jacobus Meydenbach (1491) has also been credited with the authorship, though he was but the editor of a somewhat later, better known, edition. Bodenheimer (1928, 1929) briefly reviews the latter and later editions from an entomological viewpoint. (Insects were not mentioned in the smaller, earlier edition). Soil-dwelling insects mentioned included ants (Fig. 19), true cicadas (as well as Cercopidae), scarabaeoid beetles and field crickets. The *Hortus Sanitatis* spawned various other herbals in the 16th Century, but, like the "Bestiaries" that were still popular, these contributed nothing to the advancement of science, pedobiological or otherwise. In the "Bestiaries" the religious and moral emphasis became, if anything, even greater and led to the publication of works virtually devoid of interest in biology, such as the *Reductoria Moralia* of Petrus Berchovius, 1521 (see Bodenheimer, 1928, 1929). Soil-inhabiting animals mentioned therein included the same old range of ants, "ant-lions," cicadas, crickets (deadly poisonous insects!) and so forth.[16] The *Hortus Sanitatis* also encouraged more practical books like the *Commentario* of Pietro Andrea Mattioli or Matthiolus (1548) and the *Naturalis Historiae* of Adam(us) Lonicer(us) (1551). The former, at least in some later editions, includes an illustration showing earthworms (Fig. 20) and support for the view that the amphisbaena has only one head, though reference to other soil fauna is virtually lacking. The latter work (see also Bodenheimer, 1928) mentions ants and scarabaeoid beetles (notably the Rose Chafer, *Cetonia*), crickets, "earth flies" and "earth fleas". It would be pleasing to think that the last constituted the earliest specific reference to Collembola (among the most characteristic of all the soil fauna), but, alas, flea-beetles are more probable, for control of garden pests was being discussed.

Between the dates of publication of these two works (which maintain a Mediaeval quality) came the first ever that we can really relate specifically to the soil fauna, though even this was marginal and dealt very largely with vertebrates. This was *De Animantibus Subterraneis* (Fig. 21), published in Basel by Georg Bauer under the alias of Georgius Agricola (1549).[17] Although generally descriptive of the fauna, the book emphasizes animals that dig or tunnel in the ground, some of which (such as rabbits and foxes) present-day soil zoologists scarcely consider as constituting part of the true subterranean fauna. Little in respect of the latter is actually discussed. The book was innovative in that it adopted an interdisciplinary, ecological approach, though to-day most would probably consider it (even though it be in Latin!) to be largely "waffle" (a feature by no means alien to many ecological writings!)

Agricola (*op. cit.*) divided his "subterranean" fauna into two main categories, "permanent" and "occasional," but this division did not apply to the entire life-cycles of the animals considered. For example, ants, wasps (*Vespula*), hornets (*Vespa*) and crickets, as well as scarabaeoid larvae, were all considered to belong to the category whose association with the underground was "permanent", whilst such insects as bees and cockroaches were but "occasional". Table I indicates those animals mentioned by him that (with the exception of *Blattae* and "*Gryllus domesticus*") we might consider to have rather more than a merely temporary association with the soil or litter. Woodlice ("*Asellus*") were, however, only mentioned as hiding in cracks in walls and in houses ("*rimis parietum & domorum latebris occulantus*"). The "*scolopendrae*" (centipedes and/or millipedes) were said to be found in [fallen] tree-trunks or in wood placed upon the ground or in sticks loose in the earth

TABLE I

Alphabetical list of German Subterranean Animals that can Conceivably be Classed as Soil Fauna, as Categorized by Georg Bauer (Agricola, 1549)

| Category* | "Classical" name used | Old Alsatian German name used | Modern High German equivalent | English equivalent | Current scientific name |
|---|---|---|---|---|---|
| Gradientum (Of Walkers) | *Asellus*† | *schefflein* | *Schäflein* | "lambkin," i.e. woodlouse, sowbug | Isopoda, Oniscoidea |
| | *Blattae*† | Wibel, *brotworme*‡, *spring wibel* | Wiebel, *s.l.* = Käfer, Brotwurm *Schabe, s.l.* | "weevils"; cock-roaches; etc. | Coleoptera; Blattodea |
| | *Formica* | *eims* | *Ameise* | ant, emmet | Formicidae |
| | *Scarabaeus* | [here] sewkefer | *Seufkäfer* | dor-beetle | *Geotrupes et al.* |
| | *Sorex* | *spitzmaus, feltmaus* | *Spitzmaus* | shrew(mouse) | *Sorex* |
| | *Talpa* | *molwurff* | *Maulwurf* | mole | *Talpa* |
| | *Vermis in Maio netus* | *meiworm*§ | *Maikäferlarve*, Engerling | May-beetle larva, Cockchafer larva, Whitegrub | *Melolontha et al.* |
| | *Vormela* | *Wormlein* | *Würmlein, Würmchen* | small "worms", grubs | Insecta (larvae) |
| Volantium (Of Flyers) | Gryllus domesticus | *hausheim* | *Heimchen* | House cricket | *Acheta domesticus* |
| | *Gryllus agrestis* | *feldheim* | *Feldgrille* | Field cricket | *Gryllus campestris* |
| *Serpentium* (Of Serpents) | Amphisbaena, Ignota | [unbekannt] | Amphisbäna | Amphisbena | [mythical - see p. 375] |
| | Τυφλινσ, Τυφλωψ | *blindschleiche* | *Blindschleiche* | Slow-worm, | *Anguis fragilis* |

(continued on next page)

TABLE I (continued)

| Category* | "Classical" name used | Old Alsatian German name used | Modern High German equivalent | English equivalent | Current scientific name |
|---|---|---|---|---|---|
| *Vermium* (Of Worms) | *Lumbricus* | reinworm | *Regenwurm* | Blindworm rainworm, dew-worm, earthworm | Lumbricidae |
| | Spongylis | *engerle* | Engerling | whitegrub | Scarabaeoidea (larva) |
| *Not on List* (but referred to in text) | Aranei nigri | – | "schwarze" Spinnen | "black"(?=wolf) spider | Lycosidae? |
| | *Scolopendra* | – | Hundertfüssler, oder ?*Tausendfüssler* | centipede, or ?millipede | Chilopoda, or ?Diplopoda |

*Omits categories Natantium (Of Swimmers), which are irrelevant, and *Daemonum* (Of Demons), which includes only the entry "*Dęmon subterraneum truculentus*" (Malevolent subterranean demon) or(Malevolent subterranean demon) or "*bergteufel*" (mountain devil), or the less evil "*bergmenkel/kobel/guttel*" (gnomes, goblins, fairies, etc.).

†Referred to only from buildings, and, except for "*Asellus,*" not soil-associated.

‡*cf.* Swedish "*brödetäre*".

§Said to have only 4 legs.

("*scolopendra in truncis arborum, aut in lignis supra terram locatis, aut inpalis terrae infixis*"). "Black" spiders ("*Aranei nigri*"), which I take to mean wolf spiders (Lycosidae), inhabit holes in the ground, as do field crickets ("*Gryllus agrestis*"). It was observed that the latter (and cockchafers or "*Vermis in Maio*") dig in dry earth in order to construct their burrows for the summer (House crickets for the winter also); field crickets die before winter; cockchafers in early autumn. It is also of interest to note that even in this scientifically-based work, credence is given to the existence of various subterranean demons. The (unknown) amphisbaena is also mentioned, presumably still in its dread, mythical Mediaeval form (see Note 6). Though Agricola's small book, as the first treatise on soil zoology, may be said to constitute something of a landmark in biological science, it had no impact on the study of soil animals, or of ecology generally, either at the time or subsequently. It has, in fact, rarely been cited.

*De Differentiis Animalium*, by the Oxford physician Edward Wotton (1552), should now be briefly mentioned for its refreshing style. It was, however, but a concise account of classical, zoological knowledge freed from the clutter of Mediaeval embellishment, and cannot be said to have contributed anything new. The soil-inhabiting animals were virtually the same as those mentioned by Aristotēles. Nigidius' account of the burrowing and capture of crickets (see p. 382) as well as a reiteration of their alleged medicinal properties, however, is given.

About the same time, the Swedish Archbishop Olaf Ster (Olaus Magnus Gothus) published his treatise on Scandinavia, including an account of its animals (Ster, 1555: Book XII). In compelete contrast to Wotton, this was in the old, almost Mediaeval, tradition. Of soil-inhabiting animals, only ants were considered, though a fair range of their types of "nests" was covered. It was stated that a red (poisonous) species lived in mole-hills in meadows. Bodenheimer (1928), who refers to the above, also notes that Hieronymus Cardanus (Geronimo Cardano), in 1559, cited Albert von Bollstädt (see p. 387) on the question of true ant-lions, and stated that West Indian ants inflict painful bites.

Bodenheimer (1928) also mentioned the fact that Johann Colerus, in his "Household Book" of about 1500, referred to damage to plant roots by insects (for which remedies were prescribed), and he also draws upon the behaviour of ants in relation to weather prediction. Bodenheimer likewise draws attention to the local, but notably original observations of Dr.


Fig. 22. Mole-cricket, *Talpa Insetto* (now *Gryllotalpa*) from Ferrante Imperato (1599).

636 Vlyſsis Aldrouandi

Bicipitem verò eſſe Scolopendram verum non eſt, ſed bicipitē poëta dixit, quòd talis videa E
tur: nam vt Ariſtoteles teſtatur & experimento quotidie deprehendi poteſt, Scolopendra ex
vtraq; parte graditur, tanquā vtrimq; caput habeat vnum, etiam ſi in duas partes diſſecta ſit,
tunc enim altera pars in caudam, altera mouetur in caput. Sed dum graditur, remorum in-
[a] Lib. 7. hiſt. plant. c. 11. ſtar, latos mouet pedes, quos alarum in modū geſtat, ſicuti poëta dixit. [c] Theophraſtus Sco-
lopendras ſcribit reperiri circa radices gladioli, quia, inquit, congregantur facillimè in eam.
Quibuſdam in regionibus tanta copia increuere, vt fugati ab eis populi proprios deſeruerint
[f] Li. 8. c. 29. lares, quod Trerienſibus contigiſſe ſcribit Theophraſtus teſte [f] Plinio: idem de Rhytienſi-
bus prodidit & Ælianus. Quæ in hac tabula num. 1. depingitur Scolopendra eſt marina, la-
to corpore, ſubcaſtaneo, velut pedibus innumeris, longiuſculis, aurei coloris. Num. 2. co-

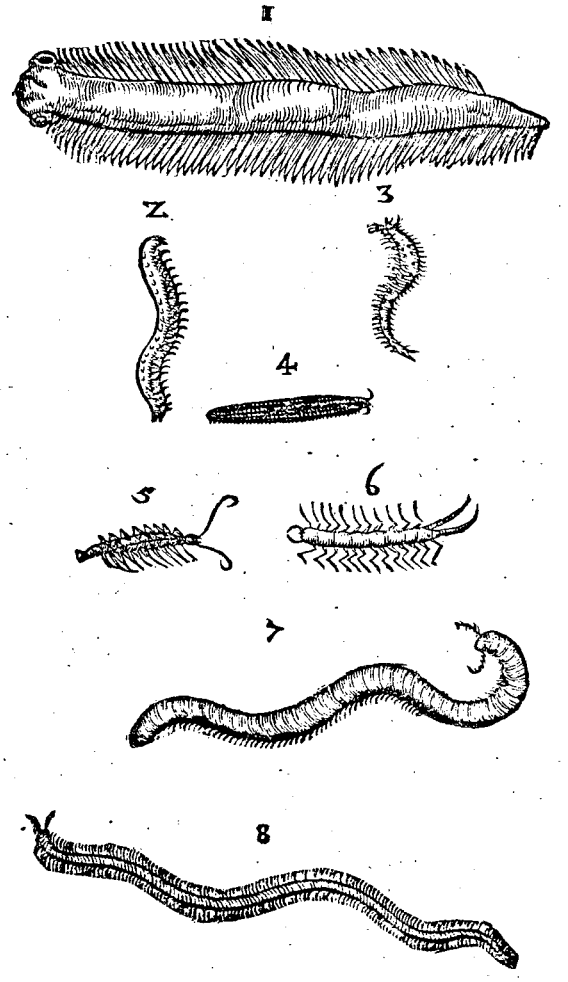


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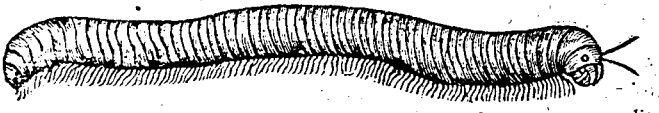
Fig. 23. A page from *De Animalibus Insectis* by Ulysse Aldrovandi (1602), showing various forms of Scolopendrae (centipedes), including millipedes and marine polychaet worms (I). [Original in Lyman Collection, McGill Univeristy, Macdonald College Campus.]

LIB.2. *minimorum animalium Theatrum.* 199

Maxima terreſtris Scolopendra, ea quam vides craſſitie & longitudine eſt; color totius corporis ex fuſco nigricante ſplendens. Singulis inciſuris pedunculus appendet luteus, *id eſt*, in ſingulis lateribus ſexaginta prorſum & retrorſum æqua facilitate promovet. Num et caput verſus ingreditur, & in caudam; ideoque à Nicandro & Rhodigino biceps dicitur. Partem inter caput & alvum non ſimplicem ſed multiplicem habet: quo fit, ut præciſum hoc genus vivere poſſit. Irritatus hic Scolopendra tam acriter mordet, ut Ludovicus Atmarus (qui nobis eum é Libya dono dedit) quamvis chirothecis duplicique linteo munitus, vix eum manum perentem ferre potuerit; altè enim in linteum os forcipatum adegerat, diuque pendulus vix tandem excuti permiſit.



Horum alium ex nova Hiſpaniola allatum linea quædam flammea medium per dorſum ornat, atque æneus later pilorumque color commendat: habet enim capillares pedes, atque armatim ſe tollens celerrimè currit. Hoc ſumma admiratione dignum eſt, quum natura huic animalculo caput minimum dederit, memoriam tamen, vimque rationis æmulam, neque congio, nec urceo, ſed ampliſſima quâdam menſura tribuiſſe: cum enim innumeri adſint pedes quaſi remiges, & à capite veluti clavo alij permultum diſtant; novit tamen quiſque officium ſuum, & pro imperantis capitis mandato in hanc vel illam partem ſe conferunt.

Alius item ad nos ab Auguſtini promontorio ex India perlatus, corpore nonnihil atque pedibus major, qui ſeptuaginta liveſcentibus inciſuris, & bis totidem ſpadiceis pedibus conſtabat.

Plures Scolopendras reperiri non dubito, omnium ferè colorum, præter viridem: quamvis etiam Ardoynus de viridi mentionem facit. Inſita ſingulis proprietas (ex Theophraſti ſententiâ) ad Gladioli herbæ radices ſeſe conferre. Bubulas autem exuvias meretur Robertus Conſtantinus, eumque ſecutus Stephanus, nec non Ardoynus ipſe; qui Scolopendram primùm ſerpentem, deinde octipedem, tum in cauda cornigerum, ultimò tardigradum eſſe comminiſcuntur. Taxandi Rhodoginus, Albertus & Avicenna, quòd nullum Inſectum ſupra viginti pedes habere temerè affirmant, illique numero Scolopendram alligant. Quamvis etiam Nicandro biceps dicatur his verſibus:

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Fig. 24. A page of "Scolopendrae" (myriapods) from *Insectorum Theatrum*, completed by Thomas Moffet in 1589 (Moufet, 1634, posthumous). [Original in Lyman Collection, McGill University, Macdonald College Campus.]

Johann Bauhin (1598) on "*Scarabaeus majalis*" (a geotrupid dor-beetle, illustrated), and what were clearly scarabaeoid larvae, made when graves were being dug near Mompelgard (Würtemberg). About this time, too, (? 1593), the Neapolitan physician Ferrante Imperato (1599) included, in his book of natural history curiosities, a reasonably good illustrated account of the "*talpa insetto*" (i.e., the mole cricket, *Gryllotalpa*, Fig. 22). The closing years of the 16th Century also saw the invention, in 1590, of the microscope by the Dutchman Zacharias Jannsen, which, if one may be permitted to turn a phrase "opened up a whole new can of worms"[18] for all of the biological sciences, and ultimately led to the discovery of the true nature and diversity of the soil fauna.

In China, the classical *pen-ts'ao* pharmacopoeia was restructured along biological rather than pharmacological lines, to produce the *Pên-ts'ao Kang-mu* of Lia Shih-Chên, completed in 1596 (Konishi and Itô, 1973). It referred to ants of three or four kinds, termites, burrowing (polyphagid) and other cockroaches, earwigs, mole crickets, field crickets, ant-lions and various kinds of beetles, such as Carabidae, Elateridae, Silphidae and Scarabaeoidea (including coprophagous species) and their larvae. Instructions were given on how to collect many of these insects. In the Orient, however, general knowledge of the soil-associated (and other) fauna had made virtually no advance since "Mediaeval" times and, indeed, never did so until caught up in the wake of 20th-Century western scientific advances.

The advent of the 17th Century may be said to have heralded a new era of invertebrate zoology, and of entomoogy (*sensu lato*) in particular. This has a direct bearing on the recognition of the more prominent members of the soil fauna. It did not, however, bring with it any real pedobiological advance.

The earliest two textbooks of entomology ever written both really belong to the 16th Century as they were too early to take advantage of the microscope. That of the wealthy Italian, Ulysse Aldrovandi (1602), *De Animalibus Insectis* (Fig. 23), has priority of publication, but the first to be "ready for press" (virtually completed 3.III.1589) was the *Insectorum Theatrum* (Fig. 24), compiled by Thomas Moffet, Moufet or Muffet, the London-born, much travelled physician of Scottish parentage who became a physician at the English court. The work itself, though not published until long after its compiler's death (Moufet, 1634), was known to some authors much earlier, and there may even have been an abortive, imperfect continental edition in 1598 (Raven, 1947). It combined Moffet's own observations with previously unpublished, posthumous manuscripts of Edward Wooton (above), the Swiss zoologist Conrad Gesner, and particularly of the illustrator and collaborator, another English physician, Thomas Penny (*not* Penn, as given by Bodenheimer, 1928, and Beier, 1973). The English translation (under the name of Muffet) did not appear until yet another quarter-century had passed, when it was combined in a single volume with reprints of the Reverend Edward Topsell's (1607, 1608) "Histories" of "Four-footed Beasts" and of "Serpents" (Topsell, 1658).

Both Aldrovandi and Moffet included invertebrates other than terrestrial arthropods. In the case of the latter author, these were restricted mainly to various kinds of worms, but the former dealt in addition with slugs and, quite extensively, with echinoderms. As much of Aldrovandi's tome, in contrast to the smaller volume of Moffet, was taken up with all manner of non-scientific (though often fascinating) material, the latter was, for the most part, scientifically the more satisfactory, though it, too, left much to be desired. Both dealt with a fairly wide range of soil- and litter-inhabiting animals, which, apart from the earthworms and slugs, are accounted for along with others by Bodenheimer (1928, 1929). Although the

publication of these works constituted a great stride forward for entomology, knowledge of the biology of the animals concerned was, nevertheless, advanced very little. Moffet (Moufet, 1634), among soil-associated animals mentioned (and often figured) the following, in addition to earthworms: ants (which are categorized in an almost Mediaeval fashion), mole crickets (said to spend most of their lives in damp soil and to collect grains of wheat and oats, possibly for the winter), earwigs, various kinds of beetles (such as scarabaeoids, including their dung balls, ground-beetles, elaterids and staphylinids, as well as the subterranean larvae of some of these, such as wireworms and whitegrubs), field crickets and cicadas (whose soil-inhabiting nymphs were not emphasized). In addition to these insects there was mention of mites on geotrupid beetles (see also Oudemans, 1926) and of millepedes, centipedes, isopods and burrowing spiders, as well as scorpions. Aldrovandi (1602), besides discussing earthworms and slugs, covered much the same range of soil-associated arthropods as Moffet. He noted that chafers (*Melolontha*) dig "nests" in dry earth, assuming that, as with burrowing bees and digger wasps, they oviposit there. He also referred to and figured earth nests of Geotrupidae and mentioned root-feeding by whitegrubs and mole crickets. When writing on cicadas, he mentioned the amphisbaena in connection with Níkandros (see p. 376), but he dealt with it more fully, and illustrated it, in his posthumous, 1606, volume on reptiles and serpents, maintaining that the animal did indeed have two heads, contrary to the declarations of other authors (Druce, 1910).

In the same year that Aldrovandi (1602) published his *De Animalibus Insectis*, there appeared in Strassburg the anonymous *New Feld- und Ackerbau*, a revised and "modernized" version of Petrus de Crescenzi's *Ruralium Commodorum* of the early 14th Century (see p. 387), advising on how to deal with various pests, including "earth lice", whitegrubs and ants (Bodenheimer, 1928). In the following year, Schwenckfeld (1603), in the 6th book of his *Theriotropheum*, relating to the fauna of Silesia, dealt with insects in an alphabetical, but very comprehensive manner (*cf.* Bodenheimer, 1928). Soil-associated animals mentioned included the following: "*Ascarides terrenae*" (various insect larvae including whitegrubs, cutworms, and probably the maggots of bibionid Diptera, all of which damaged fields and cut off roots); "*Cantharis formicaria latior*" (*Cetonia aurata*, the Rose chafer, and its white-grub-like larva and pupa living commensally in ants' nests); "*Culices fematarii*" (various small, manure-inhabiting dipterous flies); "*Curtilla*" (mole cricket, *Gryllotalpa gryllotalpa*, a pest of roots which builds nests in the earth and lays yellowish eggs therein[19]); *Formica* (ants generally; life history given; the idea that ants become winged when older is perpetuated); *Fullo* (here meaning the Common earwig, *Forficula auricularia*, lives under tree-bark; the idea of propensity to creep into human ears perpetuated, and remedies given); *Gryllus agrestis* (= *G. campestris*, Field cricket; digs in dry earth and spends the summer underground in holes); *Scarabaeus pilularius* (= *Geotrupes stercorarius*, dor-beetle; makes big balls of dung, using its feet, and lays its little larvae therein to protect them from winter cold); *Scarabaeus bufonius* (= *Carabus auratus*, a large ground-beetle; lives where toads are plentiful; people believe that they copulate with these; they are likewise poisonous[!]); *Spondylis* (whitegrubs, *Melolontha* and similar larvae; garden pests which lie in the earth near plant roots which they completey devour; used by anglers as fish-bait).

We have already referred to the Reverend Edward Topsell in connection with the English translation of Moffet (see p. 400), but his *Historie of Serpents* (Topsell, 1608) should perhaps receive brief mention here. This work was based mainly on the work of Conrad Gesner (see p. 400), but, despite its title, includes some information on invertebrates, virtually all, with the

exception, so far as we are concerned here, of his notes on scorpions, taken from a pre-publication copy of Moffet. He does, however, mention a "discourse of Wormes" by his contemporary, Dr. Thomas Boreham. This does not now appear to be extant (Raven, 1947), which is a pity, as it would seem to have been the first treatise on earthworms as such, other than that attributed to Dame Juliana Barnes (see p. 390).

Before concluding this section, we should perhaps briefly mention Francis Bacon of Verulam (St. Albans), one of the most noted philosophers of his age, if only to note that, in his posthumous *Sylva Sylvarum* of 1627, he presented some observations and researches on insects (most of which he pronounced to be generated in filth) and earthworms. Despite his erudition, however, he had nothing to contribute to knowledge of the soil fauna (see Bodenheimer, 1928). Bodenheimer (*op. cit.*) also refers to the 1645 *Zootomia Democritaea* of Marco Aurelio Severino, which includes some observations on the anatomy of crickets and (?) earwigs.

## MID-17TH TO MID-18TH CENTURIES

Although Francis Bacon (above) had introduced new philosophical concepts, it was not until the 1640's that we see the beginnings of the "Rise of the Naturalists" (the "Bionomic Era" of Bodenheimer, 1928). Like other developments, this did not come about suddenly, but one particular name may be mentioned here, that of Dr. Thomas Browne (later Sir Thomas Brown - without an "e"!). This worthy English scholar began to raise biology to a scientific level by questioning "authority" - almost "for the first time since Aristotle", according to T.H. White (1954), though John Scot (see p. 384) apparently found himself in disfavour on a similar account several centuries previously. In his *Pseudodoxia Epidemica*, which went through several subsequent editions, Browne (1646) refuted, or at least cast doubts upon, many widely accepted beliefs (though, paradoxically, he was a firm believer in witchcraft and in the validity of the Ptolemaic concept of the universe!). Apart from debunking mythical beasts, such as the basilisk (and the amphisbaena) Browne made a number of sound observations. Among these he noted that the (soil-associated, adult) earwig, *Forficula auricularia*, is winged, not apterous, as generally supposed. He also noted the occurrence (though not specifically in connection with soil) of the "red-coloured summer spider" or "tainct" (later "taint" or "tant", presumably a trombidiid earth-mite, identified by Oudemans (1926) as being *Acarus holosericeus*, described and named much later by Linnaeus (1758) and now the type-species of the genus *Trombidium*. This is probably the first report of a recognizable, free-living, soil-associated mite.[20]

Before proceeding further, we should perhaps mention here that knowledge of the tropical fauna was increasing at this time. Particularly notable were the writings of Georg Marcgraf, some of which were published posthumously (Marcgraf, 1648; see also Bodenheimer, 1929), though others have only recently come to light. Apart from mentioning the termitophagous activities of the South American ant-eater, various kinds of Brazilian insects are referred to. These included digging scarabaeoid beetles (illustrated with numerous parasitic or phoretic mites on the pronotum) and the jigger flea (*Tunga penetrans*) which affects human feet by way of the soil - as was known to the early Peruvians (*cf.* Morge, 1973) and had been known to Europeans since the early 16th Century (*cf.* Kevan, 1977).

Such reports of this period really belong to an earlier age, and the same is true of the third textbook of entomology to be published, that of John Jonston (1653), a much travelled Silesian physician of Scottish extraction. The book (Fig. 25, 26) was really a combination and condensation of Aldrovandi (1602), devoid of "non-scientific" matter, and Moffet (Moufet,

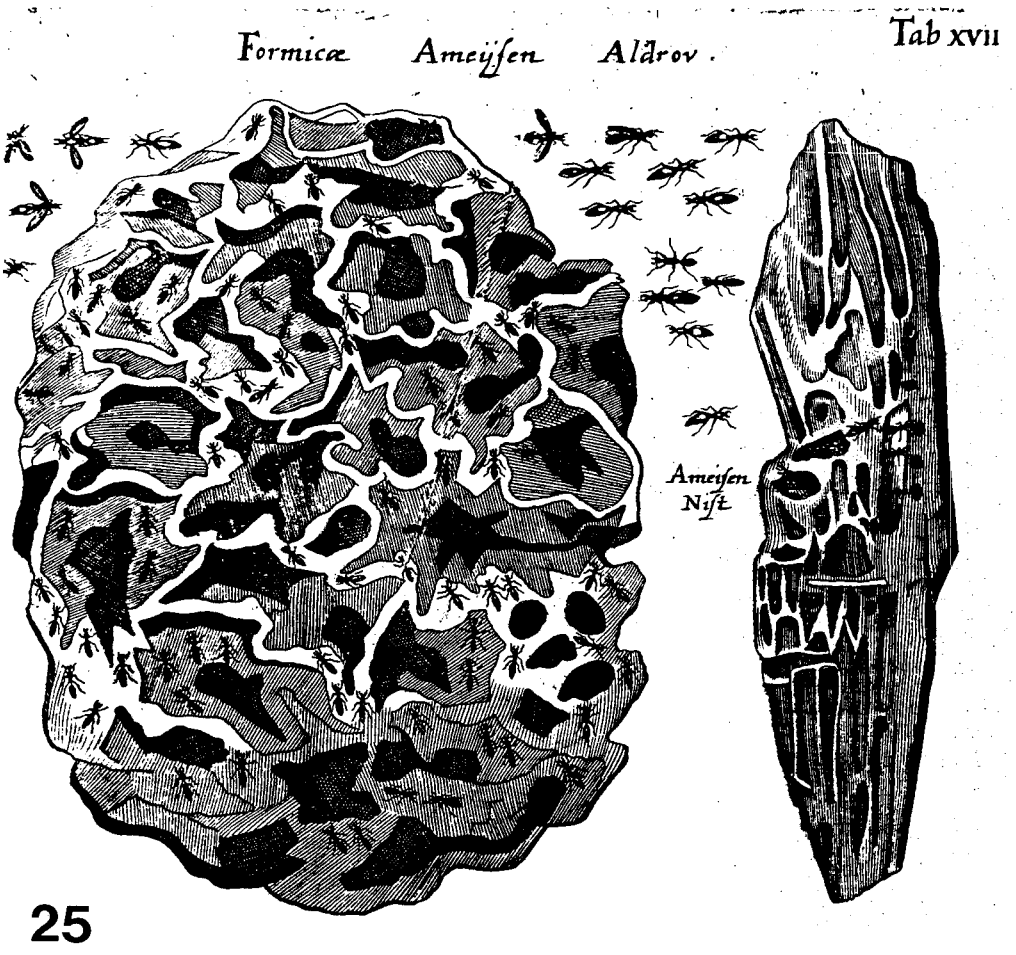


Fig. 25. Ants and their habitations. The upper part of Pl. XVII (opposite p.114) in the third text-book of entomology (Jonston, 1653); from among the illustrations copied from Aldrovandi (1602). [Original in Lyman Collection, McGill Univeristy, Macdonald College Campus.]

1634). It added nothing to what these two authors had included about soil invertebrates. To his volume of four (not three as indicated in his title) "books" on insects, etc., Jonston appended two more, culled from other authors, embracing serpents and dragons. These latter indicated that belief in mythical Mediaeval dragons, basilisks, hydras and so on, were still current, if declining. The "*Amphisboena*" (*sic*) was, however, no longer a two-headed monster (Fig. 26, lower), but had taken its place among rational legless, burrowing reptiles, along with the rather similar "*Scytale*" and "*Caecilia*".[21]

It was shortly after the appearance of Jonston's work that the first free-living nematodes were discovered by Borel (1656). Although these were vinegar eelworms, *Turbatrix aceti*, and not soil-inhabiting, their recognition had very important implications for soil zoology. Fragments of the history of soil nematology will be found in Overgaard-Nielsen (1949) and, to a minor extent, in Thorne (1961) and Chitwood and Chitwood (1974).

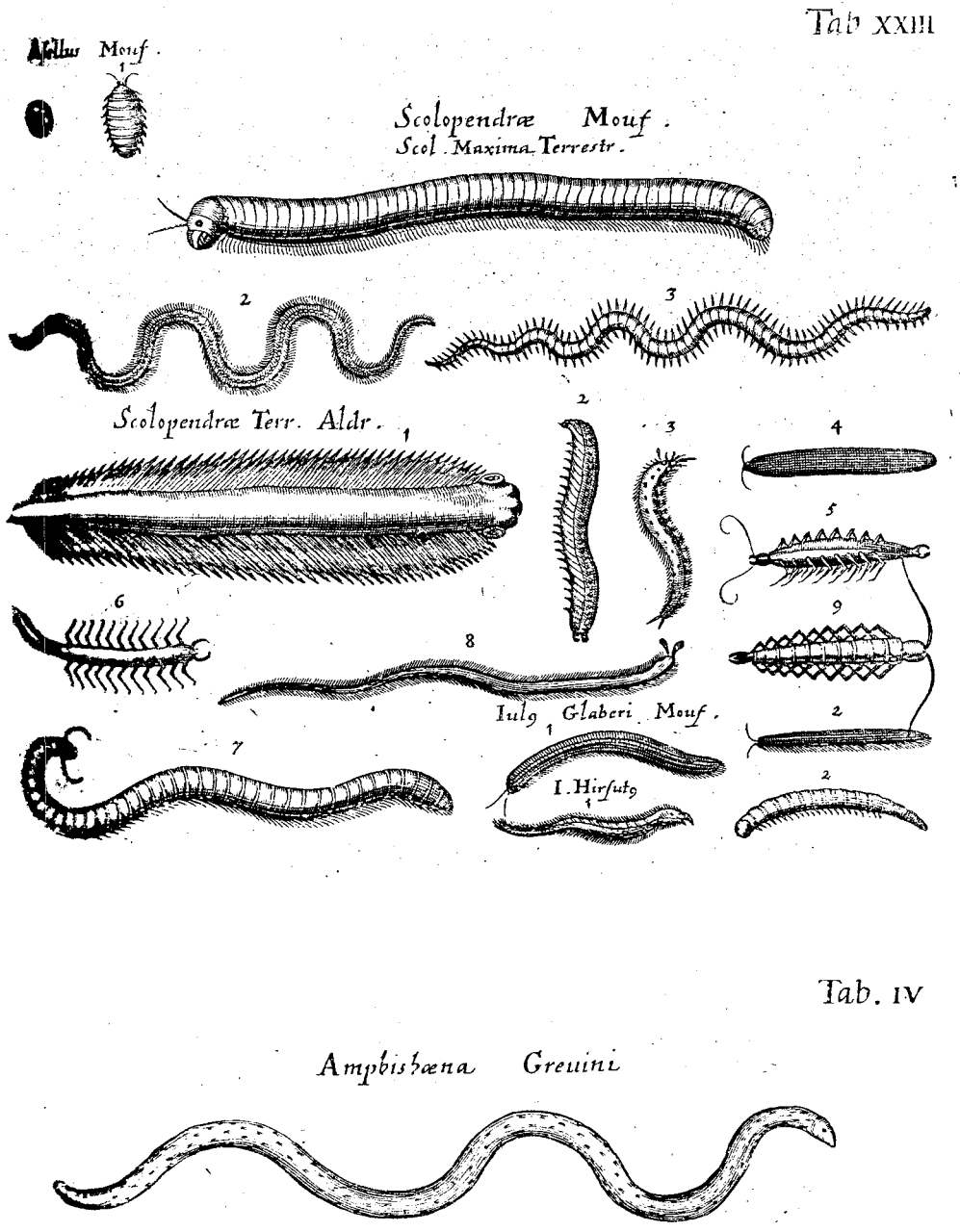


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Fig. 26. Above, "*Asellus*" (woodlouse, presumably *Armadillidium*) and "*Scolopendrae*" (myriapods, including marine polychaet worms) from lower part of Pl. XXIII of Jonston (1653); illustrations taken from Moufet (1634) and Aldrovandi (1602) as indicated. Below, one-headed "*Amphisboena*" from upper part of Pl. IV of Jonston's appended book on serpents. [Original as Fig. 25.]

The closing years of the sixth decade of the 17th Century also saw further discoveries in the tropics. Bontius (1658) briefly mentioned a few marginally soil-associated, East Indian arthropods, such as scorpions, cockroaches, ants, scarabaeoid and other beetles. Rochefort (1658), besides cockroaches, discussed West Indian termites (mainly in wood) and the already well-known jigger fleas (*Tunga penetrans*). Piso (1658) noted the occurrence of several root-feeding insect pests of sugar-cane and cassava in Brazil.

Sperling (posthumous, 1661) might now be mentioned, if only for his somewhat novel approach to zoology in presenting the subject as a sort of catechism in the form of statements, questions and answers. Many kinds of insects were referred to, but only the clever, industrious, corn-gathering (!) ants concern us here (*cf.* Bodenheimer, 1928). Goedart (1662, 1667) however, made one or two important observations, and he is generally regarded as being the first naturalist for many centuries to rely mainly on his own observations, rather than on written "authority" (though this distinction might more properly be claimed by Bauhin, 1598, above). Part I of his work (1662) gives a good illustrated account of the biology and ecology of the mole cricket, *Gryllotalpa*, and its subterranean nest and eggs. (Bodenheimer, 1928, who discusses the complex authorship of the work, notes that Goedart claims to have invented the name of the insect.) Part II (1667) contains a very good account of the crane-fly, *Tipula paludosa*, and its leatherjacket larva, correctly suggesting a three-year life-cycle; he also mentions a four-year cycle for the May-beetle (*Melolontha*) with its root-feeding larvae. Part II is also important from the point of view of soil acarology and nematology as it draws attention to, and illustrates for the first time, acariform mites and rhabditiform nematodes (Fig. 27), which are shown in the decaying remains of an ink-cap (*Coprinus*) fungus.[22]

An increasing number of relevant observations were made by various authors during the latter part of the 17th Century. Some of these may be briefly commented upon in the form of the following list:

Hooke (1665): described and gave the first good illustration of a cryptostigmatic mite (Fig. 28) associated with mosses and fungi; Oudemans (1926) identified this member of a dominant group of soil organisms as "*Acarus*" *geniculatus*; Hooke (1665), in addition, reporting again on the vinegar eelworm *Turbatrix aceti* (see p. 403), also discovered the nematode *Panagrellus redivivus* that occurs in wallpaper paste, an important prelude to the discovery of species directly associated with soil (*cf.* Goedart, 1667, above).

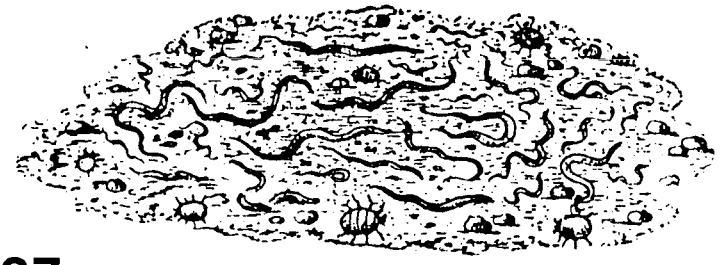
Anonymous (1665): was the first report from North America of cicadas, the holes left by their emergence from the soil, and their exuviae (Bodenheimer, 1929: 159, gives later references also).

E. King (1667): gave a fairly detailed account of the biology of ants, including the pupal nature of "ants'-eggs".

Charleton (1668): made early observations on cryptostigmatid mites on bark (*cf.* Oudemans, 1929); he also commented on various insects, including mole crickets and earwigs, but his information was taken directly from Aldrovandi (1602) and Moffet (Moufet, 1634).

Redi (1668): did not make much direct contribution to knowledge of soil fauna, but exploded the myth of spontaneous generation of insects, etc., from "filth" and other substrates, including soil; he also referred to phoretic mites on ants, both winged and wingless, and on beetles (see Oudemans, 1926; Bodenheimer, 1929).

Swammerdam (1669): amongst general observations, noted that certain invertebrates developed without metamorphosis, namely, spiders and mites (probably not soil forms), scorpions, isopods, myriapods, earthworms and slugs. It may also be noted here that, in the



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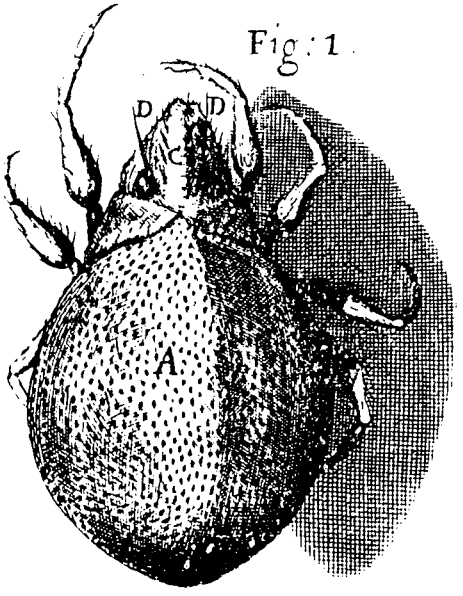


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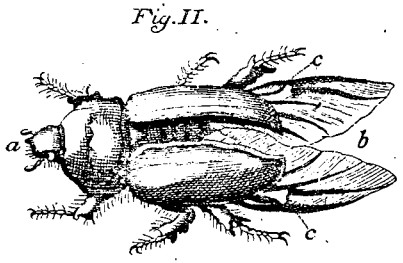


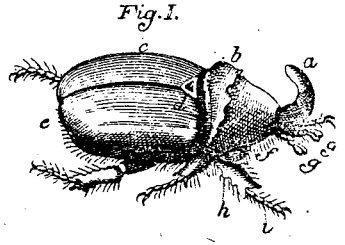


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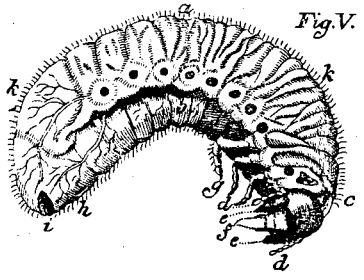





Fig. 27. Acariform mites and rhabitiform nematodes in the decaying remains of an ink-cap fungus, illustrated by Goedart (1667). Fig. 28. The "Wandering mite" illustrated by Hooke (1665); the first good illustration of cryptostigmatid mite, see p. 403. Fig. 29. Adults, eggs and subterranean larvae of the horned scarab "*Nasicornis*," from the upper part of Pl. XXVII of Jan Swammerdam's posthumous *Bybel der Natuure* (1737–38), completed by 1670. [Original in Lyman Collection, McGill University, Macdonald College Campus.]

52-years-posthumous *Bybel der Natuure* (Swammerdam, 1737–38), detailed studies on ants and their nests, and illustrations of the horned scarab beetle and its subterranean larva (Fig. 20) were published.

Wray (1670; i.e., the botanist John Ray before he changed the spelling of his name): experimented with formic acid obtained from ants. It may also be noted here that, in 1672, Francis Willughby, who was responsible for most of Wray's later, posthumous, entomological publication (Ray, 1710), died.

Kircher (1675, 1680): attempted to relate "science" with the animals of the *Holy Bible* and to dismiss Redi's (1668) work (above), maintaining that Noah's Ark could not possibly have accommodated representatives of all known living creatures, so that spontaneous generation must be accepted for many; insects, etc., arose from dead material in the proper proportions; six classes of such animals existed; from *soil* came earthworms and slugs, etc., and from excrement and cadavers emerged scarab (and other) beetles (as well as wasps and bees); another group included ants and crustaceans (which would include isopods). [An earlier work of Kircher (who was a Jesuit priest), dating from 1665 and entitled *Mundus Subterraneus* ... (in 12 "books"), and an even earlier one of 1657, with the same words in the title, sound like hopeful sources for the historically inclined soil biologist, but they are basically theological!]

Holger Jacobensen [1676]: as indicated briefly by Petit and Théodoridès (1962: 338) made an important study of the anatomy of the mole cricket (*Gryllotalpa*), presumably in *Acta medica Hafniensis*, but the work is unknown to me and unlisted in the principal entomological bibliographic sources.

Lister (1678): referred to the red trombidiid earth mite, called "tant" (*cf.* Browne, 1646, see p. 402), identified by Oudemans (1926) as "*Acarus*" (now *Trombidium*) *holosericeus*, though not actually *in* soil.

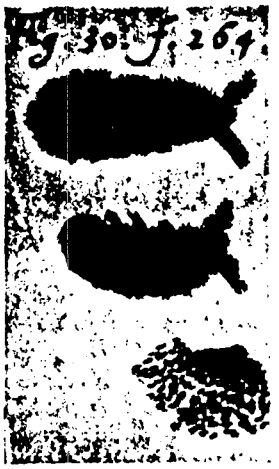
Wagner (1680): noted that the cockchafer (*Melolontha*) larva (whitegrub) was called "*Inger*" or "*Enger*" (currently *Engerling*) in German because it curled around roots, no kind of which remained undamaged by them; significantly a three-year subterranean developmental period was said to be required in Switzerland *cf.* a total life-span of four years in the Netherlands, indicated by Goedart, p. 405). The ridiculous practice of excommunicating the beetles, as at Lausanne, in earlier days was also noted (*cf.* p. 389 and Fig. 16).

Claude Perrault [1680]: in *Les Mêcaniques des Animaux*, described and discussed the alimentary canal of the mole cricket (*Gryllotalpa*), according to Petit and Théodoridès (1962: 332). He also published a small tract on *Melolontha* (*cf.* Bodenheimer, 1929: 307). Neither of these works is known to me, nor are they listed in the principal entomological bibliographic sources.

Knox (1681): was for many years a prisoner in Sri Lanka; his entomological observations included pertinent comments on ants of various kinds (some of which excavated large holes in the soil) and particularly on termites, their activities, depredations and mounds; his writings seem to have been ignored in virtually all major termitological literature, but Bodenheimer (1929) quotes him from a German translation of 1689.

Mentzel and Ihle (1683): recorded phoretic mites, identified by Oudemans (1926, 1929) as "*Acarus*" (now *Parasitus*) *coleoptratorum*, on geotrupid beetles.

Muralto (1683, 1684): discussed and illustrated the anatomy of the Wood cricket *Nemobius sylvestris*, not a burrower), the Common earwig (*Forficula auricularia*) and, more notably, the mole cricket (*Gryllotalpa*).



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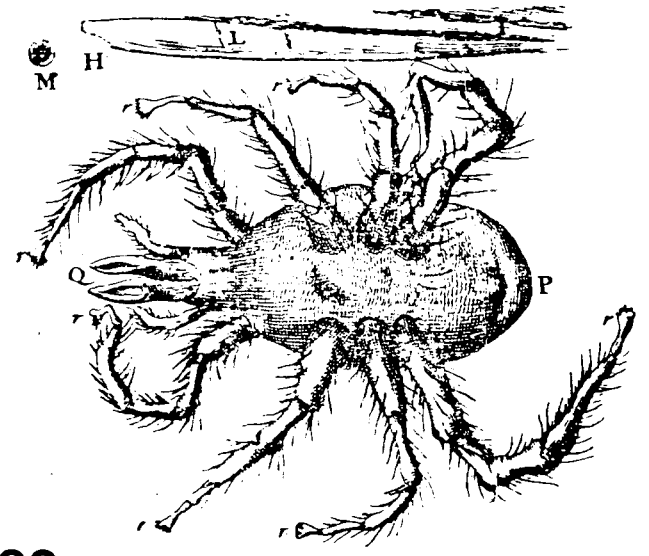


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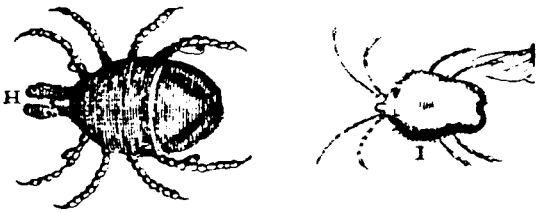


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Fig. 30. The first (?) recognizable illustration of Collembola (*Hypogastrura* on snow) by Spielenberger (1684). After Bodenheimer (1928). Fig. 31. Early illustrations of mites from Blankaart (1688). H, a species phoretic (?) on soil and other insects, *Parasitus coleoptratorum* (Mesostigmata, Parasitidae), called "Luis van een vliegned torretje" or "luis van de gekokerde vlieg"; I, Scarlet earth-mite, *Trombidium holosericeum* (Prostigmata, Trombidiidae), called "Schaarlaken-roode Aard-spinneken" or "Scharlaken-Aard-spin." Fig. 32. Phoretic (?) mite, *Parasitus coleoptratorum*, from a geotrupid dung-beetle, illustrated by James Wilson (1702).

Spielenberger (1684): published the first (?) recognizable illustration of Collembola (a species of *Hypogastrura* - Fig. 30) albeit from the surface of snow and not from soil (where Collembola constitute one of the most numerous groups of animals). Insects have been reported on snow since, at least, the times of Aristotēles and Plinius, but here their collembolan nature is undoubted(*cf.* Bodenheimer, 1929).

Griendel (1687): gave detailed figures of wingless ants and with their pupal "eggs".

Blankaart (1688): reported on various mites (Fig. 31), including those occurring on burying beetles (*Necrophorus*) and a figure of the red trombidiid earth mite, identified by Oudemans

(1926) as "*Acarus*" (now *Trombidium*) *holosericeus*, though again above ground.

Mentzel (1688): illustrated the nymphal stage and exuviae of cicadas (*cf.* Bodenheimer, 1929).

The anonymous author, referred to by Bodenheimer (1928) as Hohaus (*ca.* 1690), gave details of the biology and damage caused by mole crickets (*Gryllotalpa*).

Kämpfer [? *ca.* 1693] (1727–28): recorded observations on termites and ants in the Far East (see Bodenheimer, 1929, who quotes a German version of 1749).

Leeuwenhoek (1695): was most famous for his development of the microscope, with all that that implied for the future study of the soil fauna, but he did not contribute significantly to such studies himself. We may, however, mention his notable, detailed, illustrated account of the biology and ecology of the crane-fly, *Tipula paludosa*, and its root-feeding leatherjacket larva (*cf.* Bodenheimer, 1928). In this, he "correctly recognized the limiting circumstances of population dynamics" (Beier, 1973). Leeuwenhoek (1697) also made observations on ants, once more commenting on the pupal nature of the so-called "ants'-eggs". Each of these contributions, however, had been largely anticipated some 30 years previously by Goedart (1667) and E. King (1667) respectively (see p. 405).

Camerarius (1699/1700): again referred to Collembola on snow (*cf.* Spielenberger, 1684, above).

Carrying forward the selected list of "soil fauna" publications into the 18th Century, we may note the following:

Wilson (1702): gave a good illustration (Fig. 32) of a mite (*Parasitus coleoptratorum*) from geotrupid dung-beetles.

Poupart (1704): described, for the first time, the life-history of the unusual rhagionid fly *Vermileo vermileo*, the "ant-worm", whose pit-dwelling larvae live in a similar manner to those of myrmeleontid Neuroptera (true ant-lions).

Wilhelm Bosman [1704] of the Dutch East India Company resident in Guinea, according to Bodenheimer (1929), quoting a 1708 German version, refers in his "Voyage to Guinea ... " to ants and to termites; the former he believed had a language; the latter were said to build mounds twice as tall as a man [not an exaggeration], but he did not know if they had a "king" as big as a [full-grown] fresh-water crayfish, as a Mr. Foquenberg would have it. [The queens of some *Macrotermes* species are indeed almost as large as indicated.]

Sloane (1707): published the first of his two volumes on West Indian natural history, but only the second of these is relevant here, and this did not appear for many years (Sloane, 1725), see p. 411).

(W)ray [and Willughby] (1710) published (posthumously *per* Martin Lister) an early classification system for "insects" (i.e., terrestrial invertebrates) that began a trend towards orderly taxonomy. What might be termed soil fauna was included in the following categories:

I. "Ametamorphata" (without change)

A. 1, a: legless land animals living in earth - "*Lumbricus*" (all earthworms), slugs.
B, 1, a, x: 6-legged land animals (larger) - probably beetle larvae.
xx, *yy*: ditto (smaller not holding on to other animals) - including collembola, "booklice" and some other dubious forms.
2, a: 8-legged, with tail - "*Scorpio*"
b: ditto, without tail - "*Araneus*", "*Opilio*", ticks, mites

3: 14-legged - "*Asellus*" (isopods and amphipods)
4: 24-legged - ? "bristletails"
5, a: Many-legged land animals - myriapods

II. "Metamorphumena" (making a change)

A. No resting pupal stage - "*Gryllus*", "*Gryllotalpa*", "*Cicada*", "*Forficula*".
B, 1, a: Moult to pupal stage visible, Coleoptera or Vaginipennia – "*Scarabaeus*" (= all beetles except staphylinids)
2: Moult to pupal stage concealed - "*Muscae*" (higher Diptera)

This work also included reference to mites infesting ground beetles and Lister's appended *De Scarabaeis Britannicis* including Scarabaeoidea, Carabidae, Elateridae and Staphylinidae) and classification of British "insects".

Réaumur (1713 ?): recorded *Parasitus* mites on geotrupid dung beetles (and on bumblebees, etc.) - *cf.* Oudemans (1926).

Vallisnieri (1713): had a classification system in which his third major group of "insects" comprised those that lived in the earth and in hard substances, but this was not adopted in his later, major work of 1773 (see Bodenheimer, 1928).

Günther (1718, 1719): in a sort of quarterly almanack, referred to cockchafers (*Melolontha*, mainly swarming adults), mole cricket (*Gryllotalpa*, illustrated as having a curious proboscis), and cutworms (*Agrotis* and other noctuid caterpillars damaging vegetable roots, illustrated). A little later (Günther, 1723), he again refers to cutworms attacking roots, and to ants (*cf.* Bodenheimer, 1928, 1929).

Kolbe (1719): included reference to termites in South Africa.

Frisch (1720, 1722, 1727, 1736): in parts of a serially-published work on mainly economic aspects of entomology in Germany, made, near the beginning, observations on (burrowing) field crickets (*Gryllus campestris*), recommending their use in biological control of House crickets (*Acheta domesticus*); these, he suggested, would be driven out by their more aggressive cousins. Although this was not a practical proposition, he properly stressed that control of pests was not possible without adequate knowledge of their biology, the biological control of crickets being an example of this. Among the few soil pests considered by him was (1727) the crane-fly *Tipula paludosa*. The subterranean larvae of the Rose chafer, *Cetonia aurata*, were mentioned in the 12th part of the work (1736). Frisch (1772) also records various uropodid and gamasid mites on beetles (including Geotrupidae) in dung (see Oudemans, 1926).

Sloane (1725): in the delayed second volume of his work (see p. 409), discussed various insects associated with soil in the West Indies (mainly Jamaica), notably ants, termites, rootgrubs (scarabaeoid larvae) and the jigger flea (see also Kevan, 1977).

Linnaeus (1735): published the first, short, but regal-folio edition (Fig. 33) of what eventually, in a different form, was to revolutionize many aspects of natural history, his *Systema Naturae*. In it he distinguished the following animals that one may associate with soil:

I. QUADRUPEDIA: Ferae - *Talpa* (mole). Glires - *Sorex* (shrew).
III. AMPHIBIA: SERPENTIA (*Corpus apodum* ... ) - *Anguis* ("snakes", including *Caecilia*); here Linnaeus notes some fabulous monsters (e.g., Dragon and Basilisk, but not

CAROLI LINNÆI, SVECI,

DOCTORIS MEDICINÆ,

SYSTEMA NATURÆ,

SIVE

REGNA TRIA NATURÆ

SYSTEMATICE PROPOSITA

PER

CLASSES, ORDINES,

GENERA, & SPECIES.

*O JEHOVA! Quam ampla sunt opera Tua!*
*Quam ea omnia sapienter fecisti!*
*Quam plena est terra possessione tua!*
Psalm. civ. 24.

*LUGDUNI BATAVORUM,*
Apud THEODORUM HAAK, MDCCXXXV.

EX TYPOGRAPHIA
JOANNIS WILHELMI DE GROOT.

**33**

Fig. 33. Title page of Linnaeus' (1735) first (regal-folio) edition of the *Systema Naturae*.

Amphisbaena).

V. INSECTA: Coleoptera - *Forficula* ("*Staphylinus*" or cockroach!, and *Auricularia* or earwig), *Scarabaeus* (including *Scarabaeus pillularis* and *Melolontha*), *Carabus* (including "*Cantharellus*" *auratus*). Hemiptera - *Gryllus* (only "*Gryllotalpa*" is of present concern), *Formica* (ants), *Scorpio* (*S. terrestris*, as opposed to "*S. aquat.*" or *Nepa*; Linnaeus obviously did not know a true scorpion and deduced their taxonomic position from old descriptions). Aptera - *Acarus* (ticks, mites, etc., including *Pediic[ulus] Scarabaei* [on beetles] and *Scorpio-araneus*, pseudoscorpions), *Araneus* (spiders, etc., including "*Tarantula*" and also *Phalangium*), *Oniscus* ("*Asellus*" spp., isopods), *Scolopendria* (including *Scolop. terrestris* or centipedes, "*Scolop. marina*" or polychaete worms, and *Julus* or millipedes).

VI. VERMES: Reptilia – *Lumbricus* (including *intestinum terrae*, Aristotēles' name in Latin for earthworms, *L. latus* and the parasitic nematode, *Ascaris*), *Limax* (slugs).

Subsequent editions before the 10th (Linnaeus, 1758) need not concern us here.[23]

Réaumur (1738): made references to, and illustrated, various dipterous larvae, including some living in soil; he gave a rather full account of the life-history of the Narcissus bulb-fly, *Merodon equestris*; he also figured ant-lion larvae. Continuing his entomological *Mémoires* (Réaumur, 1740), he gave illustrated accounts of crane fly (*Tipula paludosa*) and a bibionid (? *Bibio hortulans*) and their subterranean larvae; he also discussed and illustrated "*Cicada orni*" and its nymph. A little later, Réaumur (1742) illustrated the life history of "*Formica-leo*" the ant-lion (Fig. 34); he also mentions the well known phoretic mite *Parasitus coleoptratorum*, though not on beetles (*cf.* Oudemans, 1926). Réaumur never published the last four projected volumes of his work, although his manuscripts are preserved in Paris and part of his sixth volume, written about 1743–44, and dealing with ants, was published posthumously (Réaumur, 1926).[24]

Geer (1740, 1743): for the first time, adequately described and discussed Collembola; he also gave good illustrations (Fig. 35), though these were not the first for the group, as has been stated by some (see Spielenberger, 1684, and p. 407). His specimens were found in winter on tree-bark, but this does not detract from the importance of his contribution on these typical soil hexapods. He observed their method of springing, their moulting, their exuviae, their eggs, and the presence of the unique ventral collophore.

Linnaeus (1741): unlike Swammerdam, recognized winged male from winged female ants.

Baker (1743): reported mites on earwigs and geotrupid dung-beetles (*Anoetes polypori* and *Parasitus coleoptratorum* respectively; *cf.* Oudemans, 1926; Bodenheimer, 1929).

Needham (1743, 1745): identified the nematode *Anguina tritici* that causes "ear-cockle"[25] in wheat (see also Thorne, 1961). This was the first plant-parasitic nematode to be discovered and, though the "cockle" galls occur in the ears of pannicles of grasses, they fall to the ground and the worms pass a significant part of their lives in the soil. The importance for soil zoology of this discovery, therefore, was considerable.

Linnaeus (1745): reporting on his trip to Oeland and Gothland in 1741, mentioned carabid, staphylinid and scarabaeoid beetles, ants and "ant-lions" (larvae of *Myremeleon*). His *Fauna Suecica* (Linnaeus, 1746), following the classification of his *Systema Naturae* (above), referred, amongst soil-associated animals, to mole crickets (*Gryllotalpa*) as garden pests, and to various other root-feeding invertebrates, such as slugs. The depredations of root-worms, presumably the larvae of the swift moth *Hepialis humuli*, attacking hops were noted (see also Bodenheimer, 1929). He also noted phoretic mites (such as *Parasitus coleoptratorum* and

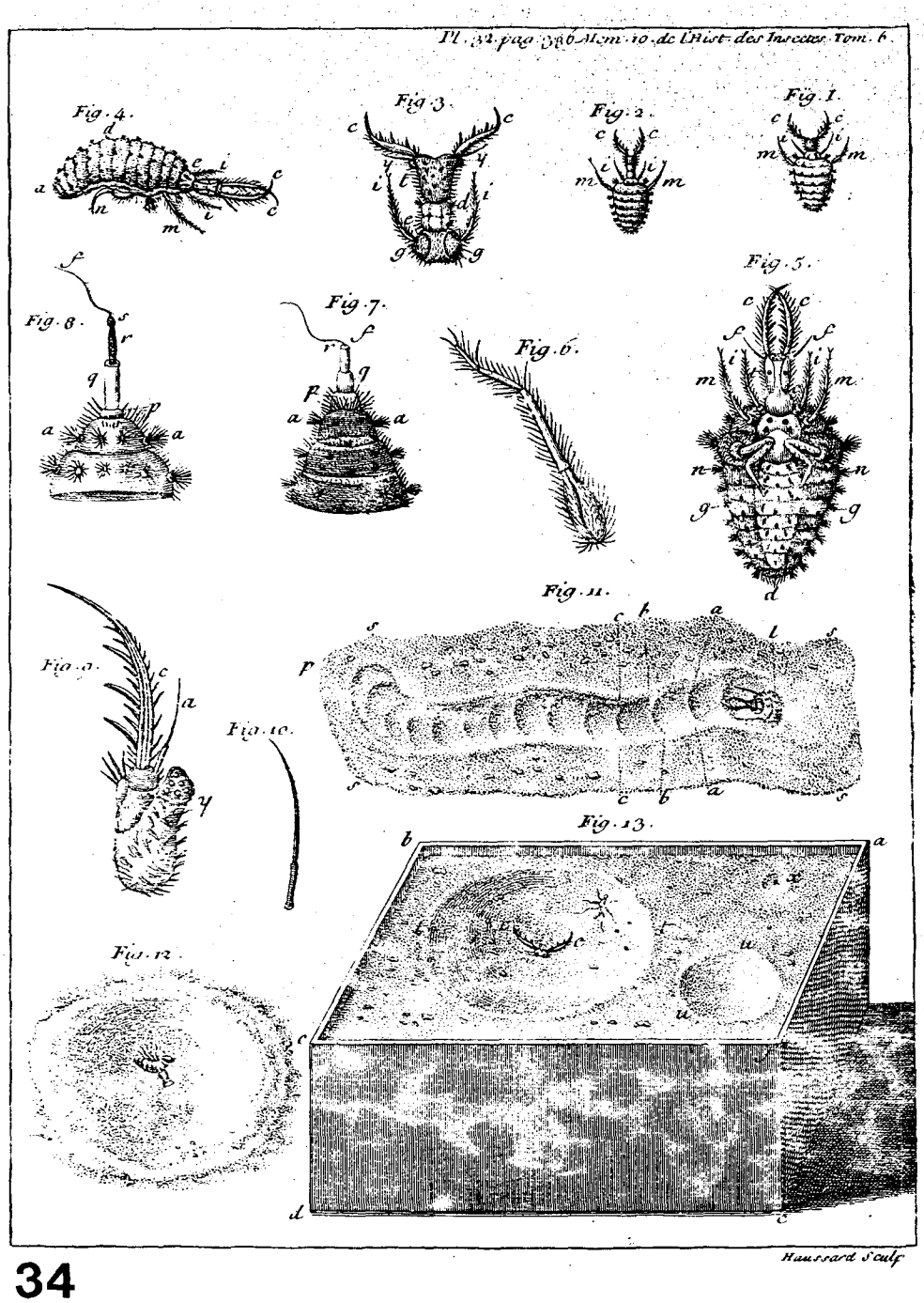


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Fig. 34. The life history of the "*Formica-leo*" *(Myremeleon formicarius)* from *Mémoirs pour Servir à l'Histoire des Insectes. VI.* (Réaumur, 1842: pl. 32). [Original in Lyman Collection, McGill University, Macdonald College Campus.]

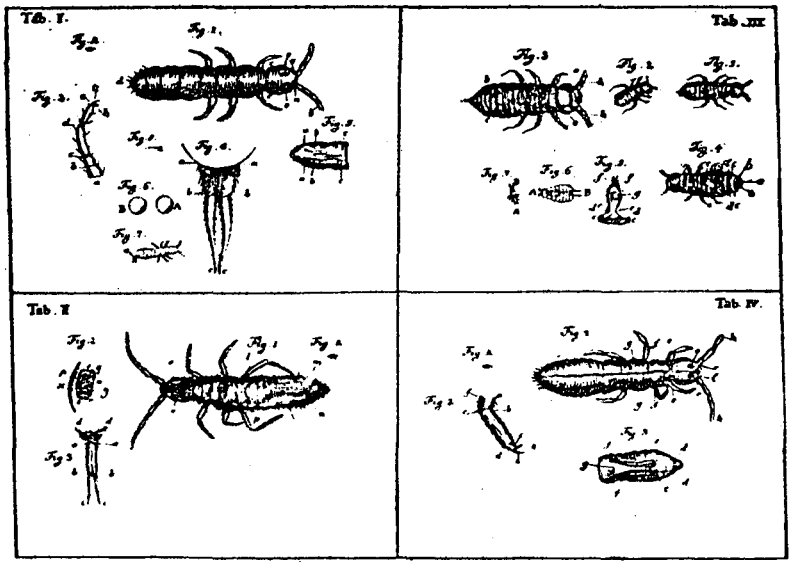

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Fig. 35. Geer's (1740) early illustrations of Collembola (see p. 412).

Uropodidae) on geotrupid dung beetles and other Coleoptera, and the red earth-mite (*Trombidium holosericeum*) and other mites within the soil ("*habitat in terra*") - see Oudemans (1926). This may, indeed, be the first record of mites actually *in* soil. The prostigmatid mite, now known as *Achiptera coleoptratus* was recorded from under stones ("*sub lapidibus*").

Gould (1747): in his account of English ants, gave information on the biology of several species; he also stated that ants are eaten by mole crickets (as well as by other enemies) and noted that millipedes and earwigs, in particular, are among the commensals inhabiting ants' nests.

Baker (1747): gave an account of the damage to pastures in eastern England by whitegrubs and cutworms.

Rösel (1749): included fine engravings and accounts of the mole cricket and field crickets.

Hughes (1750): referred to field crickets (*Gryllus assimilis*) under stones and lumps of earth in Barbados; he also discussed ants and termites there.

Hill (1752): recorded red earth mites, presumably *Trombidium holosericeum*, as being "very common under surface of earth", as was apparently the "grey rough earth acarus," a cryptostigmatid mite determined by Oudemans (1926) as "*Acarus scaber*," possibly a species of *Cepheus*, and "the little black Acarus," *Pergamassus crassipes* (*cf.* Oudemans, 1929).

Geer (1752): gave another account of the rhagionid dipteran *Vermileo*, the "ant-worm fly" referred to much earlier by Poupart (1704), see p. 409.

Réaumur (1753): gave yet another illustrated account of the same insect.

Rösel (1755): described true ant-lions (Myremeleontidae) and illustrated his account with engravings very similar to those of Réaumur (1742, see p. 411), but of even higher quality. Rösel died in 1759, but some time prior to that he had prepared material for his fourth volume

(Rösel, 1761) which showed phoretic mites on *Necrophorus* burying beetles (*cf.* Oudemans, 1926).

Kalm (1756a): gave a very comprehensive account of the "17-year" cicada (as "Gras-Hoppor") in eastern North America. The same author (Kalm, 1756b, 1761) again referred to the same insect and to field crickets, *Gryllus "niger...* " (mostly *G. pennsylvanicus*, sometimes *G. veletis*), the latter overwintering in the soil, on one occasion at a depth of "ten inches" (not piled up to that depth on the surface as mistranslations imply). Kalm is one of the earliest authors to state that he actually dug for invertebrates in the soil! Among the overwintering insects that he found beneath the surface were various kinds of ants, carabid and scarabaeoid beetles and their larvae (including June-beetles and whitegrubs, geotrupids and horned scarabs). Native, litter-dwelling (as well as imported, domiciliary) cockroaches are also mentioned. Kalm's so-called woodlice, however, were not isopods but ticks.

Osbeck (1757): commented upon several kinds of "*Scarabaeus*" beetles and the substrates in which they occurred in Spain. Reference is also made to Spanish field crickets (see also Bodenheimer, 1929).

Adanson (1757): observed various insects during his sojourn in Senegal, and among these were termites (*cf.* Bodenheimer, 1929). Apart from noting their destructiveness, describing fruitless efforts to combat their ravages, suggesting arsenic and fire for the purpose, he also made observations on the internal structure of termitaria. He was astute enough to conclude that the majority of the termites that were most destructive to his possessions were not of a kind that build conspicuous mounds; he noted their covered galleries. Reading Adanson, one gets the impression, perhaps for the first time, that here was an author who had some appreciation of the intricate association between the soil and its (termite) fauna.

We have now reached that point in zoological history, when Linnaeus (1758) published the 10th edition of his *Systema Naturae*. There was, indeed, no momentous biological discovery associated with this event, but the almost universal adoption of binominal nomenclature for all animals, which followed within a remarkably short time, ushered in a new era. So far as the soil fauna was concerned, the only immediate impact was to add a few more generic names to those listed in earlier editions of the work (and eventually to provide a reference point for validating the various names in the future). Additional, marginally soil-associated genera of Coleoptera included such as *Hister*, *Silpha*, *Elater* and *Staphylinus* (in its current sense, no longer a cockroach). We also find additions such as *Termes* (now specifically meaning termites) and the burrowing Field cricket, *Gryllus campestris*.

To conclude this section, we might just mention one, rather quaint but relevant agricultural work that really belongs to an earlier period, though published in the following decade. This is the poem, written in the early 1760's on St. Kitts, West Indies, entitled *The Sugar Cane* (Grainger, 1764). Kevan (1977) has extracted and commented on all the numerous invertebrate animals mentioned in it. These included a number of soil-related forms, such as burrowing land-crabs (*Cardiosoma*), scale insects on cane roots, ants, termites, crickets, cockroaches, jigger fleas and the human hookworm among the parasitic nematodes.

## UP TO THE MIDDLE OF THE 19TH CENTURY

After the publication of the "Tenth Edition" of Linnaeus (1758), a new, if not universal, orderliness came about the field of zoology. While anatomical and biological studies increased, it was, nevertheless, the discovery and description of previously unknown, or unrecognized,

creatures that occupied most attention and which went ahead by leaps and bounds. The "pre-Darwinian" systematic era had begun! Author after author added more and more species to the known fauna of the world, and, though the proportion was not large, many of the animals involved were associated with the soil and litter, if not as adults, then in their immature stages.

Clearly it would be profitless to attempt to enumerate in detailed succession the new discoveries in the manner I have adopted hitherto in this review. We must confine our attention to the more significant events for soil zoology and to the relevant publications. For the general trends of the period, with many specific examples from entomology (though few mention the soil fauna even indirectly), the reader is referred to Tuxen (1973), who begins a little earlier, and to Lindroth (1973), who ends a little later than does this section. For an exhaustive account of developments in acarology from 1759–1804, see Oudemans (1929). A full bibliography of the literature on oligochaet annelids (including terrestrial forms) to 1894, is given by Beddard (1895); Stephenson (1930) gives no historical review for these creatures; Reynolds and Cook (1976) limit their brief remarks to taxonomy.

Before proceeding further, however, we should remember that there were, of course, others than Linnaeus himself who crossed the "nomenclature boundary", and amongst these, perhaps the most important was his compatriot Karl De Geer, whose *Mémoires pour servir à Histoire des Insects* (so called in deference to the works of Réaumur, p. 411, and published in Stockholm) began in 1752, *before* the "Tenth Edition". The final volume, the seventh, however, was not published until the year of its author's death, 1778. It was in this volume that Geer's early observations on Collembola (see p. 413) were reprinted. The series did, of course, contain many references to various other soil- and litter-associated insects, etc., but we shall not enumerate these, other than, perhaps, to mention "*Acarus vegetans*", a uropodid mite on staphylinid beetles noted in 1768 (Oudemans, 1929).

In this period, we should also refer to the general entomological publications of such other authors as J.C. Fabricius, P. Rossi, P.-A. Latreille, W. Kirby and W. Spence, and H.C.C. Burmeister, to mention but a few. The first of these published his most important works from 1775 to 1798, but we shall mention only his *Philosophia Entomologica* ... (Fabricius, 1778). This is because that particular work is regarded by some as being the first *real* textbook of entomology, dealing as it did, with the subject scientifically and confining itself to non-marine anthropods. Rossi is included here, not only for his important example of work on localized faunas, his *Mantissa Insectorum* ... (Rossi, 1792, 1794), but more because he was the first ever Professor of Entomology to be so designated (at the University of Pisa, 1801–1804). He did not, in fact have much direct connection with soil fauna, but the recognition of entomology as a discipline was to be of major importance to its study. Latreille's numerous revisions of the classification of arthropods, mainly between 1802 and 1829, are also of major general significance, but, from a "soil" point of view, he also devoted much time to the study of ants (Latreille, 1802).

Kirby and Spence (1815–1826) made an outstanding contribution to entomology by "popularizing" the subject without degrading it. Nevertheless, they contributed little or nothing beyond what was already known to the knowledge of the soil fauna as such. Admittedly, in the first volume (1815 [& 1816]), they considered certain soil-inhabiting species amongst the pests about which they wrote, but they added virtually nothing new. Similarly, in their second volume (1817), though they devoted 75 pages to ants and termites, they limited discussion almost entirely to their biology and behaviour, with little, if any, indication of the possible roles of these insects as part of the soil fauna.

Towards the close of the period treated in this section, Burmeister (1832) published the first (general introductory) volume of his influential *Handbuch der Entomologie*. His final (5th) volume did not appear until much later, in 1855.

We might now mention a few publications of more particular interest (direct or indirect) for a study of the soil fauna, that appeared during the period considered here. We may begin by noting Spallanzani's (1769) account of free-living nematodes, to which he again referred many years later, in 1787 (*cf.* Chitwood and Chitwood, 1974). Two references by O.F. Müller (1773, 1776) are also notable as they were the first to recognize the distinctness of that extremely important group of soil animals, the enchytraeid oligochaet worms. "*Lumbricus*" (now *Lumbricillus*) *lineatus* and "*L.*" *minutus* (of dubious identity) were the species involved, both from near the seashore (*cf.* Reynolds and Cook, 1976, who give a brief history of oligochaet research generally). Also concerned with "worms," once more with the "ear-cockle" nematode of wheat, *Anguina tritici*, we may also mention Roffredi (1775) and Scopoli (1777), who, respectively, began to unravel the life-history, and named the genus, though not the species. [The latter was not done until Steinbuch (1799) worked mainly on a related species, *A. agrostis* - see Thorne (1961).]

In the meantime, Schrank (1776, repeated 1781) was writing about mesostigmatid mites, such as *Pergamassus crassipes*, and Collembola, like *Onychiura ambulans*, in soil under flower-pots, and mites like *Hologamasus lichenis* under lichens (see Oudemans, 1929); and O.F. Müller (1786 - *cf.* Chitwood and Chitwood, 1974) made the first observations on truly free-living fresh-water nematodes (many of which may occur in the water-film around soil particles).

Another group of predominantly soil-inhabiting animals that were written about quite extensively by European travellers to the tropics were termites. Notable among such authors were König (1779) in respect of southern India and Sri Lanka (Fig. 36), and Smeathman (1781) regarding tropical West Africa (Fig. 37). Fletcher (1922) translated König's paper and commented upon that of Smeathman; Thakur (1984) briefly notes that König was probably the first author to investigate termites *scientifically* in Peninsular India and Sri Lanka (though there had been much earlier reports from the latter by Knox, p. 407), and he clarifies the nomenclature. Fungus-gardens, ectoparasites, the use of termites as human food, etc., are all mentioned. Sparrmann (1784) [1783] also wrote about termites in Africa, but in respect of South Africa. Among other things he observed their "piercing the soil."

More significant, perhaps, and published a few years later (though mostly written earlier) came the first edition of *The Natural History and Antiquities of Selborne* (G. White, 1789). In this, White (see also Note 26, p. 440) not only made keen observations on mole crickets (Fig. 38), field crickets, harmful scarabaeoid and tipulid larvae, other insects and injurious slugs, but stated that "worms seem to be 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 fibres of plants, by drawing straws and stalks of leaves and twigs into it; and most of all, by throwing up such infinite numbers of lumps of earth called worm-casts, which, being their excrement, is a fine manure for grain and grass ... the earth without worms would soon become cold, hard-bound, and void of fermentation; and consequently sterile ... "[26] Here, then, we finally see the beginnings of a clear understanding of the interaction between the soil and its inhabitants!

Nevertheless, though the book was an immediate best-seller (and was even published within three years in a German translation in 1792, the year before White died), this particular piece

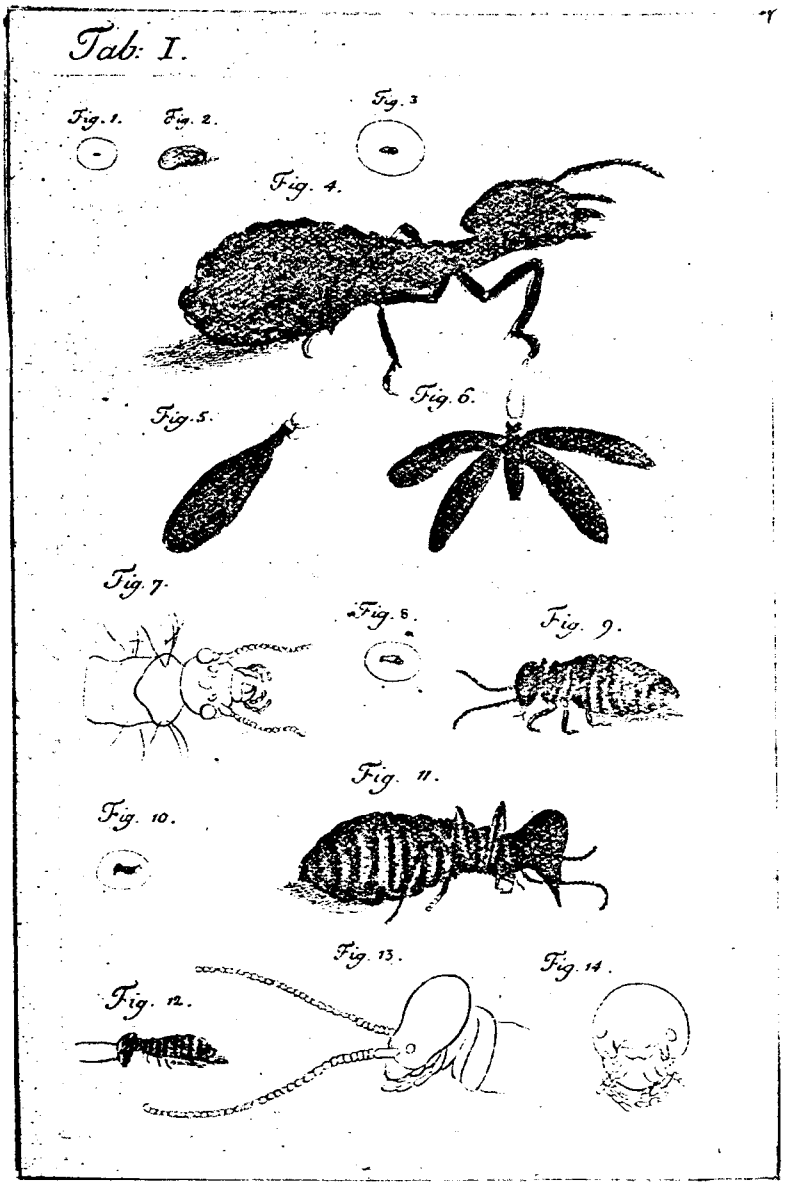


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Fig. 36. Termites from south India and Sri Lanka illustrated by König (1779). Nos. 10 and 11 are of *Hospitalitermes monoceros* (König), from Sri Lanka; nos. 12–14 are of *Anacanthotermes viarum* (König), from South India; the others are of uncertain identity.

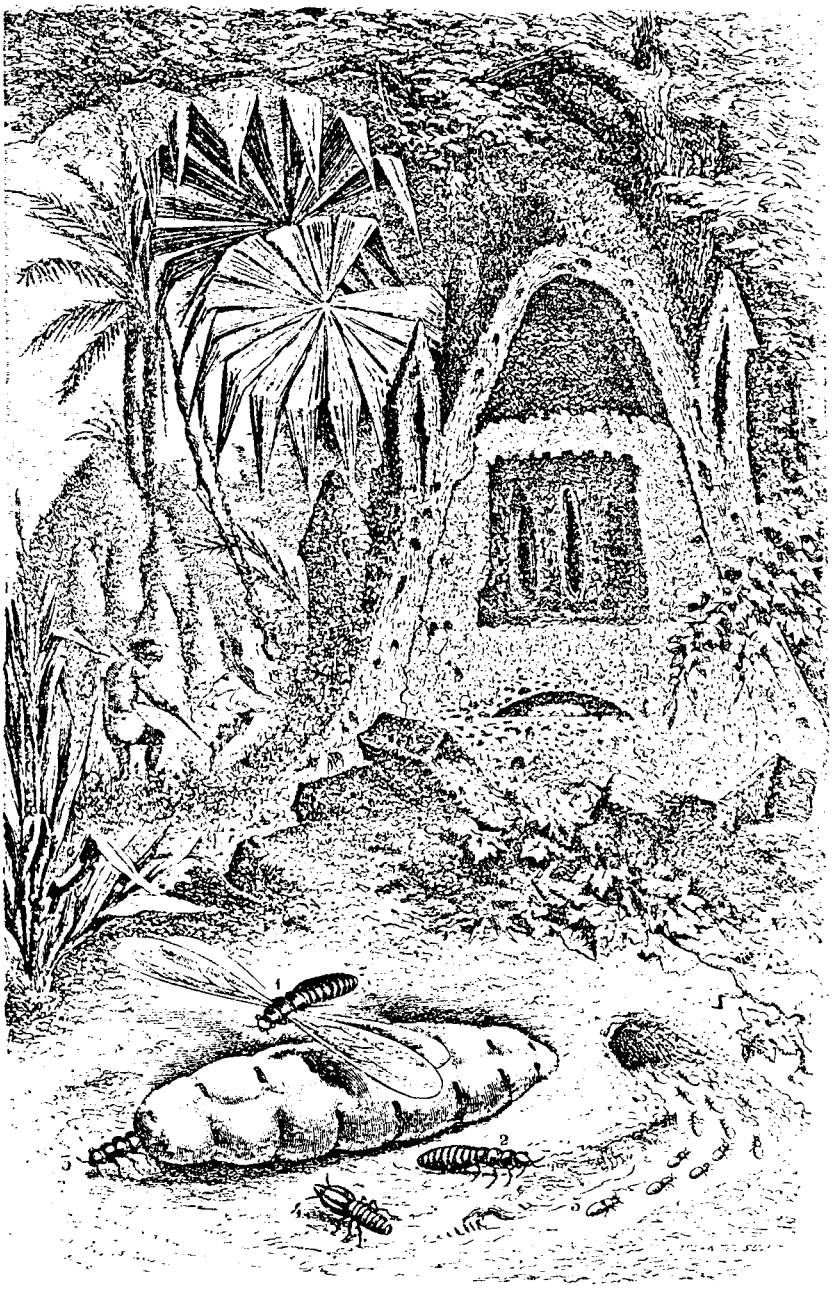

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Fig. 37. The illustration of the large, mound-building West African termite, *Macrotermes bellicosus*, from Smeathman (1781). Smeathman tells us that, in certain "English" parts of West Africa, termites had the dubious distinction of being dubbed "Bugga Bug"!

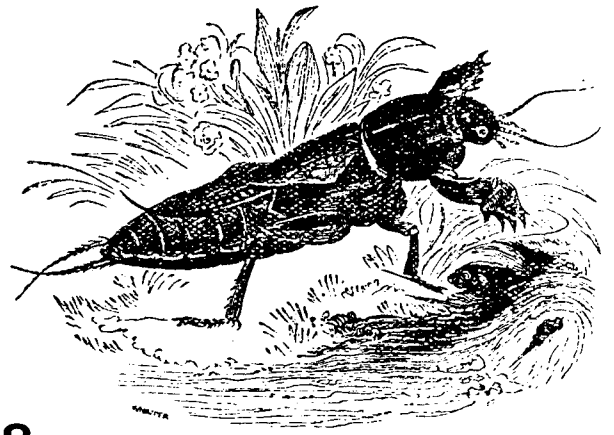

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Fig. 38. Mole-cricket (*Gryllotalpa*). Illustration from an early edition of Gilbert White's (1789) *Natural History and Antiquities of Selborne.*

of wisdom was not followed up for almost half a century, except for the plagiarism by Bingley (1803 and subsequent editions, see Note 26), until Charles Darwin read a paper on the subject to the Geological Society of London on November 1st, 1837, soon after his return from his famous voyage with H.M.S. *Beagle* (Darwin, 1840). — And that did not arouse much immediate interest either!

Meanwhile, general systematic and biological works like those on ants by Latreille (1802) and Huber (1810), and on mites by Schrank (1803–04) and Hermann (1804), went on; Morren (1829) was experimenting with water relations of earthworms; Henle (1837) described the terrestrial oligochaet genus *Enchytraeus* (type species *E. albidus*) from decaying seaweed, sewage beds and compost heaps; Bourlet (1839, 1841, 1842) and Nicolet (1841, 1847) had begun to lay the foundations for the study of important group of soil organisms, the Collembola; and Koch (1835–38, 1844, 1847) did the same for myriapods (and other non-insect arthropods). One may note, too, that Dujardin (1842) wrote about Nematomorpha (gordiid worms) and larger mermithid nematode parasites of insects (his new genus *Mermis*), which can be associated with soil; and then later (Dujardin, 1845), while dealing chiefly with endoparasitic helminths affecting vertebrates, he referred to free-living, soil-inhabiting rhabditiform nematodes, as well as to the plant parasite, *Anguina tritici*. Hoffmeister (1842–45), too, was beginning to distinguish between various species of lumbricid earthworms.

By this time, however, Ehrenberg (1837) had published his tract on the "living soil", drawing attention to the possible role of protozoa and other micro-organisms therein, and Darwin (1840) had pointed the way to the scientific study of earthworms. Thus, soil biology, as such, may now, perhaps, be said to have begun at last, however modestly. One should not, however, be misled by the title of a paper by Schiødte (1849), "Specimen faunae subterraneae", for this, though an important landmark of its own, dealt with cave-dwelling, not soil invertebrates.

## 1850 TO 1900

By the middle of the 19th Century, real knowledge of the soil fauna as such was, in general, only a little advanced from what it had been in the days of Aristotēles. Larger or more conspicuous animals that inhabited the soil were reasonably familiar - such as moles, legless lizards (even true amphisbaenids!) and amphibia, earthworms (though most of these were simply lumped together as "*Lumbricus*", certain slugs, isopods and myriapods, and a modest array of larger insects, such as scarabaeoid and various other beetles and their larvae, cutworms, cicada nymphs, ant-lion larvae, mole crickets and burrowing field crickets, crane-fly, bibionid and other fly larvae, and, of course, various kinds of ants and termites. Incidental knowledge had, however, begun to accumulate regarding smaller creatures, such as Collembola, mites (especially those that lived on insects), enchytraeid worms and nematodes, though mostly as little more than curiosities. Beyond the earthworms, and possibly ants and termites, there was little concept of a soil-fauna community. Other animals were considered largely in isolation, Ehrenberg's (1854) atlas of soil inhabiting protozoa, etc., being an exception.

A noteworthy early contribution to nematology, including free-living forms, was that of Diesing (1850–51), later revised (Diesing, 1861). Also in relation to nematodes, a note by Berkeley (1855) was of considerable interest as it focussed attention on an unidentified "vibro" attacking the roots of cucumbers, probably the first discovery of a plant-parasitic eelworm other than those causing ear-cockles of cereals and wild grasses (*Anguina*), which had again received attention shortly before by Hardy (1850). [J. Kühn's (1857) *Anguillula* (now *Ditybachus*) *dipsaci* on teasel is often considered to be the "second" plant-parasitic nematode.]

Termites were also receiving further attention from a systematic point of view with the first monograph on the group by Hagen (1855–60), while more information on soil-inhabiting nematodes continued to accumulate. For example, Schulze (*in* Carus, 1857) described the soil-inhabiting *Diplogaster micans*); Gervais and Beneden (1859) gave us more on the ear-cockle eelworm (*Anguina tritici*); H.J. Carter (1859) mentioned tropical free-living nematodes while writing on parasites of humans and, economically very importantly, Schacht (1859) noted the occurrence of the cyst-forming, root eelworm (*Heterodera schachtii*, though not then named[27]) on sugar-beet. Claus (1862) and Eberth (1863) also contributed to our knowledge of free-living nematodes, by which time, however there were only about 80 species known, most of them marine (Overgaard-Nielsen, 1949). Lest it be thought that no progress was being made at this time in the area of integrated soil biology, one should mention here the writing of Post (1861–62), who again drew attention to the important role of living organisms in the soil, but the time was not yet ripe for detailed investigations of this kind. More traditional work of importance during the immediate period was the initiation of the continuing work of Schiødte (1861–83) on the larvae of Coleoptera, very many of which live in soil or litter, decaying vegetation, etc., and which were largely unknown at the time. Koch (1863) also (posthumously) laid the foundations for a better understanding of the myriapods. (His son continued in this field later).

A real beginning was also made on a concerted study of free-living nematodes (including many soil forms) by Bastian (1865). Schneider's (1866) monograph on nematodes in general also appeared about the same time, but it was Bütschli (1873) who provided the basis for the present-day classification of free-living nematodes, of which he included 61 soil and fresh-water species, 30 new (Overgaard-Nielsen, 1949). An interesting discovery was also made about this

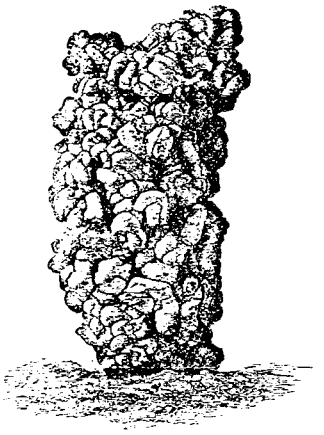
time, when Lohde (1874) first observed nematode-trapping fungi in the soil. Then came the first of J. G. de Man's publications dealing specifically with soil nematodes (Man, 1876), of which he described about 50, most new (Overgaard-Nielsen, 1949). This author continued to publish on free-living species until 1921 (Thorne, 1961). Interest in terrestrial annelids, especially earthworms, was increasing about this time, as indicated by the works of Eisen (1871–1873), who was to continue with their systematics for many years, and of Perrier (1872, 1874), who also did some experimenting with them.

A milestone belonging to this period, for students of the soil fauna, was the publication of the *Monograph of the Collembola and Thysanura* (which included Microcoryphia and Diplura) by Lubbock (1873).[28] Such biological and ecological information as was available was included, though it was mainly a systematic work, as was customary (but necessary) at the time. By the end of the decade, Plateau (1876) had studied digestion in myriapods; Hensen (1877) had published the first important paper on the role of earthworms in soil fertility since Darwin (1840); Vejdovský (1877, 1879), in two works, with which I am unfamiliar, began to put the enchytraeid annelids in order; and P.E. Müller (1879), who invented the terms "humus form", "mull" and "mor", stressed that these latter were biological, not merely physico-chemical, systems, in which the fauna in general (not merely earthworms), together with other organisms, was intimately involved (see also P.E. Müller, 1884, 1889).

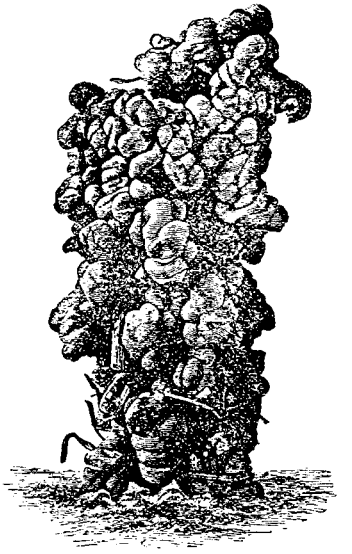
Darwin (1881), with his customary procrastination, now published *The Formation of Vegetable Mould through the Action of Worms* (Fig. 39), which over-shadowed other valuable but slightly later contributions on the subject by Hensen (1882) and Baur (1883). Vejdovský (1885) also made further studies of earthworms and other oligochaets (but not much on Enchytraeidae as he had already dealt with these, as noted above). It is probable that Darwin's book, rather than stimulating further research on the interaction of fauna and soil, tended, by its authoritativeness, to give the impression that there was little more to be said on the matter - except where earthworms were rare or absent. Drummond (1887, 1888) developed the hypothesis that termites were the tropical analogues of earthworms, but soil fauna studies as such did not burgeon forth as might have been expected.

We should now turn our attention again to other groups of animals that are extremely abundant in the soil, namely the myriapods and the mites. In respect of the former, Latzel (1880, 1884) published a very important monograph for central Europe. Knowledge of mites was gradually accumulating as a result of the efforts of various authors, but one in particular, Antonio Berlese, should be mentioned. His *Acari, etc.*, in Italia reperti, published over many years (Berlese, 1882–1903) included large numbers of soil-inhabiting species. Before his major contributions were made[29], however, Michael (1884, 1888) had published an extremely important monograph on the British "oribatid" (Cryptostigmatid) mites, which laid the foundation for the study of these typical and abundant soil- and litter-inhabiting creatures.

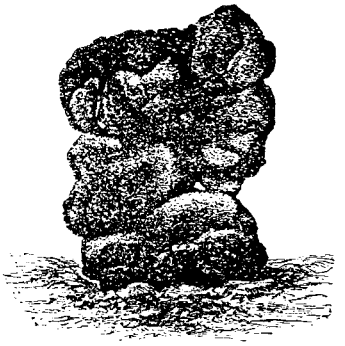
Towards the close of the 19th Century we should refer to further work on economically important root-feeding nematodes, for instance, the description of the root-knot eelworm of coffee *Meloidogyne exigua* by Goeldi (1887) in Brazil, and a fine monograph on the Sugar-beet eelworm, *Heterodera schachtii*, by Strubell (1888). One of the earliest workers to realize the important role of the fauna in comminution of litter and in humus formation was Keller (1887). Another was Kostȳchev (1889), who recognized that passage of organic matter through the bodies of invertebrates (earthworms, millipedes, sciarid fly maggots), even if little chemical change occurred, was important, the excrement being more readily broken down by fungi. Related to this, though scarcely realized at the time, were the studies on the biology of



Tower-like casting from near Nice, constructed of earth, voided probably by a species of Perichæta : of natural size, copied from a photograph.



A tower-like casting, probably ejected by a species of Perichæta, from the Botanic Garden, Calcutta : of natural size, engraved from a photograph.



A casting from the Nilgiri Mountains in South India ; of natural size, engraved from a photograph.

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Fig. 39. Famous illustrations of earthworm castings published by Charles Darwin (1881); from photographs by Dr. King, when keeper of the Botanic Gardens, Calcutta.

UNTERSUCHUNGEN

ÜBER DIE

BODENFAUNA IN DEN ALPEN

INAUGURAL-DISSERTATION

ZUR

ERLANGUNG DER PHILOSOPHISCHEN DOKTORWÜRDE

VORGELEGT DER

HOHEN PHILOSOPHISCHEN FAKULTÄT DER UNIVERSITÄT ZÜRICH

(MATHEMATISCH-NATURWISSENSCHAFTLICHE SECTION)

VON

KONRAD DIEM

AUS HERISAU, APPENZELL A.-RH.

BEGUTACHTET VON DEN HERREN PROF. DR. A. LANG
PROF. DR. K. KELLER

ST. GALLEN
ZOLLIKOFER'SCHE BUCHDRUCKEREI
1903

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Fig. 40. Title page of Konrad Diem's (1903) thesis on the Soil Fauna of the Alps. The work was reprinted the same year in *Jahrbuch der Naturwissenschaftlichen Gesellschaft St. Gallen 1901–1902*: 234 pp.

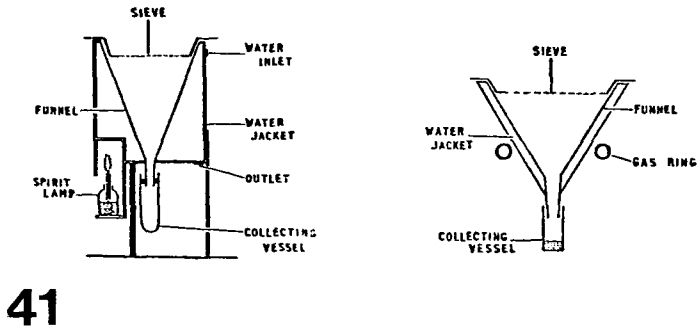


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Fig. 41. Berlese funnels for extracting soil arthropods. Left, original pattern of Berlese (1905); right, early gas-operated modification. After Kevan (1962a).

millipedes by Rath (1890, 1891). Further investigations on the effects of earthworms on soil fertility were also carried out by Wollny (1890) and Djémil (1896), while various other earthworms studies were undertaken by Bretscher from 1895 until the end of the century, when he submitted for publication a paper on their biology, which appeared the following year (Bretscher, 1901).

## 1900 TO 1945

The 20th Century opened auspiciously from the point of view of soil zoology, for, under the direction of Professor Conrad Keller (see above), Konrad Diem undertook a comparative ecological study, from 1900 to 1902, of the animals inhabiting Swiss alpine soil and litter. In his doctoral dissertation (Fig. 40) for the University of Zürich (Diem, 1903), he briefly defined the term "*Bodenfauna*" (soil fauna) for the first time, and it would seem that his thesis was the very first attempt at an integrated faunistic investigation of soil and litter habitats anywhere. Though his methodology was quite unsophisticated, he considered not only the more conspicuous animals (earthworms, myriapods, gastropod molluscs), but also Collembola, nematodes and enchytraeids as best he could. Additional, less thoroughly treated groups were beetle larvae, fly larvae and "others". Mites seem to have been ignored. Indeed he admits to having difficulties with the smaller forms of life.

Another important step forward at about this time was the invention of the "Berlese funnel" for extracting mites and other small arthropods from soil and litter (Berlese, 1905). Berlese's name is still widely, but erroneously used for virtually all apparatus of a similar nature, but the original, water-jacketed funnel was heated, eventually by a gas-ring from *below* (Fig. 41), whereas all modern devices are unjacketed and heated (by an electric bulb or other device) from *above*. These are modified from the "Tullgren funnel" (Tullgren, 1917).

During the early years of the century, general interest in earthworms continued. Parker and Metcalf (1906) and Hurwitz (1910) were concerned with the reactions of these to salts and to acids respectively. Russell (1910) and Baugé (1912) again stressed the question of earthworms and soil fertility. Wieler (1914) also concerned himself with earthworms and soil reaction.

The publication by Russell (1912) of the first edition of *Soil Conditions and Plant Growth* "provided an enormous stimulus to the comprehensive study of the soil and its living organisms, but at that time not much could be included on the role of animals other than earthworms ... "

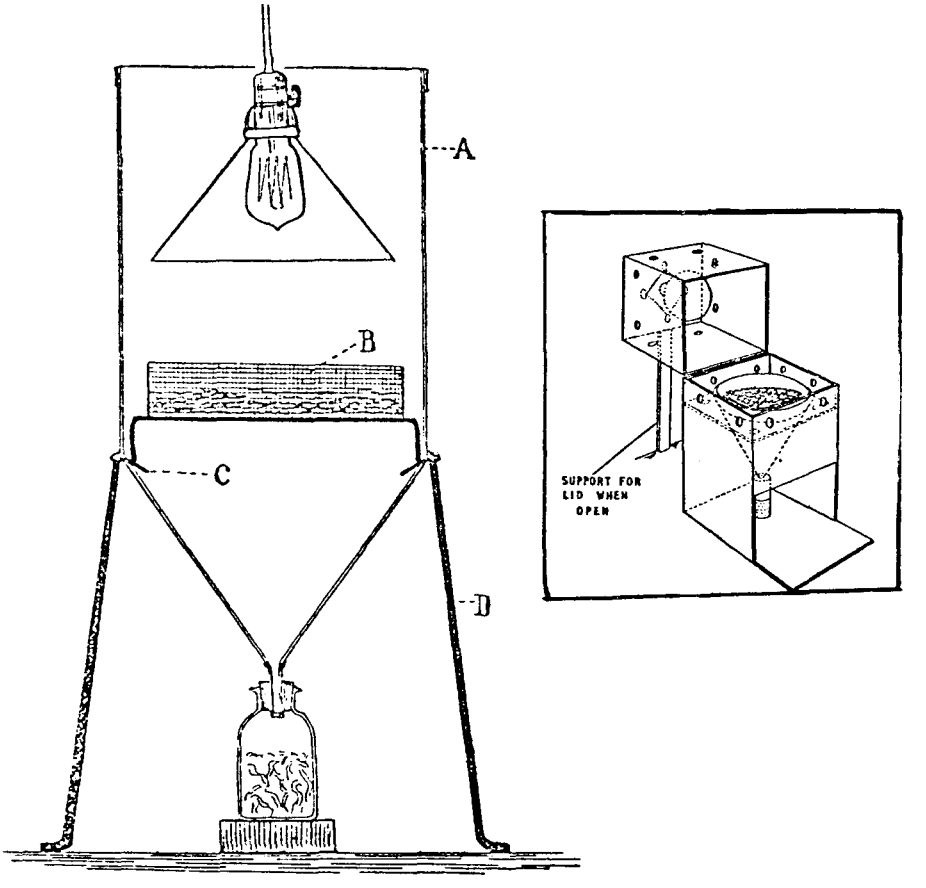
(Kevan, 1962a), and there was little enough of that. A sort of "two solitudes"[30] attitude on the part of self-styled soil scientists on the one hand, and of zoologists, on the other, seems to be traceable to this period. The former, for a long time, seldom paid attention to animals smaller than earthworms (which they ignored if they could), whilst the few zoologists who deigned to get their hands dirty were considerably retarded in their recognition of the pedological significance of the soil fauna. Most early studies by the latter had a direct or indirect bias towards crop pests, mostly insects or nematodes.

One of the earliest comprehensive studies of insects (and other arthropods) in the soil was that of Cameron (1913)[31] in which the principal finding was that gravitational soil water was destructive, and capillary soil water favourable, to them. The paper was not concerned with effects of the fauna on the soil. On the other hand, Cobb (1915), in a pioneer paper attempting to popularize "nematology" (the word was introduced into the language here), suggested, though no basic information was available, that nematodes presumably bore an important relationship to the fertility and biology of the soil. (He was in error, however, in his opinion that the great majority of soil species possessed an oral "spear" and were injurious to plant roots). He estimated that, in an acre of North American alluvial soil, there may be 3,000 million nematodes in the top 3 inches (7.5cm). Cobb (1917, 1918) gives further estimates of nematode populations in sand and soil.

While the First World War restricted work on the soil fauna (as it did other endeavours) in most places, even in neutral countries, we may recall the appearance of Tullgren's (1917) funnel for extracting small arthropods (Fig. 42), and note the invention of another type of funnel for soil-inhabiting nematodes (Fig. 43), that of Baermann (1917). The latter was originally for retrieving the larvae of parasitic hook-worms from tropical soils, but it was subsequently used for nematodes generally, including those occurring in the faeces of vertebrates.

Probably the first Canadian contributions to integrated soil entomology were also published at this time, those of Cameron (1917a, b), though the larger of these related to work done previously in England. They stressed the importance of soil moisture and aeration, as well as of other factors, on soil insect ecology.

Over the next decade or so, no major stride forward was made in the study of the soil fauna, but we may mention a few publications of interest. Morris (1920) began his investigations on soil insects, reporting on their occurrence in permanent pastures; Jegen (1920) discussed the significance of enchytraeid worms in humus formation; Buckle (1921) investigated the fauna of arable land; Arrhenius (1921), Moore (1922) and Phillips (1923) were concerned with the effects of soil reaction (pH) on earthworms, whilst Salisbury (1923) looked at the question from the opposite viewpoint, the influence of earthworms on soil reaction and stratification; Micoletzky (1922) gave the fullest account to date of free-living soil nematodes; and McColloch and Hayes (1922) discussed the *reciprocal* relations between soils and insects. The year 1922 was also notable for the first serious attempt to use "wet" extraction methods for soil arthropods (Fig. 44), as introduced by Morris (1922a) for the purpose of his studies on these animals in arable land (Morris, 1922b, 1927). M. Thompson (1924) also undertook an extensive study on soil arthropods. Soil nematode investigation, especially on applied aspects also began to forge ahead. The distinctiveness and great importance of the Potato root eelworm (later called the Golden nematode in America) came to the fore, the name *Heterodera rostochiensis* being bestowed upon it by Wollenweber (1923); see papers by Wolleenweber (1924) and Morgan (1925). Thorne (1927) investigated mononchid eelworms in arable soils in

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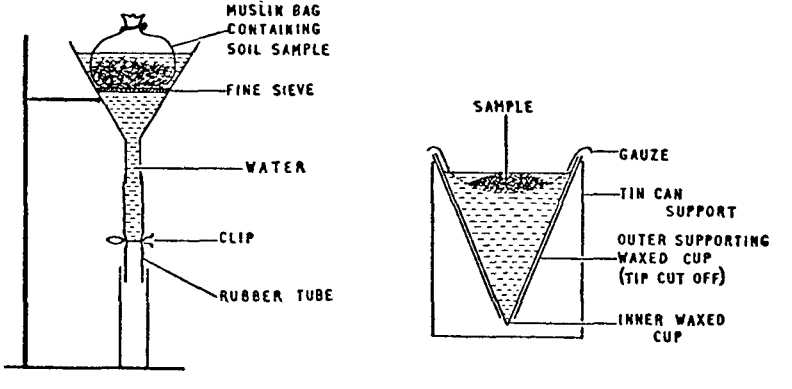


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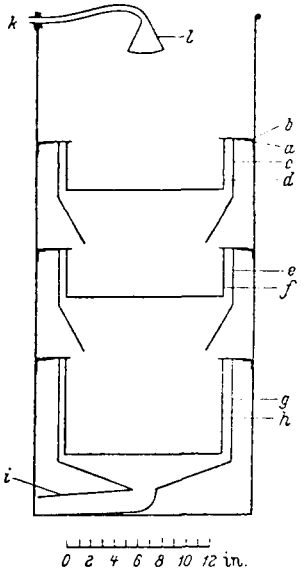
Fig. 42. Tullgren funnels for extracting soil arthropods. Left, original design, after Tullgren (1917); inset, right, modified version of Haarløv (1947), after Kevan (1962a). Fig. 43. Baermann funnels for extracting soil nematodes. Left, basic pattern of Baermann (1917); right, Anderson and Yanagihara field pattern. After Kevan (1962a).

Fig. 44. Morris "wet" extraction apparatus for soil arthropods; after Morris (1922a). a, ledge; b, shelf; c, first funnel; d, first sieve with holes 3–5 mm in diameter; e, second funnel; f, second sieve, with holes 1–5 mm in diameter; g, third funnel; h, third sieve, with 50 meshes to the inch; i, outlet; k, inlet; 1, rose. Fig. 45 Ladell flotation apparatus for extracting soil arthropods; after Ladell (1936). a, cylinder in which soil is mixed with liquid; b, conical head fitted to the top of the cylinder, with a watertight connexion; c, combined stirrer and air bubbler supporting two sieves; d, stirring mechanism; e, air pump; $e_1$, manometer; f, small electric motor for stirring; g, soil sedimentation tank; h, glass reservoir containing the solution; i, Büchner funnel; j, filter flasks; 1, discharge outlet of cylinder; 2, handles; 3, rubber ring; 4, central tube of hollow stirrer; 5, hexagonal box of stirrer; 6, air tubes; 7, air outlet; 16, threaded collar; 17, hexagonal nut; 18, brass tube connexion; 19, flanged tube; 20, hexagonal back nut; 21, brass boss; 22, iron strap; 24, crank; 25, connecting arm; 27, chute; 28, lip; 29, overflow pipe; 30, discharge outlet of tank; 31, handles; 32, tap funnel. Fig. 46. Flotation apparatus for extracting soil arthropods. Above, Salt and Hollick (1944) apparatus (A. sieving; B. actual flotation; C, separation of arthropods from vegetation). Below, large-scale tanks of Cockbill *et al.* (1945). Both after Kevan (1962a).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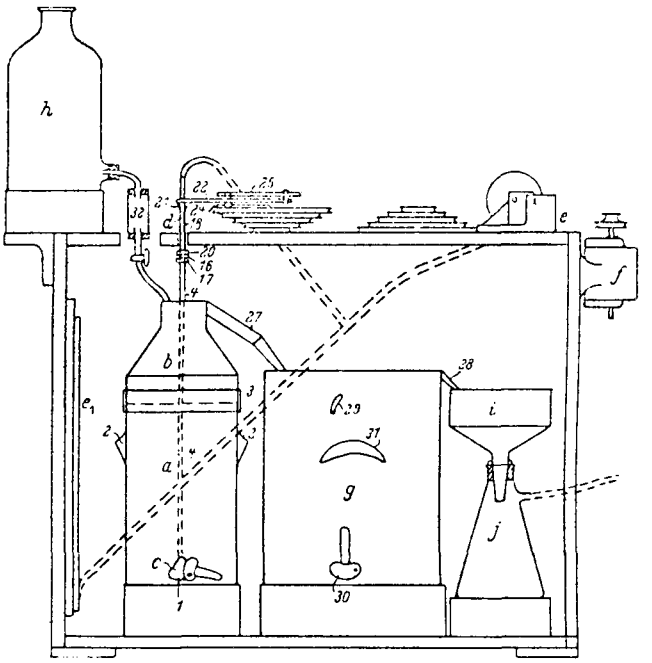
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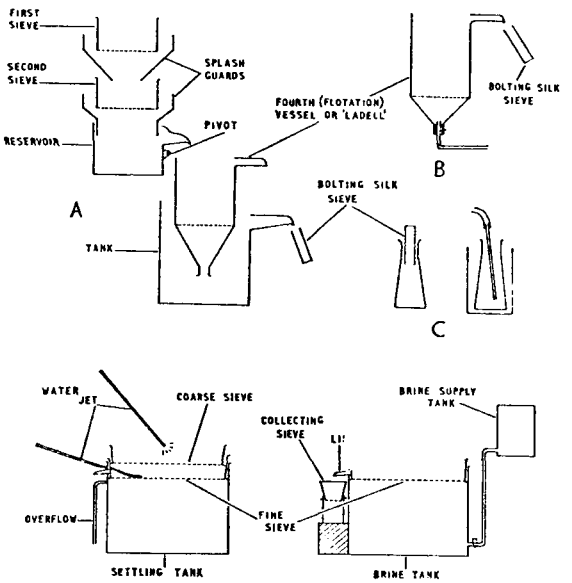
FIRST SIEVE
SECOND SIEVE
SPLASH GUARDS
RESERVOIR
PIVOT
FOURTH (FLOTATION) VESSEL OR 'LADELL'
BOLTING SILK SIEVE
A
B
BOLTING SILK SIEVE
TANK
C
WATER JET
COARSE SIEVE
BRINE SUPPLY TANK
COLLECTING SIEVE
OVERFLOW
FINE SIEVE
SETTLING TANK
BRINE TANK

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the United States, and Cobb (1927) summarized what was known about "nemas" (nematodes other than parasites of vertebrates) in general. Even in China these animals were receiving attention in soil (H.D. Brown, 1929). An important paper was published by Handschin (1926) on the Collembola of subterranean communities. Oudemans (1926, 1929) published the first two parts of his historical bibliography of mites. A little-known, annotated bibliography of cryptostigmatid or "moss" mites by Jacot (1929) should also be mentioned, and, so as not to forget earthworms, we should note an important contribution by Stöckli (1929) on the significance of these in soil formation.

In concluding our brief review of the 1920's, we should also refer to the comprehensive study of insects and other invertebrates in the soils of pasture and arable land by Edwards (1929), and to a characteristically American contribution to soil entomology – a machine (albeit still hand-operated) to facilitate the rapid recovery of insect larvae (specifically elaterid wireworms) from the earth (Lane and Shirck, 1928). Power-driven apparatus of increasing complexity was introduced later, but this will not be considered further here (for references, see Lang, Akesson and Carlson *in* Kevan, 1955: 351–355).

The beginning of the next decade was notable for the appearance of one of the classics of soil zoology, *The Fauna of Forest Soils*, by C.H. Bornebusch (1930), which had a very great impact on the study of the role of animals in forest soil ecology. In the same year, too, Mail (1930) stimulated interest in the effect of low (winter) temperatures on the survival of soil insects. Driedax (1931) published further investigations on the significance of earthworms for plant growth, and, in the same year, Nazaroff (1931) advanced the interesting theory, later generally accepted (Machado, 1983b), that large masses of spongy brown ironstone in lateritic areas of the African (and other) tropics were a result of "the ferruginization of termitaria". Ulrich (1933) made a notable quantitative comparison of the macrofauna of forest litter between good and poor stands of trees. Kollmansperger (1934) included extensive ecological information in his thesis on German earthworms; and Rommell (1935) gave a positive example of the role of myriapods in mull formation.

It was about this time that Jacot (1935, 1936), first in a short, popular article and then by a scientific paper, began his eloquent, but not very successful, attempts to interest North American biologists and/or pedologists in the fauna of soil and litter (especially of forest and woodland) for its own sake and from a pedological viewpoint.

Frenzel's (1936) monograph on invertebrates of all groups in meadow soils was the next large work in the field after that of Bornebusch. It appeared in the same year as Ladell (1936) proposed a new, rather complicated type of flotation apparatus for recovering insects and other arthropods (Fig. 45). In the following year, Ford (1937) published an important ecological paper on population fluctuation in Collembola and mites. A significant Canadian contribution on populations of soil insects was that of K.M. King (1939). Jacot's (1939) discovery that phthiracarid mites hollow out conifer needles without apparent external change in their form was also significant. Jacot (1940) also produced a very commendable, comprehensive review of animals in soil and litter, but again he seemed unable to influence American biologists or pedologists to any appreciable extent.

As the Second World War progressed, the need for food production focussed attention on the soil (except for large areas where this was being fought over). Even papers like that of Joachim and Kandiah (1940), comparing soils derived from termite mounds with those of adjacent land, took on added significance, as did Adamson's (1943) review of termites and soil fertility. Even the mole (*Talpa europaea*) and its relationship with earthworms and other soil

invertebrates received its share of attention (MacDougall, 1942). From a pedological viewpoint, the microscopic investigations of humus by Kubiëna (1943) showed the abundance and importance of the excrement of soil invertebrates for further decomposition of soil organic matter, Gisin (1943), in neutral Switzerland, published the results of an extensive study of the ecology of Collembola, and Starling (1944), in the eastern United States, studied the ecology of pauropods, a little-known group that proved to be much more abundant in the soil than had generally been believed. In England, however, intensive wartime studies of crop pests had been in progress, particularly on wireworms (elaterid beetle larvae) which were of special importance in crop fields that had previously remainded unploughed for long periods. From these studies came, not only ecological information aimed at pest control, but the well-known flotation soil-extraction technique of Salt and Hollick (1944) and the large-scale flotation tanks of Cockbill *et al.* (1945) - see Fig. 46. And, of course, there was no lack of interest in earthworms and soil fertility. This even stimulated the reissue of Darwin's (1881) book on the subject, with a foreword by Sir Albert Howard, in which the latter expressed strongly his opinions against the use of "artificial" fertilizers.

Meantime, in neutral Sweden, extensive studies on the fauna of forest soil and litter had been undertaken for some time. These resulted, near the end of the war, in another large "land-mark" publication in the annals of soil zoology (Forsslund, 1945).

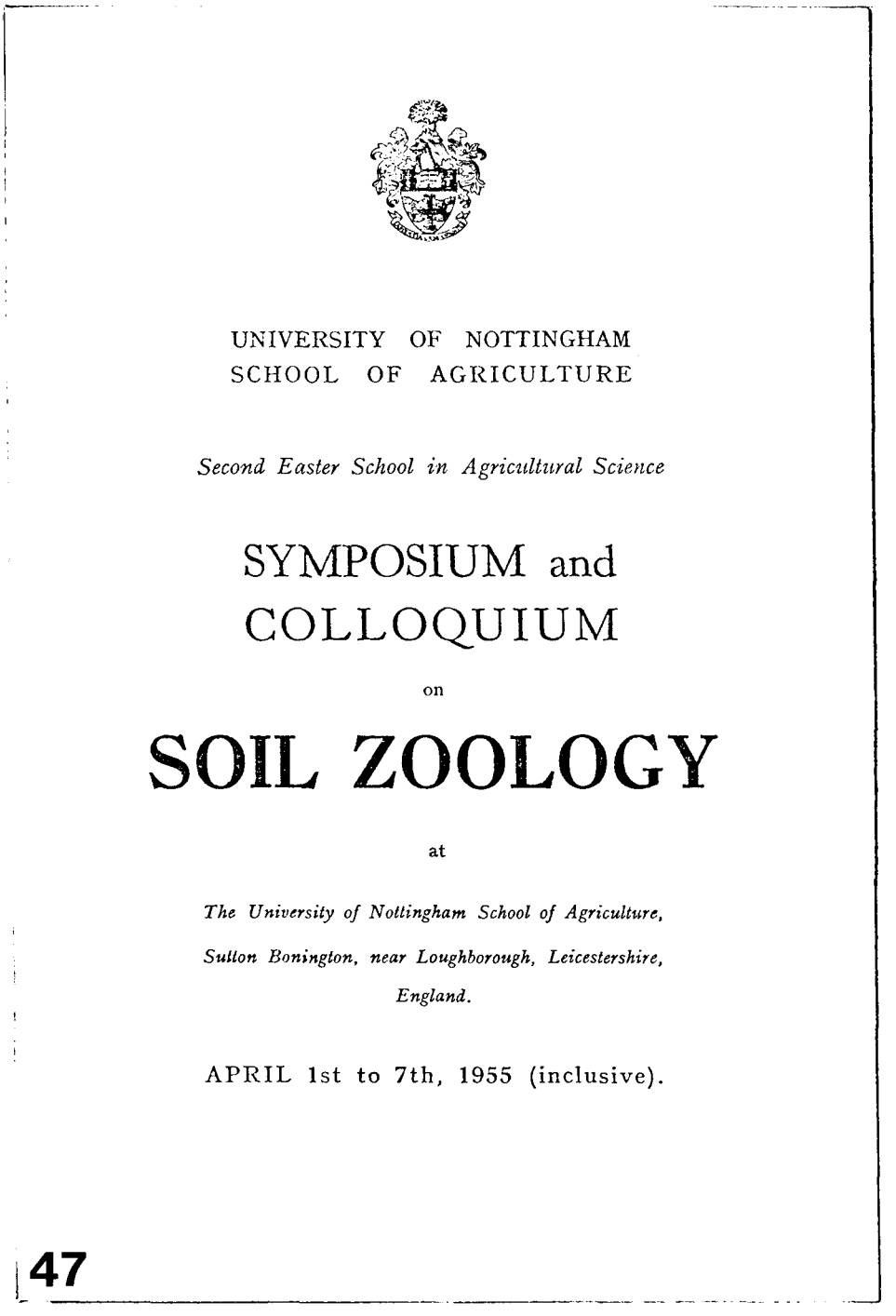
## THE POST-WAR PERIOD TO THE 1960'S

Immediately after the war there was a gradual, then a rapid, expansion of work in soil zoology, although the subject had, as yet, by no means developed into a discipline like fresh-water biology. Pearse (1946) in the United States, Fenton (1947) in the United Kingdom, and Gilyarov (1947) in the Soviet Union, produced important contributions on forest soil faunas. Salt *et al.* (1948) continued with studies on pasture soils.

There was also considerable renewed interest in earthworms and their reciprocal relationships with soil conditions (Evans and Guild, 1947, 1948; Evans, 1948; Guild, 1948; Dawson, 1948; Dutt, 1948). Scandinavia, where soil fauna studies had always been pursued with vigour, continued to produce impressive results. Haarløv (1947) modified the Tullgren funnel so as to increase its efficiency (Fig. 42, inset); his was the basis of numerous subsequent modifications, improvements and adaptations. Weis-Fogh (1948) related distribution of Collembola and mites within the soil profile to pore-space, using an elegant, new technique. Overgaard-Nielsen (1948) introduced new methods for nematode and rotifer extraction, and Forsslund (1948) recorded unprecedented numbers of arthropods from forest soils.

The same year also saw the publication of Kubiëna's (1948) influential *Entwicklungslehre des Bodens*. Although this was not the first time that this author had drawn the attention of other pedologists to the importance of small arthropods in humus formation, nor was it to be the last, it may be said that it was now, more than at any time previously, that "soil scientists" were made to sit up and take notice of soil and litter fauna, other than earthworms, in the process of soil formation.

The next few years saw the burgeoning of major works on the soil fauna. In addition to those in more restricted fields, like that on the soil nematodes by Overgaard-Nielson (1949), they included books covering a wide field: Gilyarov's (1949) *Osobennosti Pochvȳ ... v Evolyutsii Nasekomȳkh*, dealing with the soil as a milieu for insect evolution; Franz's (1950) *Bodenzoologie ...*, largely relating to the importance of soil fauna for cultivation; Kühnelt's



UNIVERSITY OF NOTTINGHAM
SCHOOL OF AGRICULTURE

*Second Easter School in Agricultural Science*

SYMPOSIUM and
COLLOQUIUM

on

SOIL ZOOLOGY

at

*The University of Nottingham School of Agriculture,*
*Sutton Bonington, near Loughborough, Leicestershire,*
*England.*

APRIL 1st to 7th, 1955 (inclusive).

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Fig. 47. The historic, pale buff cover of the programme for the first international meeting of soil zoologists in 1955.

(1950) *Bodenbiologie* ..., a general text on the soil fauna, later translated into Spanish and English, and Delamare Deboutteville's (1951) *Microfaune du Sol* ... with an emphasis on tropical as well as temperate conditions and taking into account soil formed above ground level on trees. At this time too, there appeared another large research report on the (mainly arthropod) fauna of temperate (beech) forest soil, which was to become a classic (Drift, 1951). Then Hartmann (1951, 1952) stressed the importance of soil fauna in his books on forest soil ecology. Soon afterwards came another important book, mostly relating to soil and litter fauna, but one which is not widely known to soil zoologists, and even less to pedologists, partly because of its title, *The Biology of the Cryptic Fauna of Forests* (Lawrence, 1953), and partly because it relates mainly to southern Africa. Also regionally restricted was *Fauna Pochv Latviĭskoĭ* SSR (on the soil fauna of Latvia) by Eglitis (1954). Although it would seem invidious to try to select any papers from the scientific journals, for particular mention, the valuable review by Birch and Clark (1953) should perhaps be excepted.

Pedological works, such as those of Kubiëna (1953), Handley (1954) and Wilde (1954), now referred more and more to the importance of the soil fauna in humus formation, but it was the year 1955 that saw Soil Zoology finally emerge as a discipline on its own. In the previous year, almost exactly 30 years before this present meeting, I undertook, at the instigation of Professor E.G. Hallsworth, to organize the first[32] international colloquium in the field, to take place from the 1st to the 7th April, 1955, at the University of Nottingham School of Agriculture, Sutton Bonington, near Loughborough, England (Fig. 47). The meeting - registration fee, *then*(!), 10 shillings (*ca.* $2), accommodation - (all meals included!) £ 1.5.0 (*ca.* $5) per diem! - was an unqualified success, bringing together scientists from many countries (though mainly European) and its proceedings (Kevan, 1955) published in record time, became "out-of-print" almost at once and are now very hard to obtain on the second-hand market. The Sixth International Congress of Soil Science, at its meeting the following year, fostered a greater interest than hitherto in the soil fauna, and there were several papers given in this field (International Society of Soil Science, 1956). This led to an ongoing series of international Soil Zoology colloquia, beginning in association with the 15th International Congress of Zoology in 1958 (International Congress of Soil Zoology, 1959; Murphy 1962) - see also Note 32.

From the time of the 1955 meeting onwards, too, soil animals also became emphasized in several major works on animal ecology, such as those of Tischler (1955), Macfadyen (1957, 1962) and Balogh (1958), in at least one introductory zoology textbook (Moment, 1958), and in some general books on soil, such as those of Russell (1957), though the United States Yearbook of Agriculture, *Soil* (Stefferud, 1957), had very little space devoted to the subject, which was symptomatic of an unexpectedly retarded general interest in North America. Though both Canada and the United States had had in the past, and continued to have, their proponents of soil zoology (as distinct from those who worked with soil pests) they lagged far behind Europe, both western and eastern, in the field. Courses and research in Soil Zoology, as such, were, however, introduced by me into the McGill University (Macdonald College) programme in 1958–59, where they uniquely continue. Canadian perspectives of the times were also published (Kevan, 1959–61, 1962b).

In the late 1950's and in the 1960's, there was a very large increase in the number of publications on soil fauna in scientific periodicals. Of these, I will mention only a review by Kühnelt (1963), and a paper dealing with an important development in arthropod extraction technique by Kempson *et al.* (1963) - see Fig. 48. Significantly, however, many books and

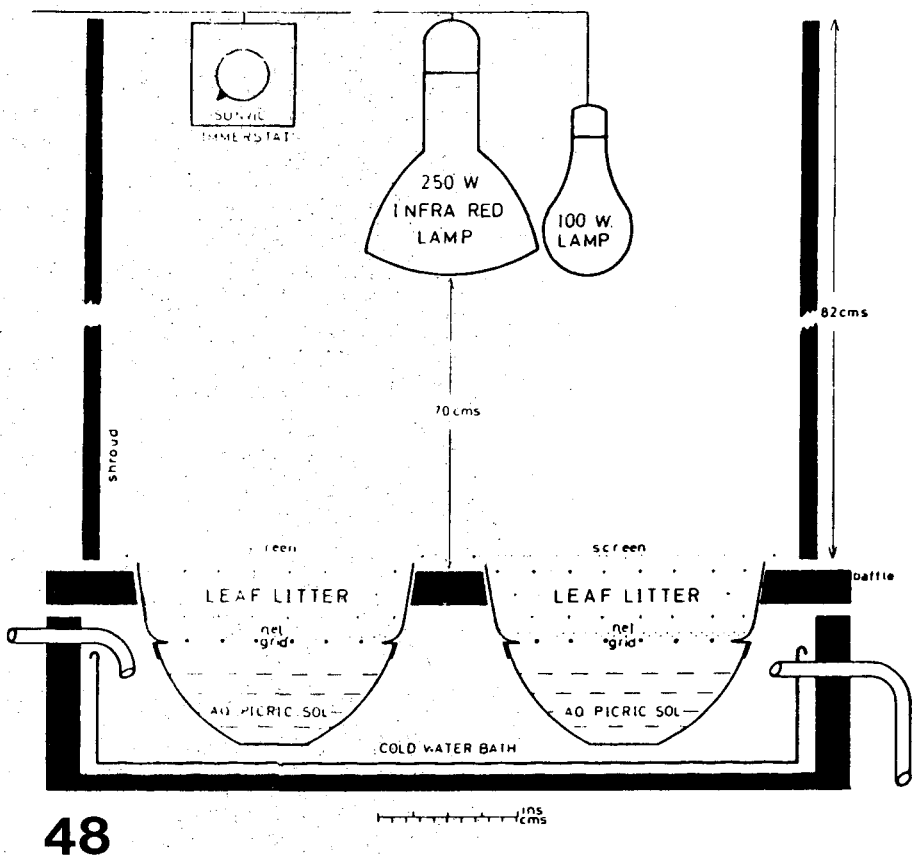


Fig. 48. Extraction apparatus for small soil and litter arthropods; after Kempson *et al.* (1963). Slightly modified versions of this type of equipment have resulted in the recovery of some of the highest recorded numbers of soil arthropods per unit volume.

monographs (other than taxonomic works, which we will not cover here) devoted, wholly or in large part, to the soil fauna appeared. Some of these were quite general, others restricted in their topics; some were large, some small; some placed an emphasis on humus formation, soil fertility etc., while others did not. They included: Paclt's (1956) book on the biology of apterygote Hexapoda, important soil animals; the Spanish and first English editions of *Bodenbiologie* (Kühnelt, 1957, 1961); a text by Nosek (1957); a "popular" book by Farb (1959); a research monograph by Haarløv (1960); Godfrey and Crocroft (1960) on the mole; *Principles of Nematology* by Thorne (1961); a book with an agricultural bias by Kipenvarlitz (1961); a general introductory text by Kevan (1962a), with an amended edition in 1968; a South American faunal series edited by Delamare Deboutteville and Rapoport (1962–68); texts by Schaller (1962, 1968) and Bachelier (1963), *The Physiology of Earthworms* by Laverack (1963); small "popular" works by Dunger (1964) and Palissa (1964); a localized account for the central Volga region by Aleïnikova (1964); a voluminous tome on soil biology generally by G. Müller (1964); and, by contrast, a little booklet for amateurs by Moreau (1965); Gilyarov's (1964, 1965) monograph for the identification of soil insect larvae and handbook for diagnosing

soil types according to their fauna; a small highschool teaching manual by Pramer (1965), and a slightly more advanced introduction to soil life generally by Jackson and Raw (1966); a large monograph by Loksa (1966); a thesis with special reference to tropical Africa by Maldague (1967); a collection of specialist papers on various aspects of soil biology edited by Burges and Raw (1967); a text by Brauns (1968); and other works by Dunger (1968) and by Lamotte and Bourlière (1969), the last being of considerably wider significance than to purely soil ecology.

Meanwhile, further colloquia, symposia, etc., were being held in many places, internationally, nationally and locally. Some of the proceedings of these meetings were published as follows: Arnol'di *et al.* (1958), Murphy (1962), Dunger (1962), Klapp and Wurmbach (1962), Doeksen and Drift (1963), Rapoport (1966), Bȳzova *et al.* (1966), Minkevičius *et al.* (1966), Graff and Satchell (1967) and Aleĭnikova (1969). It is also interesting to note the widening interest in the soil fauna that was developing among non-zoologically oriented scientists. An address by P.W. Murphy to the Seventh International Congress of Soil Science at Madison, Wisconsin, 1960, on the role of animals in soil formation, was prepared for inclusion in one of the general sessions, though the text was never published (Kevan and Murphy, 1960; Kevan, 1961); Section II of a 1965 symposium on soil-borne plant pathogens began with an invitational address on soil fauna (Kevan, 1965); and the Ninth International Congress of Soil Science in Adelaide, 1968, opened one of its principal sessions with another such paper on soil fauna and humus formation (Kevan, 1968).

In this period, too, serial publications devoted very largely to research on soil fauna appeared. The first of these was merely an annual information bulletin (newsletter) resulting from a decision made at the Sixth International Congress of Soil Science (International Society of Soil Science, 1956). It was called *Microfaune du Sol* and began under the directorship of J. d'Aguillar in April, 1957. After the seventh number (in 1963) it was replaced by the larger and more comprehensive *Biologie du Sol*, beginning April, 1964, which eventually became *Pedofauna* in 1982 (nos. 35/36) under the direction of G. Wauthy. In the mean time, in 1961, Ekkehard von Törne, in Austria, had started the scientific journal *Pedobiologia*, and C. Delamaire Deboutteville, in France, launched *Revue d'Ecologie et de la Biologie du Sol* in 1963. Both journals remained predominantly zoological for many years.

## RECENT TIMES

During the past few years, there has been no slackening off of work on the soil fauna, and it would be quite impractical to try to review this here, even sketchily. Reference to abstracting journals and to the proceedings of congresses, etc., however, will show that the field continues to expand. One or two research publications for last year, taken at random, indicate that activity varies widely from basic preliminary surveys of the myriapod fauna of northern North America (Kevan, 1983, *c, d*) to the practical significance of the presence of heavy metals in the food of larger soil invertebrates (A. Carter, 1983)[33], both by Canadian authors, or as part of general biological studies of soils derived from loose sediments (Loub and Haybach, 1983).

Books and monographs on soil-zoological subjects since 1970 include that of Gilyarov (1970), to some extent a morphological development from his earlier book (Gilyarov, 1949); a little "popular" account for home consumption by Haarløv (1970); a specialized compilation edited by Delamare Deboutteville (1970); two soil-fauna ecology books by Wallwork (1970, 1976); a small "popular" book, more relevant to litter than soil proper, by Savory (1971); an International Biological Programme handbook on qualitative ecology edited by Phillipson

(1971); a collection of contributed papers edited by Pesson (1971); *Termites and Soils* by Lee and Wood (1971); *Biology of Earthworms* by Edwards and Lofty (1972); *Economic Nematology* edited by Webster (1972); an advanced high school-level ecological text edited by Andrews (1972) on soil organisms generally; a contribution to tundra ecology edited by Tikhomirov (1973); and introductory text for soil ecology by Richards (1974); *The Biology of Free-Living Nematodes* by Nicholas (1975); the enlarged new English edition of *Soil Biology (Bodenbiologie)* by Kühnelt *et al.* (1976); a text on soil invertebrates of the Soviet Far East by Kurcheva (1977); a small, general soil ecology handbook by A.L. Brown (1978); some account of the invertebrate fauna of brown and black soils in the Georgian Republic edited by Rekk (1979); *Nematodes in Soil Ecosystems* edited by Freckman (1982) - in which some of the contributions at last begin to consider the role of these animals in soil formation, as suggested by Cobb (1915); the Marshall *et al.* (1982) assessment of the (unsatisfactory) position of soil-faunal studies in Canada, which resulted in the present meetings; and Wallworks' (1983) little manual on earthworm biology. "Hot off the press", I may mention a review on micro arthropods and soil processes by Seastedt (1984) and a book on the distribution and ecology of Collembola (Gilyarov and Chernova, 1984) which has just reached me from the U.S.S.R. Also to appear shortly is a profusely (scanning-electron-microscope) illustrated work on European soil arthropods by Eisenbeis and Wichard (1985).

For this same period we should also mention various colloquium and symposium proceedings, including the following: Aguillar *et al.* (1971), Dindal (1973), Gilyarov (1973), Vaněk (1975), Górny (1975), Lohm and Persson (1977), C.A. Edwards and Veeresh (1978), Dindall (1980), Applehoff (1981), Veeresh (1981), Warden (1981), Satchell (1983), Lebrun *et al.* (1983), Grégoire-Wibo *et al.* (1983) and ("stop press!") Gilyarov (1984). It would also be appropriate to note an increased soil zoology content in works not primarily concerned with this; for example: in the 10th edition of *Soil Conditions and Plant Growth* (Russell and Russell, 1973); in *The Role of Arthropods in Forest Ecosystems* (Webb, 1977); in *The Encyclopedia of Soil Science* (Kevan and Hill, 1979); in *Recent Advances in Entomology in India* (Prabhoo, 1981); in *Soils, an Australian Viewpoint* (Greenslade and Greenslade, 1983); in *Laterization Processes* (Machado, 1983a, b); and in *Acarology VI* (Griffiths and Bowman, 1984).

## CONCLUSION

In the foregoing I have included scarcely a reference to taxonomic literature, catalogues or nomenclators, which may surprise those who know me primarily as a taxonomist. This is partly because the subject is a vast one without definable boundaries, and partly because I hope that currently usable taxonomic related literature (from which one can often deduce the historical background) will be covered elsewhere at these meetings.

I would, however, stress that of all aspects of soil zoology, it is taxonomy that still needs the greatest *immediate* expenditure of effort which means *adequate financial support and increasing numbers of continuing positions for qualified research workers in taxonomy.* A dozen years ago I spoke of taxonomy as being the Cinderella of the sciences (Kevan, 1973) and I will not repeat what I said then. Since that time, however, the situation, at least in North America, has, if anything, deteriorated, and the attitude or understanding (or both) of non-taxonomists to the need for taxonomy has scarcely improved (see Note 33).

This does not mean that there has been no progress in the ability we now have to identify accurately the various members of the soil fauna. Indeed, there have been, particularly in

Europe (especially in the eastern countries), considerable advances, but even so, identification is often difficult there, too, especially in the case of some groups. In most of the world, including North America, any conscientious soil ecologist inevitably becomes bogged down by taxonomic problems. If he does not identify his animals properly, his research becomes greatly reduced in value, sometimes to the point of being worthless. On the other hand, without the means of identification (except in a few groups like Northern Hemisphere Collembola), what is he to do? The answer is, of course, "first things first; become a taxonomist!". Some have indeed followed this course, but the task-masters of most do not encourage it!

Soil zoology has come a long way from the days (mostly less than a century ago) when only a few, relatively conspicuous forms (I will not say "species" as identification was seldom so precise) were recognized, or even since the time of Gilbert White or Charles Darwin, when only an inkling of the importance of animals in the humification process was evident. We have reached all manner of degrees of sophistication in chemical, physical, statistical and electronic techniques, but we still know very little about the soil fauna itself. And our ignorance will persist until we can recognize one species of soil animal, in all its stages, from another, and learn about the biology of each one that is important, and in what way it is so. This, in itself, may not be immediately evident. Sometimes we may learn some answers, but mostly we do not! It does no good, for example, to lump all the mites or Collembola together, as is often done, for every species is different and each plays a different role. House sparrows are not usually lumped together with hawks, or even with other finches, nor is "humic" acid the same as formic and/or acetic! Yet this is the way in which "data" on the soil fauna have often been presented by otherwise competent "scientists"!

Even in recent times, with a few notable exceptions, there has been, to mutual disadvantage, a general scantiness of appreciation of the fauna on the part of "soil scientists" (how many of them have ever taken an appropriate course relating to soil zoology, though a few may have a smattering of microbiology?) and a reluctance to intrude into the realms of so-called "soil science" by zoologists (though a few agricultural and forest entomologists may have been exposed to an elementary course in "soil science" – without faunal content, of course!). There is still an almost complete lack of concern or comprehension, especially, it would seem, among those who determine (financially or otherwise) the directions of research, that we are still without the means of proper identification of innumerable members of the soil fauna. Furthermore there seems to be no realization that the understanding of basic soil ecology and thus of the pedological importance of the fauna is impossible without arduous, long-term taxonomic research and application, and that even "simple" identifications are very time-consuming. The competence *could* be created, but, even where some exists, it is seldom encouraged. Nay, it is discouraged! To admit to being involved in taxonomy seems to call for an apology - if not an admission of failure to accomplish anything worth while! The pundits would have others try to run before they have learnt to crawl, let alone to walk!

How far, then, have we really come since the Sumerians, or Aristotēles, or Albertus Magnus, or Darwin, or even Konrad Diem? A little way, perhaps, though, in some respects, not very far. We certainly know more species, but what do they do? As a result of these meetings, but not overnight, perhaps we shall take one more faltering step forward! Who knows what we might take two?

Our motto: "*Es wimmelt im Boden von Unbekanntem!*" (Gisin, 1947).

## NOTES

1 The Akkadian for "ant" was given as *zirbabu*; the pale species (? termite) as *zirbabu šadi*; and the flying ant as *mutapriš*u. (Note, the Akkadians, unlike the Sumerians, did not seem to associate taxonomically the wingless with the winged ants; nor did they use a binominal system of nomenclature or seem to make much distinction between species; and their successors, in turn, were no more enlightened.) The Akkadian for (annelid) worm was *iš*qippu or *iš*qapu; for "mole cricket" (?) it was *ḫallalū*a, *ḫallalī*a or *ḫallullā*a; for "field cricket" it was *ṣaṣiru qiš*te or *ṣarṣari*; and for "dust locust" it was *erib turbuti*. One might also add a legless reptile to the soil-dwelling fauna known to the Sumerians. This was called *Muš* (generic for "serpent") *iginugal* or *Muš* iginutug; the Akkadians called it *puuḫmaḫu* or *upputum*. Scorpions (*gīr*; Akkadian *zuqaqipu*) were, of course, also well known, as might be expected, and several different kinds were distinguished.

2 Sandars' (1959) translation is entomologically a little confused, using "nymph" for "imago" and "larva" for "exuviae", but it is quite comprehensible. The Akkadian word for dragonfly from which her version is translated is *kulīl*u(m) and, for the nymph, *kirippu* (see also R.C. Thompson, 1928, who refers to both as kinds of birds!). For various Sumerian and Akkadian names for dragonflies, see Landsberger & Krumbiegel (1934). Gilgāmesh, regrettably, does not refer to the soil fauna, unless one includes scorpions as such; a passage of some length relates to the "Scorpion-men". There is, however, a mention of honey and one of flies. Otherwise, invertebrates include only the prize, finally lost, of the "flower" of immortality at the bottom of the sea. This seems to have been based on a sea-urchin, rather than a sea-anemone, for the alleged aphrodisiac properties of the former have been claimed throughout the ages.

3 The *Ṛgveda* (see Griffith, 1887) of *ca.* 1300 B.C.E. also makes reference to various kinds of "worms", for example in Book I, Hymn 191, and in Book II, Hymn 50, but these are to "poisonous" and parasitic species. The latter hymn is particularly interesting because it almost undoubtedly refers to two very important parasites of man, *Dracunculus medinensis* and *Wuchereria bancrofti*, neither of which, however, are soil-borne! The *Atharvaveda* (see Griffith, 1894), of a rather later date, ? *ca.* 1000 B.C.E., has more numerous references to "worms". A few involve plant injury, but most are concerned with flesh-consuming dipterous maggots in carrion or wounds, or with helminthic endoparasites (e.g., Book II, Hymns 31 and 32; III, 28; V, 23; VIII, 6; IX, 4; XI, 9). There is, however, in Book XII, Hymn 1, a single reference that just *might* refer to earthworms:

"The worm, O Prithivî, each thing that in the Rain revives and stirs ..."

4 *The New English Bible* translation of 1970, in Deuteronomy [II Moses] XXVIII, 42, however, uses "mole cricket" for the Hebrew *ẕelaẓal*, but this may be a mistranslation of an onomatopoeic word for a "whirring" (flying) locust of one kind or another (see Kevan, 1978: 197, 385, 467). Prof. I. Harpaz (*in litt.* 1985), however, suggests a true cricket, such as *Gryllus bimaculatus*.

5 Although of later date, it might also be appropriate here to mention the Jewish Talmud, which, like the Hebrew Scriptures, refers quite frequently to insects (Bodenheimer, 1928, 1929, 1960). Again there is virtually no unequivocal allusion to the soil fauna other than to ants, though Bodenheimer (1928) and Harpaz (1973) draw attention to the suggested biological control of these by transporting soil between (widely separated) nests in order to bring about mutual extermination by the inhabitants of each.

6 Hērōdotos (see Rawlinson, 1910) did not refer directly to the amphisbaena, but, briefly only, to gaint Libyan serpents which were possibly part of the same tradition (though they may have been pythons from the south; the *draco* was the largest of all serpents and was a constrictor). The Arabian Flying serpents, about which he has much more to say, and which had featherless wings, ere clearly not soil-inhabiting amphisbaenas though, by Mediaeval times, the two seem to have become amalgamated (Fig. 7, 8 lower). Not only did the amphisbaena have two heads, but, by then, it seized one with the other and rolled along like a hoop! At the same time, it could also be Arabian and winged like the flying serpents of Hērōdotos, and bipedal besides (*cf.* Druce, 1910; T.H. White, 1954; McCulloch, 1962; Rowland, 1973). It had illuminated eyes (in contrast to Nīkandros' description) and, in later Mediaeval times, some believed that its glance, like that of the bipedal Basilisk (discussed, for example, by the authors just mentioned), killed the beholder. An interesting feature of Hērōdotos' flying serpents was that, at the precise time of fertilization, the female seized the male by the neck and would not let go until this had been bitten through. Surely the "flying serpents" were based on (elongate) praying mantids, though I do not recall having seen this theory advanced elsewhere. Furthermore, Hērōdotos' concept, that the male gets his own back because the offspring devour the "womb" of the female, could be reconciled with the hatching of young mantids from the oötheca, regarded as a detached female abdomen!. Thus the "classical" amphisbaena was originally based on a small, burrowing, legless reptile, but the late Mediaeval version may owe its "existence" in large measure to aerial mantids! The amphisbaena reverted to its true small form (only *seeming* to have a head at each end) in the 16th Century, though, even by the end of that century, Aldrovandi accepted the two-headed concept - see Druce (1910), who cites various classical and later authors in respect of it. There is a short precis of parts of Druce's paper in T.M. White (1954). Further

ancient beliefs that may be tied in with the mantis theory are discussed by Kevan (1985).

7 Although Latin versions of the *Physiologus* included less entries than the originals (the early 11th-Century metrical version of Bishop Theobaldus - see Rendell, 1928 - had but twelve, though the ant remained - Fig. 11), fabulous beasts multiplied in the later 12th- and 13th- Century "Bestiaries," as did their mythical qualities and their importance in symbolism, both religious and moral.

8 Later (705 A.D.) he became bishop of Sherborne. Aldhelm eventually went on to greater (posthumous) achievements, as he later became a saint of the Roman Church, a position attained by remarkably few (former) inhabitants of Great Britain!

9 Aldhelm also included riddles on the so-called "*Bombix*" or "silkworm" (perhaps not actually *Bombyx* itself, but some other cocoon-spinning caterpillar); *Apis* the honey-bee; *Locusta*, the locust; "*Scnifes*," the gadfly (*Tabanus*); "*Tippula*", the water-strider (*Gerris*), called "water-spider" by Pitman (1925); and "*Crabro*", the hornet (*Vespa crabro*). In addition, his riddle on "writing-tablets" mentions "honey-laden bees"; and he has another, rather unlikely invertebrate on his list, the "*Sanguisuga*" or medicinal leech (*Hirudo*). His riddle No. 18, "Myrmicoleon", with Pitman's (1925) English version, reads as follows:

*Dudum compositis ego nomen gesto figuris:*
*Ut leo, sic formica vocor sermone Pelasgo*
*Tropica nominibus signanspraesagia duplis,*
*Cum rostris avium nequeam resistere rostro.*
*Scrutetur sapiens, gemino cur nomine fungar!*

*I long have borne a name of hybrid form:*
*Both ant and lion I am called in Greek –*
*A double metaphor, foreboding doom:*
*My beak can not ward off the beaks of birds.*
*Let wise men search out why my names are twain.*

10 In 10th-Century Byzantine illuminated manuscripts, presumably copies from much older documents, there are representations of 8-legged, chelicerate (?) arthropods called "*myrmēkion*" (see Kádár, 1978). These have been interpreted as ants (though they look more like tail-less arachnids -? pseudoscorpions much enlarged); perhaps they are supposed to be ant-lion larvae.

11 Sometimes called "Arabic" or "Islamic," but both these terms impose unwarranted restrictions of race, language and/or religion.

12 Born *ca* 1098, she became abbess of Disibodenberg (now Disenberg), in the diocese of Speyer, in 1136; she founded a new convent at Bingen in the Rupertsberg region, 1147, and died there 1179. She was famed for her visions, and prophecies and regarded as a saint, but she was never formally canonized by the Roman Church.

13 The "Bestiaries" became especially popular in England (and thereby the English part of France). The trend begun in the latter part of the 12th Century continued. Not only did fantasy increase, but so did the numbers of species mentioned, up to more than 100 (James, 1928; T.M. White, 1954, McCulloch, 1962). Among "soil" animals (other than this cricket) we begin to get further references (*cf.* Davis, 1958) to millipedes or woodlice (Fig. 13), as well as to earthworms, beetles, etc., only some of which had appeared earlier, not in the Latin versions of the *Physiologus*, but in Byzantine Greek copies of Nikandros and Diaskoridēs (Kádár, 1978). These additions, by further transcription, became carried forward into later centuries.

14 Neither referred to the amphisbaena. The works began to appear in various translations and, more than a century later, in printed editions. That of Bartholomew, being the most concise, was the most popular; it was printed in over 40 separate editions from 1470 onwards. The *Liber de Naturis Rerum* was often reproduced anonymously and usually attributed to Albertus Magnus. An early Flemish translation, written (between 1265 and 1269) in metrical rhyming couplets, was that by Jakob van Maerlant; it was called *Der Naturen Bloeme* (Bodenheimer, 1928). More notable, perhaps, was the German version by Cunrat (or Conrad) von Megenberg, called *Das Püch [= Buch] der Natur*, translated in the middle of the 14th Century. This eventually, became the first printed book devoted exclusively to natural history, complete with woodblock plates (Megenberg, 1475, Bodenheimer, 1928; Morge, 1973). One of these plates included illustrations of ants and earthworms underground.

15 The *Treatyse of Fysshynge* was added to the second printed edition of her(?)*Boke of Saint Albans*, published by Wynkyn de Worde, who changed the spelling of the lady's name. The first known printed edition of the *Boke* was that of

1486, printed at St. Albans by an unknown "Schoolmaster"; it did not include this *Treatyse*. The discrepancy between textual [1485(*sic*)] and bibliographic [1496] dates given by J.E. Satchell (*in* Dindal, 1980: 848) may thus be explained. [So far as I am aware, it is pure coincidence that two Satchells are involved here; the earthworm expert does not mention his namesake, whose publisher was another Satchell.]

16 Such religious and moral works on animals later included those like *Dierum Caniculorum* by Simon Majolus, 1600 ([earth]worms, ants, "ant-lions," scarabaeoid beetles and cicadas mentioned), *Animalium Historia Sacra* by Wolfgang Franz, 1612 (a similar range of soil inhabitants, though omitting "ant-lions" and including crickets), and later, more famous *Hierozoikon* by Samuel Bochart(us), 1663 (also including references to a similar range of fauna) - see Bodenheimer (1928, 1929).

17 Georg Bauer (1494–1555) was from Saxony and was appointed physician to the German mining town of Joachimsthal in 1527. Thereafter he wrote many books on mining, metallurgy and chemistry. His interest in the subterranean fauna clearly stemmed from his interest in mines and diggings, not *vice versa*.

18 Here might also be an appropriate place to mention what appears to be a recently perpetrated fallacy regarding the 16th Century. In discussing the gall-forming nematode, *Anguina tritici*, which passes part of its life-history in the soil, and which causes what is known as ear-cockle of wheat, etc., Thorne (1961), as did others before him, suggested that the parasite was referred to by William Shakespeare, in *Love's Labours Lost* (Act I, Scene 4), when he wrote (about 1594, first performed *ca.* 1595, printed 1598), "Sowed cockle, reap'd no corn." It was not suggested that the causitive organism was known (it was not discovered until 1743), but that infected seeds would not germinate. The *Oxford English Dictionary*, however, gives no earlier than 1836 as the first use of the word "cockle" in this context. The "Corn cockle" is in fact a caryophyllaceous weed, *Lychnis galigo*, though the name has also been misapplied to rye-grass (*Lolium*).

19 Also, although hated by farmers, careful attention was paid to mole crickets and their behaviour, for barley was seldom planted in spring before their chirping was heard. It was also noted that hoopoes (*Upupa epops*) eat mole crickets. This may possibly stem from the old Greek play *Ornithes (The Birds)* by Aristophānes, in which hoopoes are said to dominate over locusts or grasshoppers (see Kevan, 1978: 267–268), for these birds could scarcely be considered to be abundant in Central Europe. It is more likely, however, that the Lapwing plover or Peewit (*Vanellus cristatus*) was meant (*cf.* Yapp, 1984). It is further noted that the head of a mole cricket worn around the neck cures fever - again probably derived from an ancient source, for the wearing of a dead orthopteriod round the neck for this purpose is mentioned in a medical "jingle" by Joseph Ursinus, 1541, as quoted by Bodenheimer (1928: 218), as well as by myself elsewhere.

20 Browne (1646) also partially exploded the fable of the (soil associated) ant and the "grasshopper" by pointing out, firstly, that a cicada, not a grasshopper, was involved (the complexities of this are discussed by Kevan, 1978), and secondly, that the former insect lives for so short a time in summer that it need not "have recourse unto the providence of the Pismire [ant] in Winter." He was confused, however, as to what was a cicada, for these are virtually unknown in his native England, and he regarded the inhabitants of "cuckoo-spit" as such. As both are Homoptera, this was not unreasonable, though he said that from "cuckoo-spit ... some kind of Locust [sic] doth proceed." Had he paid a little more attention to Aristotēles' account of the life-history of cicadas, he should have known that they emerged from the soil. Later, Erasmus Darwin took Browne to task, but that is another story!

21 The only two-headed serpent indicated was the "*Serpens Biceps*", in which both heads were at the same end of the animal, and which was apparently treated as a mere freak, as it had been previously regarded.

22 See also Oudemans (1926), who gives a Dutch title and a date of 1664; the mites he identifies as "*Hypopus*" [now *Anoetus*] *feroniarum*; the nematodes ("*slangetjes*") he says were *Diplogaster* [now *Pristionchus*] *longicauda*; both identifications were presumptuous, though credible.

23 The second edition, of 1740, substituted *Fullo* for *Melolontha* and added to the species in "*Scarabaeus*"; the genus *Cicada* was added to the Hemiptera, from which *Scorpio* was removed to the Aptera; to the last was added the collembolan *Podura* (from Geer, 1740), and the terrestrial isopods in "*Oniscus*" became "*Millipes*". The 3rd edition, also of 1740, differed little in content from the 1st. The 4th edition, of 1744, resembled the 2nd, but additional groups were added, including Diptera and Hymenoptera, to the latter of which the ants were transferred. Subsequent editions (5th of 1747, 6th and 7th of 1748, 8th of 1753, from which botanical nomenclature dates, and 9th of 1756) gradually increased in scope, but added nothing significant for our purpose.

24 The rest of this volume was to have dealt with Coleoptera. Volume 8 was to have been on orthopteroids, etc., and volumes 9 and 10 on arachnids, myriapods and annelids (*cf.* Wheeler *in* Réaumur, 1926).

25 At the time, the condition was known as "malm"; the name "ear-cockle," according to the Oxford English Dictionary, did not appear (in print) until 1836.

26 Gilbert White's brother John included in the 1802 (posthumous) edition of "*Selborne*," various previously unpublished Ms. notes by Gilbert (together with remarks by William Markwick). These included further comments on earthworms as well as on ants, bugs, etc. Bingley (1803) plagiarized, almost verbatim, both original and supplement, though in dealing with mole crickets he cited White as his authority.

27 This was not done for more than a decade, when Schmidt (1871) published his studies on the pest.

28 Sir John William Lubbock, Baronet (later Lord Avebury), who lived at Down in Kent, near Charles Darwin, was a leading figure of the day, not only as a zoologist, Vice-President of the Royal Society and of the British Association, and Vice-Chancellor (administrative head) of the University of London, but also as a prominent banker and Member of Parliament. An even greater service than by his zoological writings that he rendered to mankind was to introduce the bill which established August Bank Holiday (known also to a select few as St. Lubbock's day!). His legacy lives on, even in parts of Canada, though his name scarcely does so! As he was so busy, it is often suggested that most of his writing was done for him by one or more "ghost" writers. This monograph, however, seems to have been entirely his own work (and he has signed himself "From the Author" in a copy I possess). The excellent plates are acknowledged as being the work of a Mr. Hollick, a deaf mute, and thus unique for the times.

29 Berlese's most active period in this field was from 1897–1900. From 1904–1921 he continued to publish on all groups of mites in *Redia*, 2–18.

30 I realize that this expression will not be familiar to all. *Two Solitudes* is the title of a well-known novel by McGill University author (John) Hugh MacLennan. The book, published 1945, deals with the isolation of the "French" and "English" cultures of Québec, and of Montréal in particular.

31 Alfred E. Cameron, a Scot, came to the Canadian Department of Agriculture from England about 1916 (he was not acceptable for the armed forces on account of his club foot). Later he became Professor of Zoology at the University of Saskatchewan. Later still he was Reader in Agricultural Zoology at the University of Edinburgh, and it was there, about 25 years after his paper was written, that, as an undergraduate, I first read it and another in the same vein (Cameron 1917a) - my first taste of soil zoology. I did *not* immediately engage in this field, but I take this opportunity to express my appreciation of what I owe to my late mentor.

32 It comes as a surprise to some to find that International Colloquia on Soil Zoology are now numbered as if they began with the one held three years later at Rothamsted in 1958 (International Congress of Zoology, 1959; Murphy, 1962). Thus the last one to be held in Louvain la-Neuve in 1982 (Lebrun *et al.*, 1983) was numbered "VIII", not "IX"! This is because the Biology commission of the International Society of Soil Science seemed to consider that they had a prerogative stemming from a decision made at their 1956 congress (Int. Soc. Soil Sci., 1956) at which, for the first time, the Society had paid more than scant attention to the matter. The numbering therefore applies only to colloquia sponsored by the Society. The intervening *International Colloquia* were as follows: II, Oosterbeek, Netherlands, 1962 (Doeksen and Drift, 1963); III, Braunschweig, West Germany, 1966 (Graff and Satchell, 1967); IV, Dijon, France, 1970 (Aguillar *et al.*, 1971); V, Praha, Czechoslovakia, 1973 (Vaněk, 1975); VI, Uppsala, Sweden, 1976 (Lohm and Persson, 1977); and VII, Syracuse, New York, U.S.A., 1979 (Dindal, 1980). Colloquim "IX" will be in Moskva, U.S.S.R., 1985. It may also be noted that the 1955 colloquium itself was likewise misnumbered, for it was called "The University of Nottingham *Second* Easter School in Agricultural Science," whereas it was really the *first* of its series. There had, indeed, been a not very widely publicised series of pedology seminars conducted in 1953 by guest-lecturer W.L. Kubiëna, but this was quite a small affair without published "proceedings". It may now be disclosed that it was dubbed the first "Easter School" only in retrospect, the better to promote the "second"!

33 Including some of the same myriapods (millipedes), which, like most of the other animals referred to are unidentified. This is typical of much work by "soil scientists" who emphasize "precision and accuracy of chemical analysis", but who do not even comment on the lack of this in the animal species investigated by them!

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