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The Finnish Lumbricidae (Oligochaeta) fauna and its formation

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Faunistical recording during the past c. 100 years shows that the Finnish Lumbricidae fauna comprises sixteen species, viz., *Allolobophora chlorotica, Aporrectodea caliginosa, A. longa, A. rosea, Dendrobaena octaedra, Dendrodrilus rubidus, Eisenia andrei, E. fetida, E. hortensis, Eiseniella tetraedra, Lumbricus castaneus, L. festivus, L. rubellus, L. terrestris, Octolasion cyaneum* and *O. tyrtaeum.*

Faunal formation among the Lumbricidae in Finland was traced through indirect evidence based on the up-to-date ranges, present ecology, modes of dispersal and reproduction of the species. The Finnish ranges are in general continuous with those of the species in the adjacent countries, implying affinities with distributional history. Habitat spectra of marginal species populations were worked out to assess the ecological requirements for the pathways of northward dispersal of the species in Finland. Post-glacial phases of geomorphology, climate, vegetation and human impact on the environment are discussed in relation to dispersal and habitat occupation of the species.

The most widely distributed Lumbricidae in Fennoscandia are the eurytopic *D. octaedra* and *D. rubidus* and stenotopic *E. tetraedra* that live among litter or close to the soil surface where they are exposed to forces (e.g. floodings, wind, visits by ungulates and birds) that can facilitate passive dispersal. Man-made habitats play no major role in their habitat spectra and records from localities without any considerable human impact indicate a good ability for passive dispersal without man's agency. Anthropochory may be of secondary importance in their post-glacial dispersal northwards. They reproduce parthenogenetically, i.e. one worm or viable cocoon may be sufficient to establish a population. These species may represent an old faunal element in the study area.

The majority of Lumbricid species in Finland are deep-burrowers. In the northern parts of their range at least they are closely associated with man-made habitats. Many of them occur in Finland only in areas which were long submerged post-glacially. Long-distance dispersal jumps due to anthropochory from one man-made habitat to another, biparental reproduction (with some exceptions) and life cycles taking place in deeper soil layers are characteristic for them. Many of them are nowadays expanding their range. Since agriculture, trade connections and so on constituting human activities which may facilitate their dispersal have been maintained in Finland only for some thousands of years, deep-burrowing species such as *A. longa, Eisenia* species, *L. festivus* and *O. cyaneum* confined to man-made biotopes in S Finland may represent a young faunal element.

Lumbricids seem to have dissimilar distributional histories in Finland where the faunal formation is still in progress, particularly due to increasing human activities (e.g. trade, intensive land use, agricultural, horticultural and forestry practices, soil transportation) that facilitate earthworm dispersal and create new habitats for them.

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1. Introduction

The Finnish Lumbricid fauna is low in species and it can be taken as a marginal element for the more diverse earthworm fauna of Central and Southern Europe. Endemic species are lacking here and the species present are post-glacial immigrants that have invaded there, either spontaneously or in association with human activities. Fossil and subfossil lumbricids are unknown in Finland, but we may obtain some clues to the processes involved in faunal formation from data on the recent populations of species.

Since the pioneering observations on the Lumbricidae of Finland by Spoof (1889) many additional faunistic surveys have been undertaken. Karppinen & Nurminen (1964) summarized faunistical and ecological information up to the beginning of the 1960s and outlined the Finnish ranges for the species. Since those days additional faunistic, ecological and genetical data have accumulated and the status of many species and subspecies has been amended, thus calling for corresponding changes to the distributional maps and the nomenclature of the species in Finland as well. All these, together with information on post-glacial changes in climate, vegetation, geomorphology and the arrival and activities of man are considered in tracing indirectly the post-glacial formation of the Lumbricidae fauna in the study area.

2. Material and methods

2.1. Study materials

Faunistic records referring to the Lumbricidae in Finland are taken from the literature and additional information is supplied by the inspection of about 1 000 samples of earthworms preserved in the zoological collections of the Universities of Helsinki, Turku and Oulu. Unpublished observations and samples by the author are also considered. All the records and sample sites have been located to the squares of the UTM grid system in order to produce up-to-date distributional maps for the species.

Data on qualitative and quantitative aspects of the populations of lumbricid species in different parts of Finland is mostly based on the papers by Siivonen (1946), Karppinen & Nurminen (1964), Terhivuo & Valovirta (1974a, 1978), Hæggström & Terhivuo (1979), Terhivuo (1984, 1989), Hæggström (1985, 1986) and Bouché et al. (1988). Data on the ranges and ecology of lumbricids in the areas adjoining Finland has mostly been compiled from Julin (1949), Stöp-Bowitz (1969), Ljungström (1964), Nordström & Rundgren (1973, 1974), Perel (1964, 1979), Timm (1970, 1987), Malevič (1976) and Terhivuo (1982 and unpubl.)

2.2. Nomenclature adopted

Many aspects concerning the classification and nomenclature of the Lumbricidae are debated today and many species seem to be rather complexes of species or polyploid strains than taxonomically clear-cut units. Problems often arise from the fact that some species reproduce only biparentally, some are parthenogenetic polyploids, while in some species both biparentally and parthenogenetic strains are encountered in different parts of their range. These discrepancies also apply to some of the Lumbricidae species found in Finland.

In the present paper I have followed the recommendations by Sims (1983) and Sims & Gerard (1985), so that the nomenclature is according to these workers. Some contradictionary viewpoints indicated in other taxonomical reviews are briefly mentioned. As the nomenclature adopted in earlier faunistical surveys of the Lumbricidae in Finland is highly variable, the following review may be warranted. I introduce the genera and species in alphabetical order without any implication as to their possible evolutionary relationships.

The number of species in the genus *Allolobophora* is now reduced so that only the type-species *A. chlorotica* (Sav.) is recorded in Finland. For additional information on the synonyms for the species see e.g. Gates (1980).

In the genus *Aporrectodea* the three species reported from Finland are *A. caliginosa* (Sav.), *A. rosea* (Sav.) and *A. longa* (Ude). The *A. caliginosa* complex, or the *Allolobophora trapezoides* complex as considered by Gates (1972) is an enigma. According to Zicsi (1982) and Sims & Gerard (1985) the four major morphological forms, namely *caliginosa* (syn. *turgida*), *trapezoides*, *tuberculata* and *nocturna* are phenotypic forms of *Aporrectodea caliginosa*. Gates (1972) holds that the *trapezoides* complex consists of three separate species, namely *tuberculata*, *turgida* and *trapezoides*, which should be taken as members of the genus *Allolobophora*. Bouché (1972) attributes *A. caliginosa* (with two subspecies, viz., *alternisetosa* probably equalling *tuberculata* and *meridionalis* corresponding to *trapezoides*) and *A. longa* to the genus *Nicodrilus* , but, *A. rosea* to the genus *Allolobophora*. Perel (1976, 1979) lumps *A. caliginosa*, *A. rosea* and *A. longa* into the genus *Nicodrilus*.

Only one species of the genus *Dendrodrilus* occurs in Finland, namely *D. rubidus* (Sav.). Of the four main morphological forms, *rubidus*, *subrubicundus*, *norvegicus* and *tenuis*, the first three mentioned were often considered as distinct species in the genus *Dendrobaena*, and *tenuis* was known as *Bimastus tenuis* or *Dendrobaena tenuis*. Zicsi (1982) and Easton (1983) give them as subspecies of *Dendrodrilus rubidus*, but, e.g. Gates (1979), Perel (1979) and Sims & Gerard (1985) recognize them only as morphs or forms of one species, namely *D. rubidus*. The ranges of *rubidus*, *tenuis* and *subrubicundus* widely overlap in Finland (Terhivuo & Valovirta 1974a) and elsewhere (Sims & Gerard 1985). No clear-cut ecological differences have been pointed out between them, and some of the populations reproduce biparentally, others parthenogenetically (Muldal 1952, Omodeo 1952), indicating that they may not be distinct taxonomical units. The status of the form *norvegicus* is also obscure; it is probably a member of the *Dendrodrilus rubidus* complex (Sims & Gerard 1985), whereas e.g. Julin (1949) and Stöp-Bowitz (1969) consider it a distinct species.

The genus *Dendrobaena* comprises one species that is found in Finland, viz., *D. octaedra* (Sav.) that is also the type species of the genus. For synonyms for it see e.g. Stöp-Bowitz (1969).

The genus *Eisenia* now involves three Finnish species, namely *E. fetida* (Sav.) and *E. andrei* (Bouché) which were earlier considered as two colour morphs or subspecies of *E. fetida*, and *E. hortensis* (Mich.) which was known, among other alternatives, as *Dendrobaena veneta* ssp. *hortensis* and as *Dendrobaena hortensis* (see Easton 1983). According to electrophoretical surveys and breeding experiments by Jaenike (1982), Robotti (1982) and Øien & Stenersen (1984) *E. fetida* and *E. andrei* are two distinct species. On the other hand, no ecological, distributional or morphological differences (besides the colouration of the posterior end) between the two species have been reported.

The genus *Eiseniella* involves only one Finnish species, namely *E. tetraedra* (Sav.). For the forms described on the basis of the male pore translocations see e.g. Terhivuo & Valovirta (1977).

The genus *Lumbricus* involves four species recorded in Finland; *L. castaneus* (Sav.), *L. festivus* (Sav.), *L. rubellus* Hoffm. and *L. terrestris* L. For the synonyms of these species see e.g. Stöp-Bowitz (1969) and Easton (1983).

The genus *Octolasium* is now corrected to *Octolasion* as suggested by e.g. Stöp-Bowitz (1969). Easton (1983) lists *O. lacteum* and *O. tyrtaeum* as two distinct species, but according to Sims & Gerard (1985) *O. lacteum* is a subspecies of *O. tyrtaeum*. The Finnish *Octolasion* species are *O. tyrtaeum* (Sav.) and *O. cyaneum* (Sav.).

The data on which earthworms are classified mainly originates from morphological studies undertaken during the past few centuries. New tecniques in chromosome staining, as well as enzyme electrophoresis, have been applied to the Lumbricidae rather recently. For instance, the pioneering papers by e.g. Muldal (1952), Omodeo (1952, 1955) and Jeanike (1982) have, however, had a profound impact upon recent earthworm taxonomy and classification. For the chromosomal status of the earthworm species studied up to the beginning of the 1980s see e.g. Casellato (1987).

3. Results and discussion

The Lumbricidae species recorded in Finland are allochthonous since the last Quaternary glaciation exterminated all those present in an earlier era. Due to the lack of fossil and subfossil earthworms, the faunal formation can be traced only through indirect evidence. I have used the following data sets in discussing the distributional history of the species; the up-to-date ranges and habitats for the species in Finland and the neighbouring areas, the modes of reproduction, dispersal strategies, ecological versatility of species, post-glacial geomorphological phases in the study area, post-glacial changes in the climate and vegetation there, and the influence of human activities on the dispersal of the species and the environment.

3.1. Ranges, habitats and reproduction of the Lumbricidae

The up-to-date ranges for the sixteen Finnish Lumbricidae species in eastern Fennoscandia and nearby areas are indicated in Figs. 1–14.

Allolobophora chlorotica (Fig. 1) has a southwestern range in Finland. In the USSR it is not recorded north of lat. 60°N (Malevič 1976, Perel 1964, 1979). Fig. 1 may show distributional affinities between the Finnish populations of the species and those in Sweden and/or Estonia.

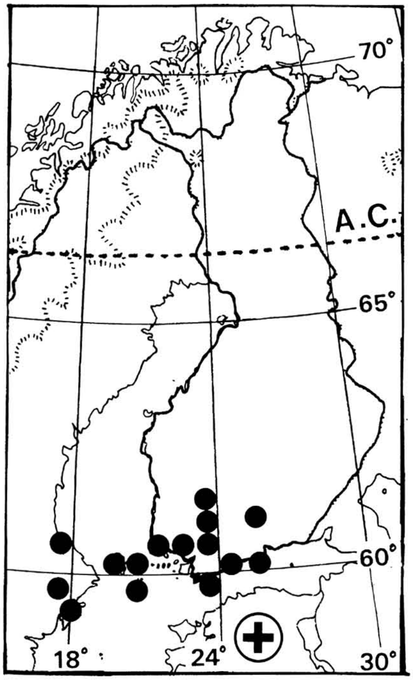

Fig. 1. Range of *Allolobophora chlorotica* in Finland and the nearby areas. The Finnish records are derived from the faunistic literature and from the samples in the zoological museums of the Universities of Helsinki, Turku and Oulu. Records referring to Sweden are redrawn from Julin (1946) and Ljungström (1964) and those for Norway are taken from Stöp-Bowitz (1969). The presence (+) or absence (–) of the species in the areas adjacent to Finland is according to Timm (1970, 1987) and Malevič (1976). Additional data on the occurrence of the species in the USSR (Perel 1964, 1979, Malevič 1976) are indicated in the text. A.C.= Arctic Circle.

A. chlorotica is a rare stenotopic species in Finland and it seems to disperse most efficiently anthropochorously. It occupies mull and clayey soils in luxuriant deciduous forests, meadows, pastures and road-banks. It is recorded in greenhouses and gardens and occasionally even in limnic habitats (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974a, 1978, Hæggström & Terhivuo 1979, Terhivuo 1989). It is a diploid that reproduces only biparentally (Muldal 1952, Omodeo 1952, Vedovini 1973).

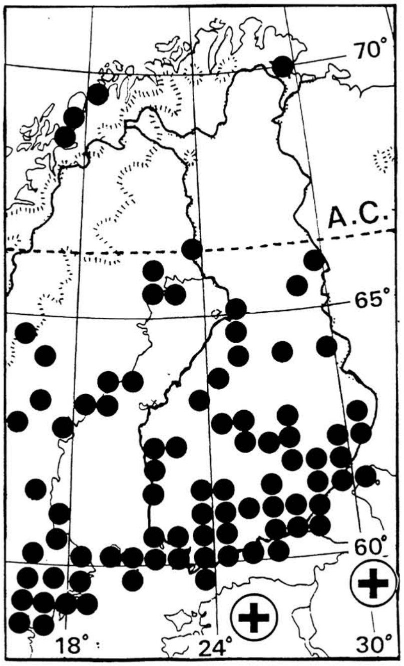

Fig. 2. Range of *Aporrectodea caliginosa* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

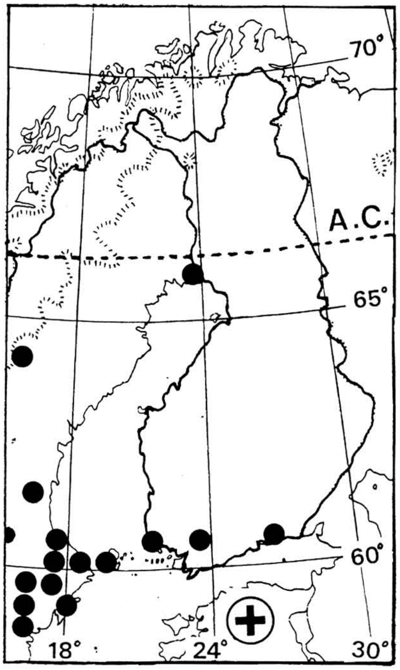

Fig. 3. Range of *Aporrectodea longa* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

Aporrectodea caliginosa (Fig. 2). In the present context the *caliginosa* complex is considered as a whole. Both in Sweden (Julin 1949) and Finland its range extends up to about the Arctic Circle and in Norway the northernmost records refer to the Arctic Ocean coast. The latter populations maintain themselves but they evidently originate there due to human agency (Stöp-Bowitz 1969, Terhivuo 1982). Perel (1979) indicates *A. caliginosa* from the Archangel district (about lat. 63°N) and Malevič (1976) report it from near the city of Onega (about 64°N/38°E).

In southern Finland this eurytopic species is most constant and abundant in deciduous forests and meadows but it also abounds in fields, back-yards, gardens, greenhouses, etc., all of which are sites having a more or less strong association with human settlements and with the influence of mankind on fertile soils. It is sometimes present in shore alder thickets and it is occasionally found in open shore plains and coniferous forests, where edaphic and climatic conditions may be adverse (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1978, Hæggström & Terhivuo 1979, Terhivuo 1982, 1989).

Diploid, triploid and tetraploid populations are recorded in central and southern parts of Europe. Biparental reproduction is the norm but triploid strains at least reproduce by parthenogenesis (Muldal 1952, Omodeo 1952 and Cobolli Sbordoni et al. 1987).

Aporrectodea longa (Fig. 3). The Finnish localities for this stenotopic species are separate from each other and they refer to rich deciduous forests, gardens and fertile mull soils close to human settlements (Hæggström 1986). Its northern Swedish localities indicate that anthropochorously dispersed individuals can occupy and reproduce outdoors in sites far to the north of the continuous range of the species (Julin 1949). Malevič (1976) and Perel (1979) mention its occurrence in Moscow and the surrounding area up to about lat. 58°N.

Spontaneous dispersal to nearby soils is a slow process as indicated by e.g. the absence of the species

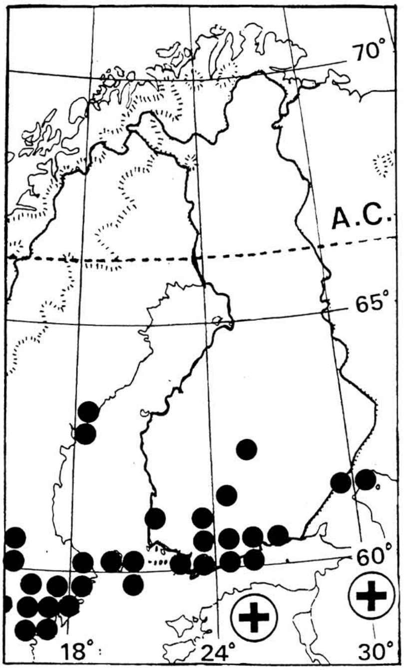

Fig. 4. Range of *Aporrectodea rosea* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

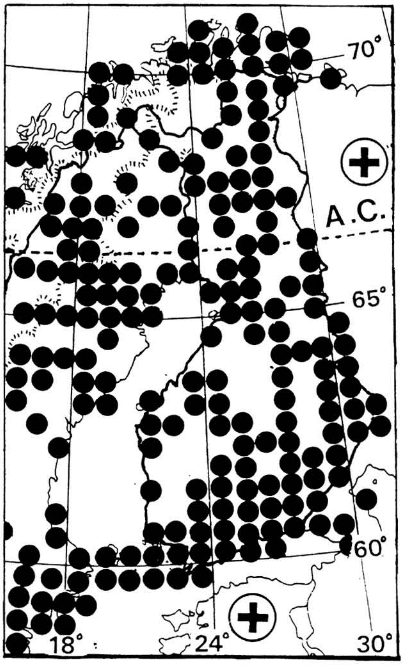

Fig. 5. Range of *Dendrobaena octaedra* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

in a great number of samples from rich soils lying close to, but being less influenced by man than in those sites where it was recorded on the mainland of Åland, SW Finland (Hæggström & Terhivuo 1979, Hæggström 1986). *A. longa* is a diploid that reproduces only biparentally (Muldal 1952).

Aporrectodea rosea (Fig. 4) extends its range in southern Finland to about 63°N as it also does in the nearby countries. Perel (1979) mentions its occurrence in the taiga zone where the northernmost records refer to the Archangel district (about lat. 63°N). *A. rosea* is rather stenotopic. It is most constant in meadows and rich deciduous forests (Karppinen & Nurminen 1964, Terhivuo 1989). In sites with a high annual input of plant material to the soil the density of *A. rosea* may approach 500 ind./m^2 (Hæggström & Terhivuo 1979). The species is also present in cultivated soils and a few records refer to coniferous forests (Nurminen 1962, 1967, Karppinen & Nurminen 1964). Timm (1970) has found it in limnic habitats.

Some polyploid *A. rosea* strains (3n, 5n, 6n, 8n, aneuploids) are considered to be male sterile and to reproduce only parthenogenetically, whereas some other strains (diploid and 10n) may be amphigonic in the southern and central parts of Europe at least (Muldal 1952, Omodeo 1952, Casellato 1987). There is a Finnish record of *A. rosea* in copula (Terhivuo, unpubl.). There are equivalent unusual records of other parthenogenetic earthworm species being found in copula as well, but copulation may not lead to the fertilization of eggs (see e.g. Sims & Gerard 1985).

Dendrobaena octaedra (Fig. 5) is distributed all over Fennoscandia and the European parts of the USSR, including numerous arctic islands (Julin 1949, Karppinen & Nurminen 1964, Stöp-Bowitz 1969, Malevič 1976, Perel 1979). It has the widest habitat spectrum of all northern Palearctic Lumbricidae species. Finnish records refer to islands and skerries (including those in the marine zone), wrack beds, shore plains, shore alder thickets, dry and moist coniferous forests, all kinds of deciduous forests, mea-

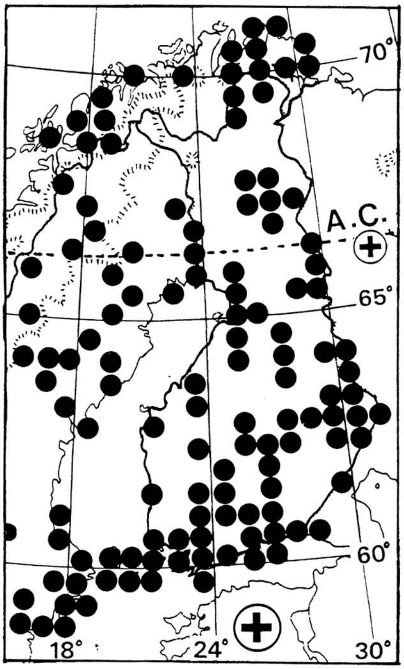

Fig. 6. Range of *Dendrodrilus rubidus* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

dows, fields, arable land, and different kinds of man-made habitats including composts, gardens and greenhouses. In northern latitudes it lives e.g. in arctic mountains, on the banks of rivers and lakes, and it may also be recorded from a variety of temporal habitats. Some finds refer to bogs that are otherwise devoid of Lumbricidae (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1978, Hæggström & Terhivuo 1979, Terhivuo 1988).

Polyploid (5n, 6n and 8n) and aneuploid populations have been recorded in Greenland and Iceland, as well as in the southern and central parts of Europe (Omodeo 1955, 1957, Casellato & Rodighiero 1972, Vedovini 1973). Hongell & Terhivuo (1989) found hexaploid specimens in southern Finland. This obligatorily parthenogenetic species exhibits great clonal diversity in Finland and N Norway; the abundant clones are eurytopic and widely distributed, whereas others prefer specific biotopes and have restricted geographical ranges (Terhivuo & Saura 1988).

Dendrodrilus rubidus (Fig. 6) is distributed in Fennoscandia as far north as the Arctic Ocean coast. In the USSR it is recorded in the taiga zone up to about 67°N (Malevič 1976). The ranges of the three main morphs, viz., rubidus, *tenuis* and *subrubicundus* overlap in Finland and specimens representing the *norvegicus* type have been recorded in N Finland (Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974a, Terhivuo 1984).

D. rubidus occupies a wide array of biotopes and its spectrum of habitats is likewise wide in northern latitudes (Terhivuo & Valovirta 1978). It is present in coniferous forest soils (Siivonen 1946, Nurminen 1967) where it lives in microhabitats such as stumps, under stones, among rotting plant material, and under moss carpets growing on stones and cliffs. It is often found in distant, but also in less remote, islands, wrack beds, shore plains, river banks, soils by ditches, shore alder thickets, deciduous forests, meadows and pastures (Backlund 1945, Siivonen 1946, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1978, Hæggström & Terhivuo 1979, Terhivuo 1982, 1984, 1989). In S and N Finland and N Norway I have often found it in wet and moist soils by rivers, brooks and springs. It seems able to withstand both fresh and brackish water. It thrives well in compost heaps and in a variety of man-made habitats including greenhouses, gardens and other rich soils close to human settlements (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1978).

Both obligatorily parthenogenetic (3n, 5n, 6n, aneuploids) and amphigonic (2n, 6n) strains have been recorded in different parts of Europe, Greenland and the USA (Muldal 1952, Omodeo 1952, 1955, Vedovini 1973, Jaenike et al. 1982, Casellato 1987).

Eisenia andrei and *Eisenia fetida* (Fig. 7) are both distributed as far as southern Finland but have no separate ranges there. The two species constitute an enigma. Recently *E. andrei* was recorded in the Jyväskylä and Hämeenlinna districts for the first time in Finland (Bouché et al. 1988). Additional specimens are present in museum collections but these have been keyed out to *E. fetida*. Some samples comprise both *E. andrei* and *E. fetida* individuals but the key character, viz., the colouration of the posterior end of the body, varies a lot. No attempt was made to identify a few more or less bleached specimens; the two species can be best identified when alive. It is noteworthy that Sims & Gerard (1985) indicate the presence of *E. andrei* only in *E. fetida* cultures. Since their ranges are the same, not only in Finland but also elsewhere, and because no ecological difference between them has been reported, I consider *E. fetida* and *E. andrei* collectively in this survey.

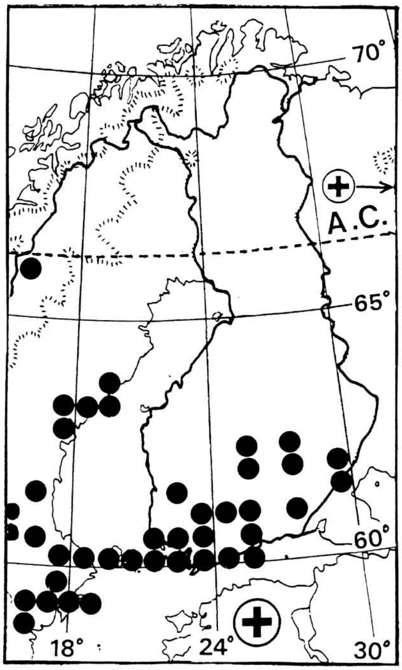

Fig. 7. Range combined from the records for *Eisenia andrei*, *Eisenia fetida* and *E. fetida* vel *E. andrei* in Finland and the nearby areas. For additional information see the text and for the data sources see the legend to Fig. 1.

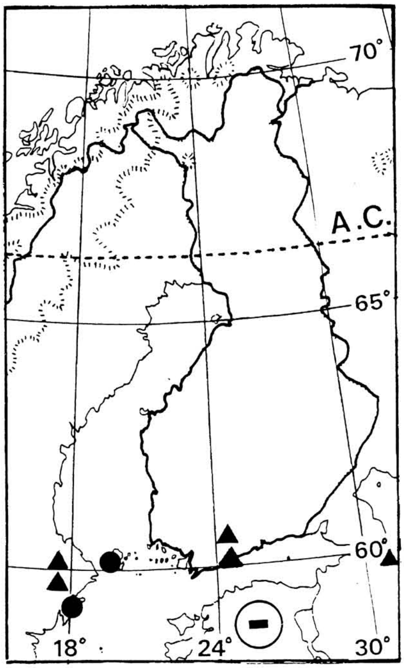

Fig. 8. Range of *Eisenia hortensis* (solid triagles) and *Lumbricus festivus* (solid circles) in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

In Norway the species complex is recorded from near the Arctic Circle (Stöp-Bowitz 1969) and in the USSR one record refers to the Kola Peninsula (Malevič 1976).

In Finland the records for the two species refer to leaf composts, manure heaps, greenhouses, waste, soils etc., these being sites with the constant addition of organic material to the soil by man. Some populations found not far from human settlements seem to originate due to man's agency. In Finland the two species are stenotopic and anthropochorously distributed.

Reproduction takes place either biparentally or by self-fertilization (Muldal 1952, Omodeo 1952, Hartenstein et al. 1980).

Eisenia hortensis (Fig. 8) was recorded for the first time in Finland in a greenhouse at the University of Helsinki botanical garden (Valovirta & Terhivuo 1976). An outdoor population of anthropochorous origin has been maintained for several years in a manure heap behind a cow-house in the municipality of Tuulos (Terhivuo 1982). Julin (1949) reported *E. hortensis* from a leaf compost in the botanical gardens at Uppsala, Sweden and Stöp-Bowitz (1969) found it in the same type of habitat in Oslo. Malevič (1976) gives one find from the Leningrad area but Perel (1979) reports it only from southern parts of the USSR. According to Muldal (1952) and Omodeo (1952, 1955) *E. hortensis* is a diploid that reproduces biparentally.

Eiseniella tetraedra (Fig. 9) is a rather stenotopic Lumbricid which in Fennoscandia occurs up to the coast of the Arctic Ocean. In the USSR the northernmost records refer to the vicinity of the Arctic Circle (Malevič 1976). It is most abundant in wet and moist alluvial shore soils, wrack beds, the banks of rivers and brooks (often under wet moss carpets along the shoreline) and it can be found in waterlogged or even limnic habitats such as the bottoms of rivers, brooks and ditches. It is found on distant treeless

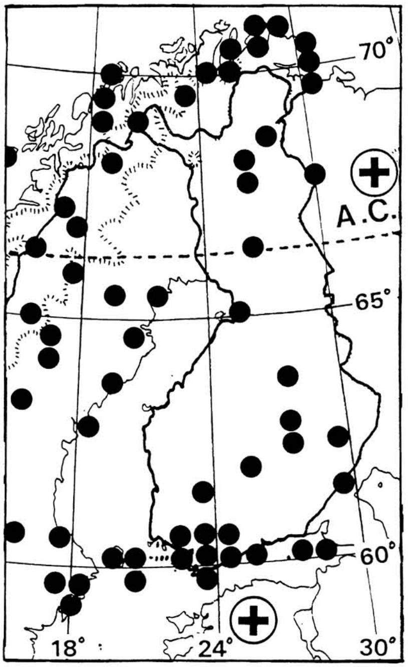

Fig. 9. Range of *Eiseniella tetraedra* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

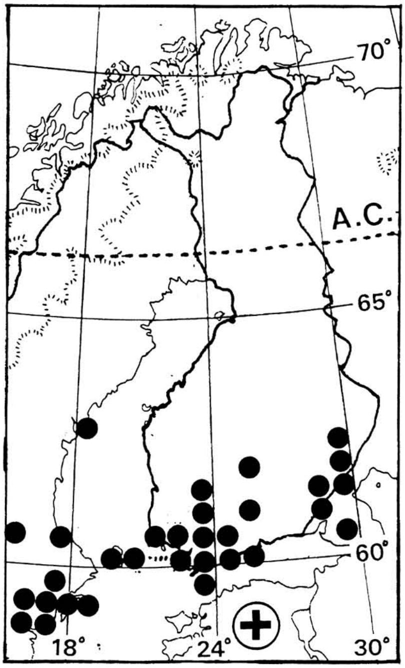

Fig. 10. Range of *Lumbricus castaneus* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

skerries in the marine zone of the Baltic and sometimes also in moist fertile mull soils rich in organic plant debris, i.e. in shore alder thickets, meadows and greenhouses (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974a, 1978, Hæggström & Terhivuo 1979, Terhivuo 1982, 1989).

This tiny earthworm reproduces only parthenogenetically. Triploid and tetraploid populations exist in central and southern Europe at least (Muldal 1952, Omodeo 1952, 1955, Vedovini 1973).

Lumbricus castaneus (Fig. 10). The records refer to southern parts of Finland where it is a constant member of Lumbricidae species assemblages in rich deciduous forests and meadows (Terhivuo 1989). It is occasionally found on shores and shore alder thickets but it is common in man-made habitats with fertile soils including gardens, greenhouses, leaf composts and waste soils near human settlements (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1978). This litter-dweller is a diploid that reproduces only biparentally (Muldal 1952, Vedovini 1973).

Lumbricus festivus (Fig. 8) has once been recorded in Finland, viz., on a roadside with transported soil material on the mainland of Åland, SW Finland (Hæggström 1985). In Sweden most records refer to southern parts of the country (Julin 1949, Nordström & Rundgren 1973) but Ljungström (1964) found it in the Stockholm area. In Norway it occurs in the vicinity of Oslo (Stöp-Bowitz 1969). It is very likely dispersed anthropochorously. It has not been recorded from the USSR (Perel 1964, 1979, Timm 1970, 1987). Probably the Finnish populations originate from either western or southern areas. Like its congeneric species *L. festivus* is diploid and reproduces only biparentally (Muldal 1952).

Lumbricus rubellus (Fig. 11) is distributed as far as the Arctic Circle in Finland but in Norway it occurs up to the coast of the Arctic Ocean. Some populations in northern parts of Norway are due to human agency (Terhivuo 1982 and unpubl.) but Stöp-Bowitz (1969) suggests that spontaneous dispersal along coastal parts of N Norway should not be ignored, either. Perel (1979) mentions it from the Archangel area.

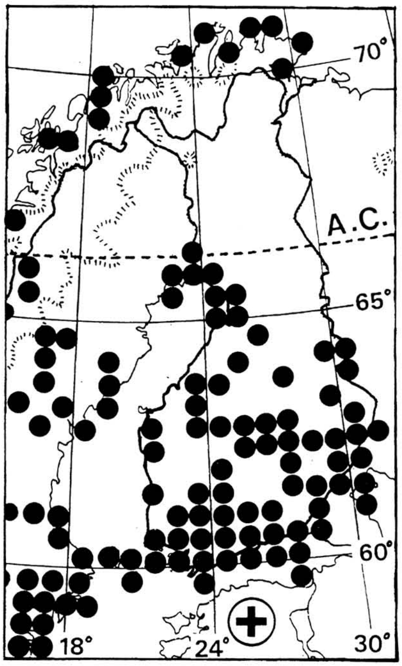

Fig. 11. Range of *Lumbricus rubellus* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

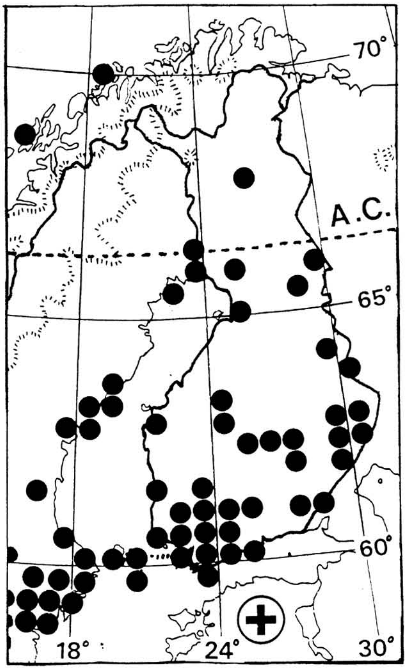

Fig. 12. Range of *Lumbricus terrestris* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

In Finland *L. rubellus* is eurytopic and occupies biotopes with great differences in environmental factors ranging from those in man-made biotopes (e.g. back-yard soils, gardens, greenhouses, composts) to those in alluvial shores, coniferous and deciduous forests, meadows and pastures. It is sometimes recorded from far-away islands and among wrack beds in northern parts of the Baltic Sea (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974a, 1978, Hæggström & Terhivuo 1979, Terhivuo 1989). *L. rubellus* is a diploid that reproduces only biparentally (Muldal 1952, Omodeo 1952).

Lumbricus terrestris (Fig. 12) has much the same range in Finland as *A. caliginosa* and *L. rubellus*. The northernmost records refer to man-made biotopes with fertile soils (Terhivuo & Valovirta 1974a, 1978, Terhivuo 1982). In southern Finland it occupies a variety of biotopes with a considerable annual input of organic plant material to the soil. It can be found in deciduous forests, meadows, pastures, gardens and greenhouses. In meadows and deciduous forests in southern Finland it comprises most of the earthworm biomass. Some records refer to coniferous forest soils and shore alder thickets (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974a, 1978, Hæggström & Terhivuo 1979, Terhivuo 1989). *L. terrestris* is a diploid that reproduces biparentally (Muldal 1952).

Octolasion cyaneum (Fig. 13) has a southwestern range in Finland implying distributional affinities with the west or some southern area. Perel (1979) mentions it from the Moscow area, but neither she nor Timm (1970, 1987) mention it from Estonia or nearby areas. Malevič (1976) has recorded one find from about 52°N/23°30′E. In Finland it lives in man-made habitats with mull or clayey soils and may be distributed to nearby sites with fertile soils (Nurminen 1962, Simola 1962, Panelius 1968 and Terhivuo 1981a). Novel populations have been recorded in widely separate localities in southern parts of the country; e.g. in the municipality of Lammi (Terhivuo 1982), at Nåtö in Åland (Hæggström 1985) and in the City of Helsinki (Terhivuo unpubl.). They are all due

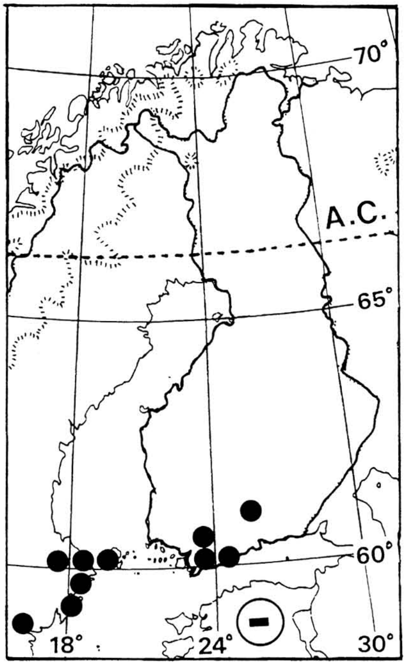

Fig. 13. Range of *Octolasion cyaneum* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

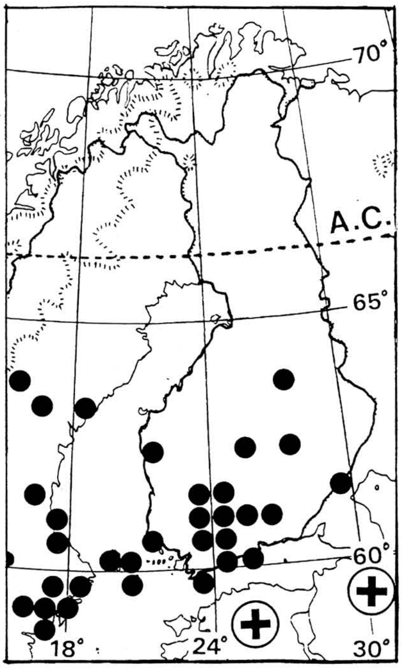

Fig. 14. Range of *Octolasion tyrtaeum* in Finland and the nearby areas. For the data sources see the legend to Fig. 1.

to human introduction. After heavy rain *O. cyaneum* can be found in great numbers on the ground. This has not, however, resulted in any uniform range in e.g. rich soils of S Finland.

O. cyaneum is a polyploid (9n, 10n, probably also other ploids) that reproduces only parthenogenetically (Muldal 1952, Vedovini 1973).

Octolasion tyrtaeum (Fig. 14) extends to about 65°N in Fennoscandia. In European parts of the USSR it is distributed to about 63°30′N (Malevič 1976, Perel 1979). In Finland it is most constant in alder woods lining shore plains in S Finland (Terhivuo 1989). It is also found in waterlogged shore soils, in banks and the littoral zones of lakes and rivers, as well as in meadows and deciduous forest soils with a high soil moisture content and rich in organic material. Some records refer to greenhouses but the species is not often found in biotopes with great human impact (Nurminen 1962, Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974, 1978, Hæggström & Terhivuo 1979). In Norway it is found only in the southern parts of the country (Stöp-Bowitz 1969). Perel (1979) indicates it from spruce forests with less acid soils in the middle Taiga zone about 60°N/40°E) and Timm (1970, 1987) reports it from limnic habitats.

According to Muldal (1952) and Omodeo (1955) *O. tyrtaeum* is a parthenogenetic species, but copulating individuals have occasionally been found (Sims & Gerard 1985).

Figs. 1–14 show that in Finland the northern limits of the Lumbricidae are not discontinuous with the corresponding margins in the nearby countries. Since no great dissimilarities in the intensity of faunistical recordings in the countries are found it seems plausible that the distributional histories of the Finnish earthworm populations are often allied to those of the same species in the neighbouring countries.

3.2. Post-glacial phases of NW Europe and the dispersal of the Lumbricidae in Finland

3.2.1. Changes in geomorphology, climate and vegetation

The retreating ice sheet of the last glaciation was followed by the formation of the Baltic Ice Lake (c. 10 500–10 200 B.P.) and the uplift of dry land areas.

During the Yoldia period (starting from about 10 000 B.P.) an arctic type climate prevailed and a tundra type vegetation occupied extensive areas in the northwestern parts of the USSR and southern parts of Sweden. A land bridge leading northwards and northwestwards to the Arctic Ocean coast of northwestern parts of the USSR was established at that time. Another dry land connection to the Arctic Ocean coast followed the coastal parts of Norway. Most of Fennoscandia was still ice covered at that time (Hyvärinen 1975).

With respect to the dispersal of earthworms to northern parts of Fennoscandia, the eastern dry land entrance was much shorter for invading populations than the western one. On the other hand, Julin (1949), Stöp-Bowitz (1969) and Perel (1979) have discussed the possibility of some hardy Lumbricidae species such as *D. octaedra* and *D. rubidus "norvegicus"* passing the last glaciation in ice-free refuges in association with some arctic plant species. This question remains unaswered, but, e.g. Perel (1979) hypothesised that the presence of *D. octaedra* on isolated Arctic islands such as Novaya Zemlya and Ostroy Kolguyev may date back to some preglacial era when these islands were part of the continent. In any case, for hardy earthworm species that can disperse efficiently without assistance from mankind an increasing amount of virgin soil was available in NW Europe c. 11 000–10 000 years ago.

During the period from about 10 000 to 8 800 B.P. a preboreal (dry and cool) type of climate prevailed and birch forests dominated in NW Europe. From this phase onwards to about 4 500 B.P. the climate gradually changed first to a boreal type (warm and dry) at the Ancylus period and then to a more maritime, warm and moist (Atlantic type) in the Litorina period. This caused the gradual development of luxurious vegetation and e.g. in the era of the Atlantic type of climate (some 7 500–4 500 B.P.) broad-leaved forests extended their ranges further northwards than they are found today. These forests hosted among others southern species of trees of the genera Tilia, *Acer, Corylus* and *Fraxinus* (see e.g. Kalliola 1973, Huttunen 1980). Climatic and edaphic factors were then evidently favourable to the dispersal of earthworm populations as well. However, coastal parts of present-day Finland and the Åland archipelago in SW Finland were still submerged, so that the lumbricid populations found there today are derived from later arrivals.

At the end of the Litorina period (c. 4 500 B.P.) the climate became cooler and more continental (subboreal type) causing a retreat in the ranges of many southern plant species, including those of the broadleaved trees mentioned above. This may have taken place in the case of some of the less hardy, southern earthworm species, but there is no indication of this. None of the recent populations or sample localities for southernly distributed species can be interpreted as being relict in nature. In fact, marginal populations are usually highly associated with human habitation.

From about 2 500 B.P. a subatlantic (cool, moist and rather continental) climate has prevailed and coniferous forests have gradually become the major biome in northwestern Europe. The intensive phase of invasion of spruce (*Picea abies*) from east to S Finland some 3 000 years ago coincides with the early agricultural practices there (see e.g. Suominen & Hämet-Ahti 1988, Rankama & Vuorela 1988).

Land uplift with changes in the sea level led to an alternation of sea and lake periods in the Baltic Basin. This resulted in discontinuities to the land connections established in the earlier era. For instance, during the Yoldia Sea period vast bodies of sea water separated Denmark and S Sweden from the central and northern parts of Scandinavia. Vast bodies of sea water are difficult for the Lumbricidae to cross without human agency. Drifting worms are eaten by fish and neither they nor their cocoons can withstand salt water for long periods. For instance, the earthworm faunas of isolated islands such as the Faroe islands (Enckell & Rundgren 1983) and Iceland (Bengtson et al. 1975), or even that in areas of Quaternary glaciation in N America (e.g. Reynolds 1976), seem to a great extent to originate from anthropochorously spread worms.

Since the drainage of the Baltic Ice Lake the formation of the Salpausselkä endmoraines gradually made an entrance permitting the plant and animal species of eastern and southeastern upland areas to migrate westwards to the slowly uplifting areas of south and southwestern Finland. Later on alternations in river and lake systems may have facilitated the migration of those species that disperse by means of water movement. Clues for such earthworm species can be obtained by studing the recent Lumbricidae fauna of isolated islands and areas of the Arctic Ocean coast lacking any appreciable human impact.

3.2.2. History of settlement, agriculture and trade in Finland

In Fennoscandia the oldest archeological data, which are from c. 10 000–9 000 B.P., are associated with the Komsa culture of the Arctic Ocean coast (e.g. Luho 1947, Huurre 1979). The so-called Boat-Axe people who lived in south and southwestern parts of Finland some 4 000–4 500 years ago may have cultivated soils as they did in more southern areas, but the oldest finds indicating definitively agricultural activities relate to the Bronze Age (3 500–2 500 B.P.) people at the end of the Litorina period. For instance, in Häme, S Finland the beginnings of agriculture can be fixed at 3 110±100 B.P. (Rankama & Vuorela 1988). However, gradual climatic distortion caused Finland to remain a sparsely inhabited country. The items indicating trade connections at that time show no evidence for the exchange of live material (Huurre 1979).

During the first three centuries (A.D.) new invaders, the Finns, adopted the vast forested areas as their hunting grounds and they also established settlements there. Agricultural practices were confined to only the most fertile soils of S Finland. Permanently settled areas remained isolated from each other for a long time. Not until the middle of the 1550s the northern coastal areas and the southern and southwestern parts of the Finnish mainland were permanently settled (Fig. 15).

From the 16th century to the beginning of the 19th century the central parts of Finland and southern parts of N Finland became permanently though sparsely inhabited (Fig. 15). Slash-and-burn cultivation, the burning of wood for tar, and frequent forest fires were important factors in the regulation of forest vegetation. For instance, heath forests have burnt approximately once in a century (Zachrisson 1977, Haapanen & Siitonen 1978). Deforested sites on rich soils and those where cattle grazed provided more favourable habitats for earthworms than e.g. heath forests that gradually became spruce dominated.

From about the 1750s to the 1860s the human population increased rapidly due to the industrial revolution reaching Finland at this rather late date. At that time intensive agricultural practices including cattle husbandry were maintained and the total amount of trade increased. In the 1850s slash-and-burn cultivation was still very common in the eastern and central parts of southern Finland (see e.g. Heikinheimo 1915). A new important plant species, namely the potato, was introduced to Finland in the 1700s, but it did not become common until the early 1800s (see e.g. Varis 1981). Novel agricultural methods and crop plants may have promoted anthropochorous dispersal of the Lumbricidae compared to those used in slash-and-burn cultivation. In southwestern parts of Finland trade connections with Sweden and the Åland islands were strong, while eastern and southeastern parts of the country were more under the influence of the eastern cultures. An economically important forest industry was established in Finland at the beginning of the 1860s. Horticulture was most intensively practiced in the urban areas of southwestern and southern Finland, where it had begun in the 1550s (e.g. Raatikainen 1981, Jalkanen 1981).

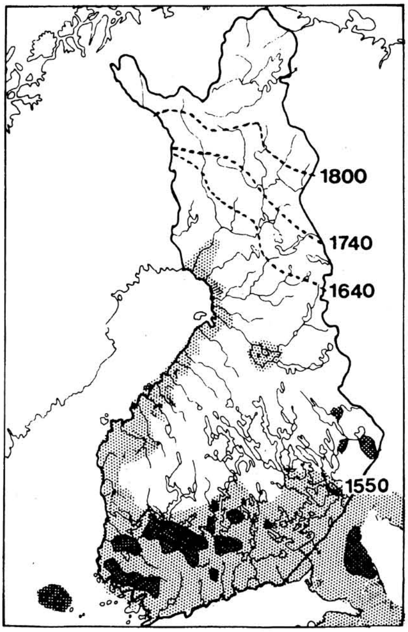

Fig. 15. Expansion of permanently settled areas in Finland. Intensive hatching indicates the permanently inhabited areas during the prehistoric era, slight hatching shows those areas settled up until 1550 and broken lines those up to 1640, 1740 and 1800, respectively. Redrawn from Kalliola (1973) and Huurre (1979).

The rate and quality of human activities in Finland imply that the last few centuries have been the most important periods for the northward dispersal of those Lumbricidae that disperse mainly or exclusively by anthropochory. Probably human activities have also encouraged the arrival of species not present there before. Besides anthropochory, man has influenced earthworm populations by creating new habitats for them, especially on fertile soils with favourable microclimatic conditions and with more or less permanent annual inputs of organic material to the soil. On the other hand, for those Lumbricidae that have

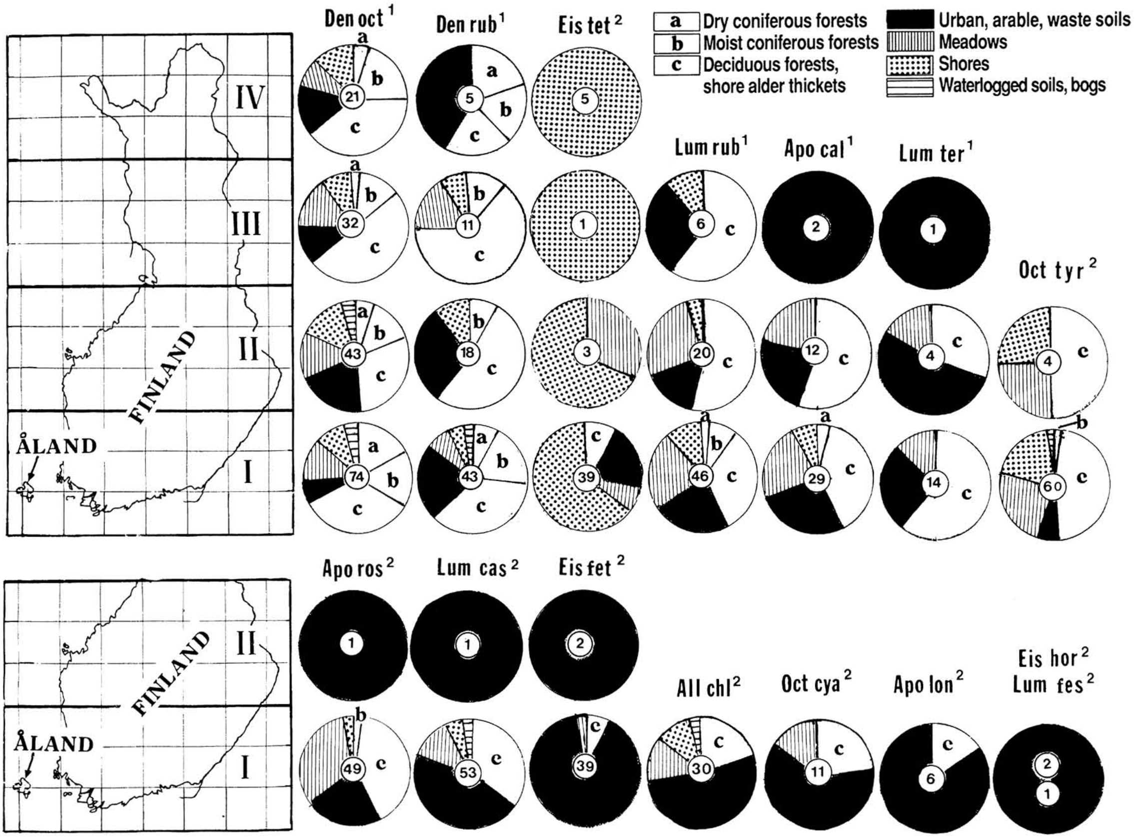

Fig. 16. Habitat spectra of the Lumbricidae species in different parts (zones I–IV) of Finland. The pie diagrams show relative proportions of different biotopes from the total biotope spectra of the species. The latter information is based either on the constancies of the species (superscript 1) in biotopes that are sampled with equal frequency in different parts of Finland (this sample procedure is explained in Terhivuo & Valovirta 1978), or on all the records of the species (superscript 2). The numbers of records are given in the middle of each diagram. Abbreviations for the species are; Den oct = *Dendrobaena octaedra*, Den rub = *Dendrodrilus rubidus*, Eis tet = *Eiseniella tetraedra*, Lum rub= *Lumbricus rubellus*, Apo cal = *Aporrectodea caliginosa*, Lum ter = *Lumbricus terrestris*, Oct tyr = *Octolasion tyrtaeum*, Apo ros =*Aporrectodea rosea*, Lum cas = *Lumbricus castaneus*, Eis fet and Eis and = *Eisenia fetida* and *E. andrei*, respectively, All clh = *Allolobophora chlorotica*, Oct cya = *Octolasion cyaneum*, Apo lon = *Aporrectodea longa*, Eis hor = *Eisenia hortensis* and Lum fes = *Lumbricus festivus*. See also the text.

previously dispersed to adjacent soils, man-made biotopes may offer novel food resources, always supposing that these species are able to compete with the anthropochorous species.

3.3. Ecological versatility of species of Lumbricidae in Finland

In chapter 3.1. I indicated that the ranges of habitats for the Lumbricidae species recorded in Finland are dissimilar. Terhivuo & Valovirta (1978) pointed out that many species occupy fewer biotopes in northern than in southern parts of their range in Finland. The rate of the shift is not, however, equal among the species. Habitat occupation of species at the northern limits of their ranges indicates the ecological requirements for the pathways used by them in extending their range northwards. Another alternative is that populations are left at these northern limits following a decrease in their range. Fig. 16 demonstrates the changes observed in Finnish species in this respect. Many species are eurytopic in southern Finland but more or less stenotopic and closely associated with man-made habitats in northern parts of their range, whereas the habitat spectra of some species do not decrease much northwards.

Earthworms are also dissimilar in respect of their vertical distribution in the soil and the kind of food resources they utilize. Dissimilar burrowing habits enable species to tap the food resources of different soil layers. Burrowing activity is related to the season and to inherent factors. Some deep-burrowing species, for instance, have an obligate diapause and some others may lie quiescent in periods of drought (e.g. Nordström & Rundgren 1973, 1974, Nordström 1975). The species of the upper soil layers are more exposed to forces facilitating passive dispersal. Ecological qualifications such as pH tolerance, rate of oxygen consumption, ability to stand periods of drought, floods and frost, capacity for interspecific competition, and mode of reproduction may be important in establishing a population.

In order to study the ecological versatility of species in relation to their dispersal I grouped the Finnish Lumbricidae according to their horizontal distribution pattern in the soil and to the type of food they utilize.

3.3.1. Earthworm species of upper soil layers

Litter-dwelling (Perel 1977, Satchell 1980) or epigeic (Bouché 1972), or surface-living (Norström & Rundgren 1973), species are mesophagous earthworms that live among litter and in the upper soil layers. Cocoons are laid there (Gerard 1964) and offspring and adults share the same substrate so that the species in all phases of their life-cycle are more subject to forces promoting passive dispersal than are species living in deeper soil layers. The Finnish species of this group comprise *Dendrobaena octaedra*, *Dendrodrilus rubidus*, *Eiseniella tetraedra* and *Lumbricus castaneus*. They are small in size, pigmented, make no permanent burrows, have a high cocoon production, a short cocoon incubation time, and a short growth period (Edwards & Lofty 1972, Nordström 1976, Nakamura 1985). Satchell (1980) considers them to be "*r*- selected".

Three of them (*D. octaedra*, *D. rubidus* and *E. tetraedra*) are distributed all over the study area. They reproduce parthenogenetically, i.e. only one mature worm or a viable cocoon is needed for the establishment of a colony. These hardy species pass the winter in frozen soils as either worms or cocoons. They exhibit no vertical migration to avoid seasonal changes in the temperature of the environment. They have none of the diapause or quiescense typical to many deep-burrowers, either (e.g. Nurminen 1967, Nordström & Rundgren 1974 and Nordström 1975).

Finnish records of *D. octaedra*, *D. rubidus* and *E. tetraedra* refer to e.g. remote skerries of the marine zone, wrack beds, and shore soils by brackish and fresh water bodies, indicating that they can spread passively by the aid of waves, floods and running water bodies (e.g Terhivuo 1982). Dispersal by wind (e.g. individuals and cocoons stuck to leaves) and by animals (e.g. in hooves of ungulates and perhaps by birds) should not be ignored, either. For instance, my observations in N Norway indicate that all three species are often found in the banks of rivers, brooks and by small bodies of water. Such sites are very often visited by reindeer whose paths criss-cross such sites.

D. octaedra and *D. rubidus* are eurytopic, whereas *E. tetraedra* is stenotopic (Fig. 16). It is noteworthy that man-made habitats do not play any major role in their habitat spectra and that their habitat spectra do not diminish much northwards. Their dispersal is not dependent on man's activities even in marginal parts of their ranges. This does not, of course, mean that man's activities have not assisted their dispersal at all. The latter process may simply be of secondary importance in their post-glacial extension of range.

Fig. 5 and the electrophoretic survey by Terhivuo & Saura (1988) suggest that *D. octaedra* may have come over to Finland from the east and/or southeast (from the USSR) and the southwest (from Sweden possibly via the Åland islands) and some populations in central parts of Finland may have originated in N Sweden.

L. castaneus, though a litter-dweller, reproduces only biparentally. Figs. 10 and 16 suggest that it is confined to southern parts of the study area and that man-made biotopes, probably also anthropochory, play a role in its northward dispersal. It passes the winter among fallen leaves etc., i.e. in sites close to the soil surface, and it can exceptionally be found on melting snow (Nordström 1975, Terhivuo 1981b).

3.3.2. Deep-burrowing earthworm species

In the present contex I consider both vertically and horizontally burrowing earthworms of the deeper soil layers as deep-burrowers. These earthworms can be grouped into endogeic and anecic (Bouché 1972), or into macrophagous and microphagous, species (Sims & Gerard 1985). They are medium to large-sized, usually less pigmented than litter-dwellers and they make permanent burrows in the soil. Satchell (1980) considers them to be "*K*-selected".

Most Finnish Lumbricidae make deep-burrows, either horizontally or vertically. Their life-cycles take place deep in the soil so that they are less exposed to the agencies important for the dispersal of litter-dwellers. But, being most constant and abundant in fertile soils where intensive agricultural and horticultural practices are also undertaken they are likely subjects for anthropochorous dispersal. Some of them e.g. the three *Eisenia* species, are totally dependent on man-made biotopes. This also seems to be true for some other deep-burrowing species at the northern limits of their ranges (Fig. 16). Recent records of faunistically noteworthy "long-distance dispersal jumps" of lumbricids in Finland refer to deep-burrowing species and they are due to anthropochory (see e.g. Karppinen & Nurminen 1964, Terhivuo & Valovirta 1974a, Terhivuo 1982, Hæggström 1985, 1986).

Inoculation experiments with *A. caliginosa*, *L. terrestris*, *A. longa* and *A. rosea* demonstrate that they can occupy good soils close to the site of inoculation but spontaneous, active dispersal within the soil or along the soil surface is no more than about ten metres or less per year (Hamblyn & Dingwall 1945, Hoogerkamp et al. 1983 and Ghilarov & Perel 1984). If we adopt a rate of some 10 m/year for active dispersal during the past 12 000 years or so, then deep-burrowing earthworms should not be in Finland at all. Consequently, active dispersal may be mainly of local significance for their northward dispersal. Supposing that deep-burrowers have "flourished" e.g. during the warm Atlantic period when favourable climatic conditions prevailed and broad-leaved forests were widely distributed recent marginal populations should be considered as relic populations. I consider this less likely because of the strong association of deep-burrowers to human habitation at the northern edge of their range where many man-made biotopes have been estabished not so long ago. At such sites they are seldom recorded in the adjacent soils.

I hypothesize that some deep-burrowing species at least represent an element of the Finnish Lumbricidae fauna that may not have arrived until after the arrival of man in Finland. The records of e.g. *A. chlorotica* (Fig. 1), *A. longa* (Fig. 3), *E. fetida* vel *E. andrei* (Fig. 7), *E. hortensis* (Fig. 8), *L. festivus* (Fig. 8) and *O. cyaneum* (Fig. 13) indicate long-distance dispersal "jumps" and strong association with man-made habitats (Fig. 16). The Finnish mainland populations of the species may have distributional affinities with corresponding species populations in Sweden and the Åland Islands or with those in Estonia or some more southern areas to which trade connections have been maintained from Finland. On the Finnish mainland the transportation of plant and soil materials, tools and machines used in agriculture, horticulture and forestry, and probably zoochory too, have facilitated their dispersal. Recent records related to e.g. the dispersal of *O. cyaneum* in Finland indicate that such processes are likely involved (Terhivuo 1981a, 1982).

Northern records of *L. terrestris* (Fig. 12) and *A. caliginosa* (Fig. 2) imply long dispersal-jumps to rich soils with human impact (Fig. 16). Anthropochory may be the most efficient mode of dispersal for them in northern latitudes, at least. *L. terrestris* resembles litter-dwellers in feeding among litter on soil surface but deep-burrowers in making long vertical burrows (e.g. Bouché 1972).

A. rosea (Figs. 4, 16), although a parthenogenetic and rather eurytopic lumbricid in Fennoscandia, is found in the southern parts of Finland where it lives in rich soils under more or less intensive human influence. Anthropochory seems to play a role in its distributional history in Finland as well.

Shore alder thickets that are included in the deciduous forest category in Fig. 16, together with shores, appear to constitute the "ecological dispersal pathway" for the parthenogenetic *O. tyrtaeum*. The species' high concentration of haemoglobin in the blood may facilitate its occupation of limnic and waterlogged habitats usually devoid of other deep-burrowers (Byzova 1975). Although it is a deep-burrower in soils rich in organic material, I have found it in shores close to the soil surface and under stones at the waterline. Its dispersal may not be strongly associated with human habitation (e.g. Terhivuo 1989).

3.3.3. *L. rubellus*

L. rubellus is a species intermediate between litter-dwellers and deep-burrowers hence it lives closer to the soil surface than deep-burrowers do (Nordström & Rundgren 1973, Perel 1977) and unlike litter-dwellers it makes shallow U-formed burrows (F. Lamparski pers. comm.) and reproduces only biparentally (Muldal 1952). It is eurytopic and can live in soils with a wide range of pH, viz., 2.4–9.0 (Olson 1928, Satchell 1955, Ljungström 1964, Hæggström & Terhivuo 1979). It also withstands brackish water and a high and low moisture content of soil, as shown by records of it from shores and coniferous forests. Its presence in remote islands suggests an ability for passive dispersal without human agency, but, according to Hoogerkamp et al. (1983), its spontaneous dispersal in the soil is a slow process. In the north (Fig. 16) it is found in separate localities with at least some human influence. My observations in N Norway indicate that tourists keen on sport-fishing can be responsible for the origin of some populations of the species found in the banks of rivers and brooks. Less strict habitat requirements may be important for the colonization of these soils. In many such sites it exceeded in numbers *D. octaedra*, *D. rubidus* and *E. tetraedra*, indicating that it is an efficient competitor.

3.4. Genetic diversity of earthworm populations at the northern edge of their range

In northern parts of their range earthworm populations are forced to cope with more extreme and unpredictable climatic conditions and with dissimilar edaphic factors compared to the less marginal areas. Mayr (1963), among others, has stressed the advantages of wide genetic variation within a population for survival in the face of temporal changes of environmental factors. In the present study area the most widely distributed Lumbricidae comprise litter-dwelling, parthenogenetic species. They lack genetic recombination and inherited genotype differences are due to mutations and to a dissimilar level of polyploidy.

Based on the electrophoretic surveying of six polymorphic loci, Terhivuo & Saura (1988) pointed out that in Finland and N Norway about every third individual of *D. octaedra* represents a novel overall enzyme phenotype and that in S Finland genetic variability is only slightly greater than in N Finland. This may be due to dissimilar mutation frequencies in the populations of south and north Finland, but it is more likely that in the latter area *D. octaedra* populations that have invaded from S Sweden and N Norway have contributed to the diversity of clone pools there.

In sexually reproducing species genetic recombination and mutations are the most important sources of genetic variability. A population consisting of a few individuals at a given site may produce a wide array of genetically dissimilar offspring. Due to recombinations taking place along the germ lines of these earthworms mutations manifest themselves more often than in parthenogetic polyploids where they may easily remain masked in the genotype. It seems to me that in deep-burrowing species the low capacity for passive dispersal without human agency, together with the isolation and scarcity of fertile soils in northern latitudes, rather than the diversity of genotypes, have limited the northward dispersal of these species in eras preceeding intense human impact at least. The many recent dispersal jumps of deep-burrowing species tend to indicate that the influences of harsh climatic conditions can be avoided in soils with good edaphic conditions for the species to some extent at least.

3.5. Dispersal of earthworms compared to that of insects

According to den Boer (1977) three main types of hypothesis concerning the dispersal of insects have been put forward. The founding hypothesis stresses that dispersal increases the rate of founding new populations and is thus of significance to the evolutionary success of the species. As an example, there are Charabidae species having populations comprising wing-dimorphic individuals (macropterous and brachypterous). Macropterous individuals have a superior dispersal power (see e.g. den Boer 1970) to brachypterous ones. The reason for individuals migrating is innate rather than related to any specific condition of the source population. According to the escape hypothesis, dispersal (migration) enables individuals to avoid current adverse conditions. The overflow hypothesis states that overcrowding in a population causes some individuals to disperse (migrate). Dispersal may also take place due to temporary events, as indicated by e.g. Palmén (1944) and Vlijm (1971). Palmén (1944, see also 1971) pointed out that specific climatic conditions e.g. high air temperature, may initiate periods of active insect flight that together with e.g. a strong wind may be the reason for the anemohydrochorous dispersal of insects in the area of the Gulf of Finland. In this case no special state of populations is involved although, of course, individuals in dense populations are more a target for forces promoting passive dispersal than those of sparse populations of the same species.

With respect to earthworms in the study area, coccons are more likely than individuals to be dispersed passively, and active dispersal in general may be of secondary importance in regard to the extension of the range of the species at least. Dispersal due to temporal events, e.g. flooding, zoochory, activities of man, etc., cannot be related to any specific state of the source population or even to the avoidance of harsh conditions. Being opportunists to some extent at least, litter-dwelling species can reach temporary food resources due to their great power of passive dispersal. However, it may be premature to state that founding a new population in an unstable environment is crucially important for them from the standpoint of their evolutionary success, especially keeping in mind that at least *D. octaedra* and *D. rubidus* are highly eurytopic, living as well in stable environments where they compete succesfully with other earthworm species (Terhivuo & Valovirta 1978). For the eurytopic *E. tetraedra* founding a new population may be more important in this respect, for the extinction rate of populations in temporary habitats such as alluvial shores may be high. It is probable that earthworms, especially deep-burrowing species, disperse passively today more frequently than in earlier eras due to increased human activity in the study area. Faunistical recording, however, is mostly able to indicate those dispersal events that are correlated with changes in the ranges of the species.

3.6. Concluding remarks and prospects

I have hypothesized that there may be an old and a young element in the Lumbricidae fauna of Finland. The precise origins of species populations can be seldom traced on the bases of the faunistical recording undertaken here for about 100 years. New information on the origin and routes of dispersal of earthworms may be obtained through tracing parthenogenetic species by means of enzyme electrophoresis, particularly in areas where human impact is negligible. On the other hand, during the past few centuries the role of man in creating unintentionally new habitats and thereby facilitating the dispersal of earthworms has become more intensive all the time. In the long run faunistic recording will reveal the arrival of new earthworm species, including those of exotic families. Records of e.g. species of the Megascolecidae and the Glossoscolecidae in Finland are preliminary signs of that process (Terhivuo & Valovirta 1974b).

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