*Chapter 38*

# The establishment of earthworm communities

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## 38.1 INTRODUCTION

The communities, roles and morphology of present-day earthworms are the fruits of a long period of evolution: present abilities or inabilities to perform certain functions or to saturate available niches are the expression of a genome inherited from their past. This chapter attempts to trace the origins of present earthworm communities from geological times.

## 38.2 THE DATA BASE

### 38.2.1 Fossils

Annelids consist mostly of soft tissues and usually decay quickly, leaving no fossils. They have chitinous setae capable of preservation but these are not peculiar to annelids and are difficult to interpret. With one recorded exception (Schwert, 1979), earthworm cocoons too are not fossilized. Traces of burrows and other marks of annelid activity survive but their origins are incapable of proof. Palaeomoders and particularly palaeomulls indicate the evolution of whole ecosystems similar to present-day types in which earthworms play a major role – nevertheless it is possible to imagine other animals playing the same role in the past.

### 38.2.2 Morphology

Morphology, based on a genetic code inherited from the past, provides evidence of adaptation to function in present-day environments. It provides a basis for classifications which, though arbitrary at first, may later be used to indicate phylogenetic relationships. The

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morphological–taxonomic procedure has led to a double systematics in which some taxa can be interpreted phyletically and others cannot (Bouché, 1972). Because similar characters indicate similar habits, it is possible on a morpho-functional basis independent of taxonomy to group species sharing more or less the same role or niche into ecological types (Bouché, 1971, 1977). Such ecological types show r (epigeics) and K (anecics, most endogeics) selection (Satchell, 1980) but also adaptations specific to soil life. Recognition of characters appropriate to each ecological type thus helps to distinguish convergent characters from both apomorphic (recent) and plesiomorphic (primitive) characters. Conversely, a phyletic interpretation, when possible, may help to explain the distribution of present ecological types. Interpretation of both phyletic and ecological data is a continuing process; nothing is definitive.

### 38.2.3   Biogeography

*Observed distribution*

The distribution of animals is independent of morphological or fossil data but the value of present distribution data is dependent on the quality of sampling. Only France has been sampled methodically. For other countries information is copious (Hungary, Belgium, Norway) or good (USSR, Italy, UK, Germany, Sweden, Australia). Elsewhere, some zones are fairly well documented while others are practically ignored. Even when information is copious, the density of sampling may be sufficient to establish the presence of species but not their absence. In France, a small territory, general though still incomplete sampling revealed three new families or subfamilies and numerous species new to science. This state of knowledge is general.

Present-day distribution is the result of three parameters: the origin of the founders, their migratory capacity and their ability to survive.

*Ability to migrate*

Endogeic earthworms have, in general, a poor capacity to migrate. Some very fragile species living in deep soil layers (oligohumic type of Lavelle) are very sensitive to desiccation and are unable to leave the soil. Other less typically endogeic species have a limited capacity for surface migration (Mazaud and Bouché, 1980) and may be caught in pitfall traps (Boyd, 1960; Bouché, 1976). Epigeic worms living in semi-permanent litter or organic matter accumulations are comparatively mobile and search on the surface for food or shelter. 'Anecic' worms are intermediate. Some leave their burrows during heavy rainfall and are able to migrate and colonize a few metres per year (Mazaud and Bouché, 1980).

For most earthworms, migration is only by dispersal into adjoining land capable of supporting them. There is no active dispersal, but passive migration has distributed some species over wide areas. Species which are active on the surface during rainfall are transported by running water as are cocoons and worms from eroded soil (Schwert and Dance, 1979). Water dispersal, leading to a pseudo-riparian distribution, is limited by watersheds which form migration barriers. Most megadrile worms cannot survive marine environments (Piearce and Piearce, 1979) but some genera, e.g. *Pontodrilus, Rhododrilus* (Jamieson, 1980), *Microscolex*, secondarily adapted to sea water, have been able to colonize oceanic islands more than 1000 km from continental land masses (Bouché, 1982). Transport by animals, e.g. moles, is generally limited to a few decametres, or longer distances by birds (Schwert, 1980). Transport by man in water affects freshwater species and species of cultivated land are commonly transported in soil attached to plants. Large worms or endogeic species which are fragile and unable to survive in disturbed soils are rarely successfully transported by these means.

*Survival ability*

The success of anthropochoric species in colonizing environments disturbed by man is well known (e.g. Ljungström, 1972) and empty niches may be created by deforestation, pesticides, waste disposal and destruction of existing habitats. They may also arise naturally from glaciation, marine emergence and sea recession. Empty niches in such virgin environments may also be occupied by migrants as in the case of the epigeic *Dendrodrilus rubidus tenuis* var. *norvegicus* in the sub-antarctic Kerguelen Islands (Bouché, 1982) where the only other earthworm present is the endogeic species *Microscolex kerguelarum.*

Overpopulation by one ecological type can have an adverse effect on the entire earthworm community (Mazaud and Bouché, 1980). The various populations of a local community adapt themselves to changes in the environment by sharing the ecological resources and filling the available niches. A precise adaptation of populations to their environment has resulted from limited gene flow; consequently immigrant allochthonal species are generally less fitted to the locality and fail to become established.

## 38.2.4 Geology and ecology

Interpretations must be capable of counter-proof (Claude Bernard) or to be falsifiable (Popper). Palaeogeographical information and ecological data provide independent sources for refuting or confirming the bio-

**Table 38.1** Names and hierarchy of taxa cited. Underlined taxa are followed by subordinate taxa.

Class: Annelida
Subclass: Oligochaeta
Orders: Lumbriculida, Tubificida, Haplotaxida
Haplotaxida suborders: Haplotaxina, Alluroidina, Moniligastrina, Lumbricina
Haplotaxina family: Haplotaxidae
  species: *Haplotaxis gordioides*
Lumbricina superfamilies: Criodriliodea, Lumbricoidea, Biwardriloidea,
  Glossoscolecoidea, Megascolecoidea

Families:

| Lumbricoidea | Glossoscolecoidea | Megascolecoidea |
|---|---|---|
| Sparganophilidae | Kynotidae | Ocnerodrilidae |
| Ailoscolecidae | Microchaetidae | Megascolecidae |
| Hormogastridae | Glossoscolecidae | Acanthodrilidae |
| Lumbricidae | Almidae | Octochaetidae |
| | | Eudrilidae |

Sparganophilidae genus: *Sparganophilus*
Hormogastridae genera: *Hemigastrodrilus, Vignysa popi, Hormogaster praetiosa, Hormogaster redii, Hormogaster samnitica.*
Lumbricidae genera: *Lumbricus, Prosellodrilus, Ethnodrilus, Scherotheca, Allolobophora, Eophila, Aporrectodea, Dendrobaena, Dendrodrilus*
*Scherotheca* subgenera: *Opothedrilus, Scherotheca*
*Scherotheca* subgenus group 1: *S. monspessulensis, S. gigas, S. dugesi,*
                        *S. dugesi brevisella*
                  group 2: *S. guipuzcoana, S. coineaui, S. corsicana*
*Allolobophora pereli, A. muldali*
*Eophila januae-argenti*
*Aporrectodea( = Nicodrilus) longa, A. longa ripicola, A. velox, A. gogna, A. balisa, A. giardi ( = terrestris), A. giardi voconca*
*Dendrobaena jeanneli*
*Dendrodrilus rubidus tenuis* var. *norvegicus*
Acanthodrilidae genus: *Microscolex kerguelarum*

geographical interpretations and phyletic reconstructions presented in this chapter.

## 38.3 INTERPRETATION

### 38.3.1 The Precambrian primary annelids

Valentine (1980) traces the origins of the main animal groups to the vermiform coelomates of 700 million years ago on the basis of fossil tracks and morpho-functional arguments concerning the coelom and hydro-

**Table 38.2** Summary of: (1) proposed relations between geological stages; (2) time in millions of years; (3) selected main events; (4) taxonomic hierarchy (not synchronous between families); (5) palaeopedological events (Kubiena, 1948) and terrestrial adaptation.

| Stages (1) | Time (2) | Selected Main Events (3) | | Taxa (4) | (5) |
|---|---|---|---|---|---|
| Quaternary | | Post-ice-age migrations<br>Extinction in ice age | | Varieties | |
| | 2 | | | | |
| Pliocene | | *Scherotheca dugesi brevisella*<br>*Hormogaster samnitica lirapora* | | Subspecies | |
| | 5 | | | | |
| Miocene | | Continent ↔ Corsica–Sardinia<br>*S. dugesi / S. gigas*<br>Massif Central ↔ Alps<br>*H. praetiosa, S. gigas* | Only South of France | Species | |
| | 23 | | | | |
| Oligocene | 36 | | | | |
| Eocene | | *Prosellodrillus, Ethnodrilus,*<br>*Opothodrilus, Scherotheca* | | Subgenus and genus | |
| | 53.5 | *Hemigastrodrilus, Hormogaster* | | | |
| Palaeocene | | *Vignysa?* | | | |
| | 65 | | | | |
| Cretaceous | | Kynotidae, Microchaetidae, Almidae,<br>Lumbricidae, Hormogastridae,<br>Ailoscolecidae, Eudrilidae, Malabrinae | | Families | |
| | 120 | | | | |
| Jurassic<br>Triassic | | Lumbricoidea, Megascolecoidea,<br>Glossoscolecoidea | | Superfamilies | |
| | 225 | | | | |
| Palaeozoic | | Lumbricina<br>Oligochaeta | | Suborder<br>Order | |
| | 570 | | | | |
| Ediacarian | | Annelida | | Class | |
| Precambrian | 700 | Burrow tracks: coelomates | | | |
| | | Metazoa<br>Eucaryotes? | | | |
| | 1400 | | | | |

(5) column labels: Aquatic terrestrial earthworms · Active mull · Moder · Gyttja · Marine worms

static skeleton. These coelomates differentiated into various lines, among them the Annelida, which appear to be represented in the fossil Ediacara fauna by *Marywadea* (680 million years), a metamerized animal. The Annelida were probably well established at the junction of the Precambrian and Cambrian (570 million years).

The evolution of the Oligochaeta by adaptation of the Annelida to epicontinental habitats can be interpreted in morpho-functional terms. The conquest of land began with an aquatic fauna which became adapted to freshwater streams. Two linked fundamental traits mark this eco-logical adaptation. First, the loss of all very mobile stages, both zygotes and diaspores. Oocytes and spermatozoa are no longer released into water, instead exchange of sperm occurs between partners. This sperm is contained in spermatophores or spermathecae to await fertilization which remains external in the ootheca where oocytes are layed. The free-living trochophore larva disappears and instead the embryo grows in the ootheca. Correlated with this, the clitellum spreads out to produce oothecae. This loss of mobility is a response to the need to avoid being carried away in water currents.

The second trait is a genetical consequence of the first. Copulation between animals with very limited mobility leads to considerable potential inbreeding. This handicap is corrected, at least partly, by hermaphroditism, polyploidism and parthenogenesis.

This differentiation of Oligochaeta from the sea annelids probably occurred in the early Palaeozoic. Among freshwater Oligochaeta, the Haplotaxida today inhabit very humid oxygen-deficient soils or penetrate far into deep soils by natural drains where they live as endogeic rheophiles. Their distribution is world wide, corresponding to their origin in Pangaea.

### 38.3.2  The Mesozoic: adaptation to terrestrial life

At the end of the Palaeozoic or during the early Mesozoic, the Oligochaeta acquired the characters adapted to true terrestrial life. First the oesophageal crushing organs, the progastral gizzard, appeared, then, freeing the anterior part, the postgastral gizzard. Earthworms obtained nourishment from various sources distributed in the soil (endogeics) then, later, from rich accumulations on the soil surface (epigeics), finally they took to mixing organic and mineral soil layers (mainly anecics).

This evolution affected the characters of the entire animal. An earthworm population living in firm burrows was subjected to selective pressure which affected organs in a linear way (pholeoiptomy); expansion of an organ in the anterior part brought about the contraction of another organ, a feature of burrow-living animals. Development of the oeso-

phageal gizzard led to posterior displacement of some genital organs and the postgastral organization was associated with a backward movement of clitellum and puberculum. This posterior displacement was, in turn, linked with indirect copulation.

Adaptation to the soil environment also entails greater development of the body wall and of the anterior septal muscles, particularly in the postgastra, better skin protection, dispersal of nephridiopores (holo-nephridia) with solfeggio-like distribution of nephridiopores, mero-nephridia, coelomic pores, and diverse arrangements of setae.

The end of the Palaeozoic and the beginning of the Mesozoic was the period of the single continent, Pangaea. Since Wegener's classic work (1920) various reconstitutions of this land mass and its evolution to the present day have been proposed. Plate tectonics and choice of absolute geographic co-ordinates have led to a modern reconstruction (Dietz and Holden, 1970) and to computer simulations (Smith and Briden, 1978).

The present classification–distribution of earthworms may be super-imposed on to Pangaea and its various stages of dissociation. Some difficulties result from the need to include all earthworms whereas one can only be confident of the phylogeny of the best-known groups. Here I use the arrangement of Sims (1980a) but the position of some families or superfamilies having only one or two species seems uncertain (Criodriloidea, Biwadriloidea, Lutodrilidae) from lack of information.

Following Jamieson (1978), I consider Alluroidina and Moniligastrina as independent from Lumbricina. These three suborders probably have their origin in haplotaxine ancestors.

If the present distribution of endemic Lumbricina is projected on to a map of Pangaea (Fig. 38.1), the distribution of the Megascolecoidea will be found to show a discrepancy. This group, well established in 'south' Pangaea, the future Gondwana, also spread into Southeast Asia where the Megascolecidae, also present in Australia, were well established. Perhaps the Acanthodrilidae (Australia, Africa and Americas) are also endemic in Southeast Asia.

This situation at the time of the Trias (220 million years) may be interpreted by various hypotheses:

(a) The present taxonomy is incorrect: this is doubtful for this level in the hierarchy;
(b) The two families spread into Southeast Asia after the junction of the Australian continent with Asia: this event was probably too late;
(c) The animals were translocated on fragments of Pacifica which drifted through Panthalassa, today's Pacific Ocean, from the Australian region to Asia and the Americas (Nur and Ben-Avraham, 1977, interpretation in Sims, 1980a). This hypothesis seems chronologi-
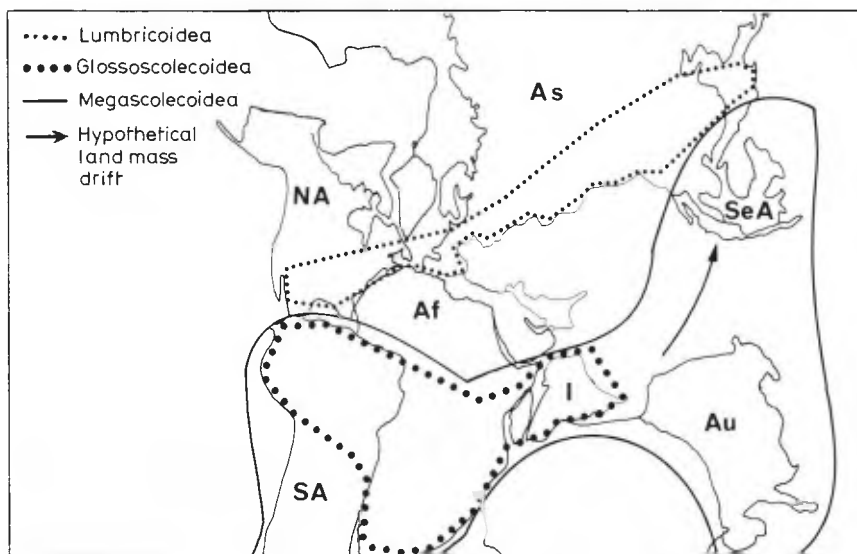
**Fig. 38.1** Present distribution of superfamilies based on endemic species in relation to Pangaea in the early Triassic (220 million years). After Smith and Briden (1978) and present area of superfamilies based on endemic species. Present continents projected on Pangaea: Af, Africa; NA, North America; As, Asia; SA, South America; Au, Australia; SeA, Southeast Asia; I, India.

cally incompatible with the total evolution of Lumbricina if Pacifica broke away from Pangaea in the mid-Permian;

(d) An inadequate interpretation of continental drift. A Southeast Asian fragment could have migrated as India, from the Southern zone (Gondwana) to present-day Asia. It must be remembered that sometimes zoological arguments are better than the accepted geological theses. Continental drift was accepted by Michaelsen (1922) and Cernosvitov (1935), while geologists generally rejected it (Wilcke, 1955). The 'impossible' migration of *Scherotheca dugesi (brevisella)* from the continent to Corsica in mid-Miocene (Bouché, 1972) provides another example. The geotectonics of Southeast Asia remain poorly interpreted and I consider this hypothesis to be probable.

Gondwana was occupied only by the Glossoscolecoidea and Megascolecoidea. The Ocnerodrilidae spread into America, Africa, Madagascar and India. The Acanthodrilidae and Octochaetidae with similar territories extend eastward to Australia. The Megascolecidae, however, settled only in the eastern part, Southeast Asia and Australia.

The Eudrilidae, a highly evolved family, seem to have differentiated from this stock at a later date, after the isolation of Africa. Laurasia, which separated from Gondwana in the Jurassic, harbours the Lumbricoidea.

### 38.3.3 End of the Mesozoic: differentiation of families

Differentiation of the families occurred, generally speaking, around the end of the Jurassic or during the Cretaceous and the disruption of Gondwana (Fig. 38.2). The Glossoscolecoidea gave rise to the Glossoscolecidae in South and Central America, the Microchaetidae in South Africa and the Kynotidae in Madagascar. Finally, the Almidae, a group with various genera which are perhaps ecologically convergent, all living in muddy soils, evolved in South America, Central Africa and India to Sulawasia.
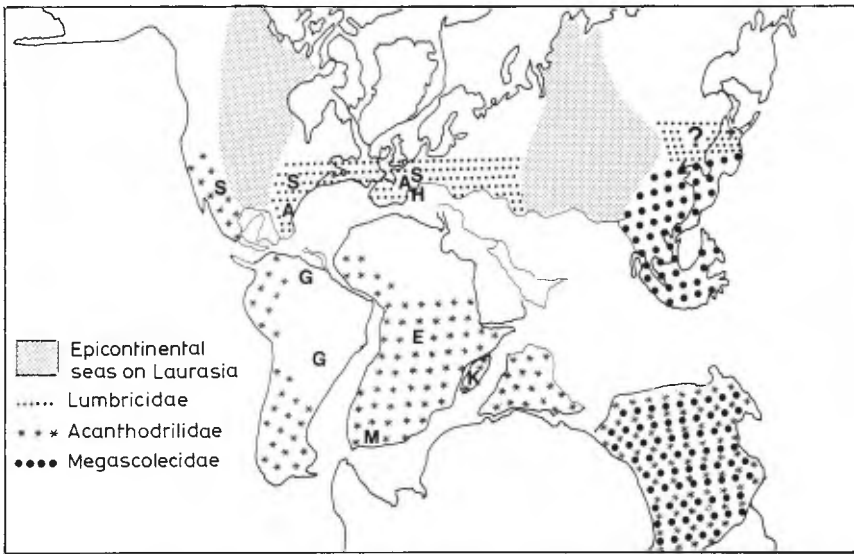


**Fig. 38.2** Distribution of families in relation to the separation of Laurasia from Gondwana in the early Cretaceous (120 million years). After Smith and Briden (1978). A, Ailoscolecidae; E, Eudrilidae; G, Glossoscolecidae; H, Hormogastridae; K, Kynotidae; S, Sparganophilidae.

The Lumbricoidea probably spread from an epicontinental sea in 'North America' to Siberia. The maximum of endemism is observed in families with different genera in America and Europe (Ailoscolecidae, Lumbricidae). The Sparganophilidae, with probably a single genus on both Atlantic shores, became established in very humid soils, and two

families are very localized, the Lutodrilidae in America and the Hormogastridae in Western Europe.

The Megascolecoidea gave rise to the Eudrilidae, peculiar to Africa, and the Acanthodrilidae spread into Western North America, bounded eastward by an epicontinental sea. Sims (1980a) provides another interpretation. The Ocnerodrilidae formed a subfamily peculiar to India. In general, the Gondwanian disruption gave rise to families or subfamilies on its fragments while the Laurasian breakup, which took place later, is today characterized by genera. This difference in hierarchical levels appears again at lower levels for earthworms living in mud (Almidae, Sparganophilidae).

### 38.3.4 The Tertiary: intrageneric differentiation

At the end of the Mesozoic and during the Tertiary, the present-day genera, subgenera and species became differentiated. The north of France
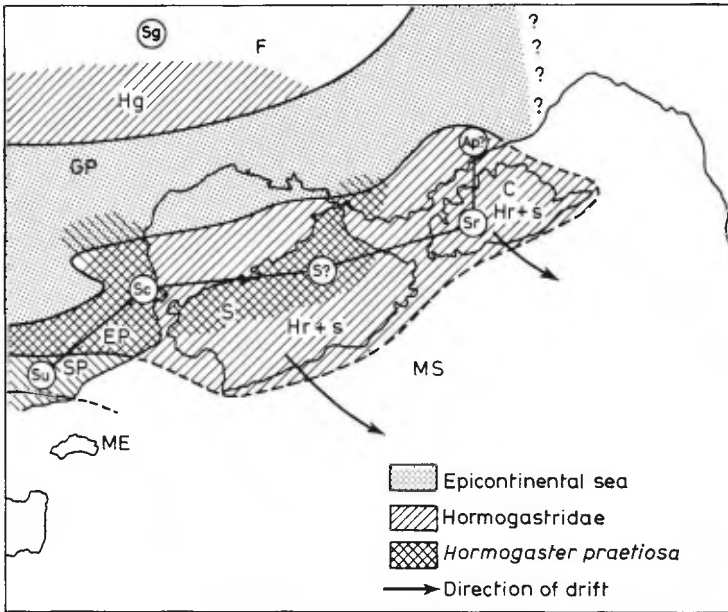


**Fig. 38.3** Approximate position of Sardinia and Corsica in the Palaeocene during separation from the continent. GP, Aquitaine–Provence gulf; SP, South-Pyrenean furrow; C, Corsica; EP, East-Pyrenean ridge; F, Continental France; S, Sardinia; Su, *Scherotheca guipuzcoana*; Sc, *S. coineaui*; S?, *hypothetical Scherotheca* sp.; Sr, *S. corsicana*; Ap?, *Allolobophora pereli?*; Sg, *S. gigas* group; Hg, *Hemigastrodrilus*; Hr, *Hormogaster redii*; Hs, *H. samnitica*; MS, Mediterranean Sea; ME, Menorca.

was deprived of fauna during Quaternary glaciations and consequently gives no information on Tertiary history but the area now forming the south of France illustrates some of the factors involved. In this zone, widely submerged by epicontinental seas in mid and late Jurassic, a great emergence occurred in the Jurassic–Cretaceous when some of the Lumbricoidea were probably able to spread into the new terrestrial territory. This land, before and during the Palaeocene, split into three zones, a 'Massif Central' in the North separated by a Lower-Provence–Aquitaine gulf from a ridge running from the East-Pyrenees to Sardinia, Corsica and the Maures (EPSACOM). This ridge was in turn probably separated from an 'Ebro continent' by a sea occupying a South Pyrenean furrow (Fig. 38.3).
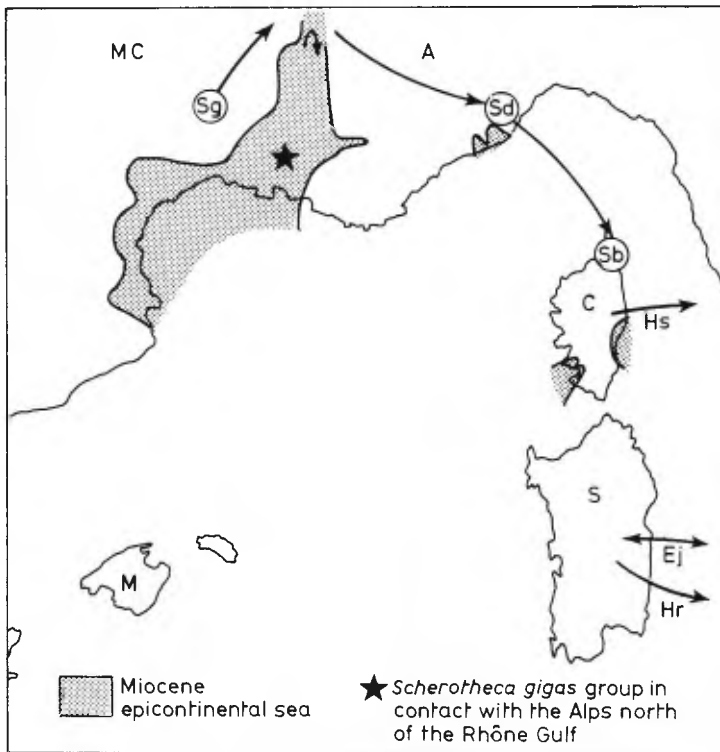


**Fig. 38.4** Migration in the Miocene and through temporary passages during the drying up of the Mediterranean during the Pliocene. Sg, *S. gigas*; Sd, *S. dugesi*; Sb, *S. dugesi brevisella*; Hs, *Hormogaster samnitica*; Hr, *H. redii*; Ej, *Eophila januae-argenti*; MC, Massif Central; A, Alps; M, Majorca; C, Corsica; S, Sardinia.

Knowledge of the Iberian fauna is poor but in the Massif Central and EPSACOM three lumbricoid groups seem to have evolved: Hormogastridae, *Prosellodrilus/Ethnodrilus, Scherotheca*. In the Massif Central land mass live: 1 *Hemigastrodrilus* (and possibly *Vignysa*); 2 *Ethnodrilus;* 3 *Scherotheca*, branch *gigas-monspessulensis*. In EPSACOM: 1 *Hormogaster* (and possibly *Vignysa*); 2 *Prosellodrilus;* 3 *Opothedrilus* and the species assemblage *S. guipuzcoana, S. coineaui, S. corsicana* with a relatively anterior puberculum (30)31–40(42) ( + *Allolobophora pereli*?).

Before the Oligocene, an island which later became Sardinia and Corsica broke away from the continent (Auzende *et al.*, 1973). Today, the distribution of *Hormogaster praetiosa* is perhaps a testimony to the former link between Catalonia-Sardinia and West Provence.

During the Miocene, contact between the Alps and the Massif Central land mass occurred allowing the *Scherotheca gigas* group to invade this new territory where it became differentiated into the species *S. dugesi*. At the end of the Miocene, the Mesogea, the present-day Mediterranean, fell to a low level (Hsii, 1972). *S. dugesi* invaded North Corsica where it is represented today by a peculiar subspecies: *S. dugesi brevisella*. *Hormogaster redii* and *H. samnitica* which were differentiated in Sardinia and Corsica, formerly the eastern part of EPSACOM, spread around and through the present Ligurian-Thyrenean sea. *Eophila januae-argenti*, today occupying Macedonia, Campania and Sardinia (Omodeo, 1961), had probably a single area during this period (Fig. 38.4).

### 38.3.5 THE QUATERNARY: DESTRUCTION OF THE FAUNA AND RECOLONIZATION

Quaternary glaciations eliminated earthworms over a large part of middle and North Europe (Michaelsen, 1903; Cernosvitov, 1935). In western Europe, and especially in France, we can see endemics as discrete isolated populations which have only been able to maintain themselves in warm micro-biotopes, including caves (*Dendrobaena jeanneli*) (Bouché, 1972). This zone of isolated population refuges lies in the middle of France with a more favourable seashore zone around Charente and Périgord (*Ethnodrilus*). There are no endemics from the area of inland ice in the Alpine mountains. Southward, the biogeographical areas reflect tertiary events and were not greatly affected by glaciation.

The recolonization of land after the ice age can sometimes be traced. For example, the group of closely related species *Aporrectodea ( = Nicodrilus) longa* (Ude), *A. gogna, A. velox* inhabits a funnel-shaped zone in the high Rhône watershed which opens on to the great North-European Plain extending from the British Isles to the USSR. Two

species are confined to the zone of refuges and did not leave the Rhône watershed while *A. longa longa* and *A. longa ripicola* spread northward (Fig. 38.5).
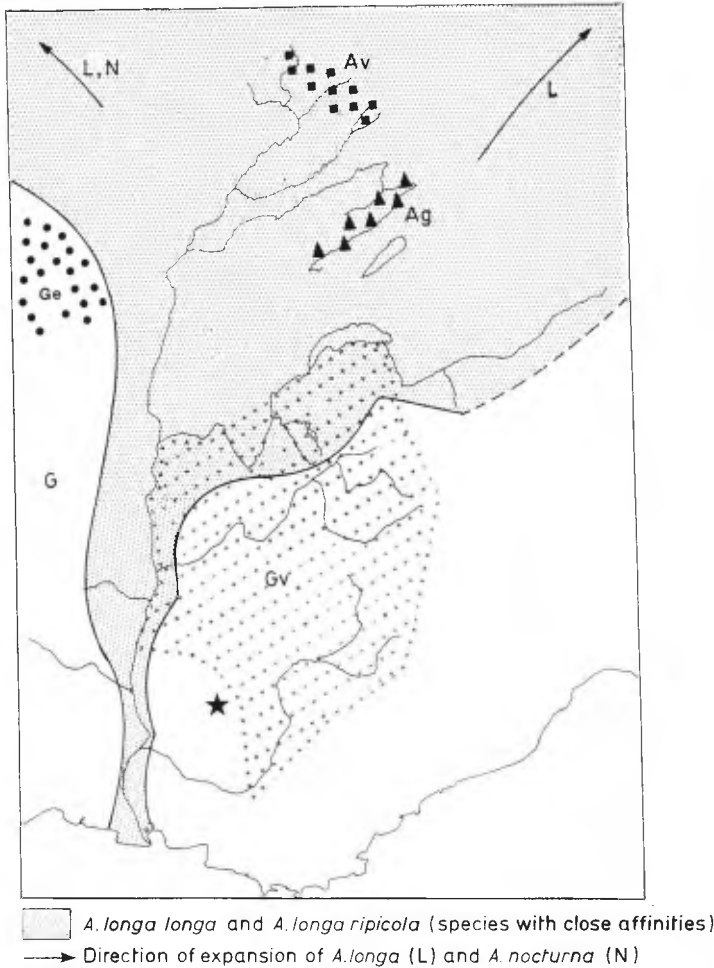


**Fig. 38.5** Post-glacial migration of *Apporrectodea* from the Rhône watershed. Av, *A. velox* (■); Ag, *A. gogna* (▲); G, *A. giardi giardi*; Ge, var. *eudensis* (●); Gv, *A. giardi voconcus* ( · ); *A. balisa* ★ (the last six are all competing species).

The territory of this group is bounded by other *Aporrectodea* which were probably competitive (*A. giardi giardi*, *A. giardi voconca*, *A. balisa*), all also anecics, and the area is shared with another anecic, *A. nocturna*, in the west. This partial co-habitation of two anecic species may be

explained by food sharing (Ferrière, 1980). While boundaries are not clearcut and the areas overlap to some extent, the species *A. longa, A. giardi* and *A. nocturna* are usually mutually exclusive (Bouché, 1972).

The north European fauna is poor and although there are some unexplained cases, for example, *Allolobophora limicola* from the Rhine watershed, including its former British tributaries, one can recognize the origin of the species in the south.

Recolonization after the ice age was followed in modern times by transport by man.

### 38.3.6 Ecological types and distribution

The evolution of the taxa was accompanied by adaptation to often precise ecological niches. It is difficult to retrace this but over such a long period it is probable that groups occupied various niches successively and alternately. This has led to morphological types which have descended from various ancestors and are more or less convergent. Direct taximetric classification of morphological data thus gives information both on present ecological similarities and on phyletic relations (Sims, 1980b; Bouché, 1980). Starting with the Haplotaxida of the endogeic type, earthworms were more or less specialized in relation to food sources. Small and narrow polyhumic worms tend to establish themselves near the surface of roots, or in the zone where organic matter is carried by drainage into pore spaces (shrinkage cracks: *Allolobophora muldali*; natural drainage channels: *Haplotaxis gordioides*). The mesohumic endogeics are in an intermediate position and ingest moderately organic soils. The oligohumic endogeics live in soils poor in organic matter of which they consume large quantities. The latter are important in tropical zones with *Vignysa popi* present in humid mediterranean soils.

These adaptations are in equilibrium with organic sources, metabolic needs and microbial life (Lavelle *et al.*, 1980) which are in turn dependent on climate. Surface organic horizons are invaded by epigeic earthworms or can be buried by anecics which contrast with other earthworms by feeding and casting in different layers. The anecic ecological type has been well established only in the Lumbricidae. Anecics create the conditions for microbial maturation of their food for, after burying, the casts are reingested (Bouché, 1981). Their burrows and cast systems favour the penetration of organic compounds by solution, by gravity in burrows, by ingestion, by traction and by excretion of metabolites (Dietz, 1979; Bouché, 1981).

The different ecological adaptations of earthworms lead to co-existence of various species which are in actual or partial competition and occupy distinct or partly overlapping niches. This scheme is probably

general and explains why the total earthworm niche is generally filled and why the areas of the various endogeics and anecics are stable. The mobile epigeics are in equilibrium with their temporary media. This scheme also explains why palaeogeographic phenomena can be observed in present population distributions and, conversely, how earthworms continued to occupy their total niche as the epicontinental ecosystems evolved. The filling of the annelid niche seems to have coincided with ecosystem development, and fossil humus types (Kubiena, 1948) are a testimony to the emergence of earthworms (Wilcke, 1955). The humus type gyttja is associated with freshwater groups, Lumbriculida, Tubificida, Haplotaxida; moder and poorly active mull are associated with endogeics while active mull is linked with anecics (Table 38.2).

## 38.4 CONCLUSION

Since the time of the Ediacara fauna, earthworm ancestors have occupied a fundamental position in ecosystems using plant organic matter which is subjected to complex transformations through earthworm/microflora interactions. Analogous interactions occur in grassland (Loquet *et al.*, 1977) and estuaries (Loquet and Dupont, 1977). The Annelida are energetically efficient with a hydrostatic skeleton, poikilothermy, reduced search for food and sexual partners, and protection by the soil environment, and have therefore filled a wide niche. One group, the Oligochaeta, has become well adapted to epicontinental life, the most successful branch being the Lumbricina with its diverse terricolous adaptations. Various ecological types representing the adaptations of different earthworm groups fill the annelid niche in emerged soils. Historical events such as continental drift, tectonic movements and glaciation, remain imprinted in many rather immobile groups. The imprint is to some extent indelible as a result of the loss of mobile stages during adaptation to terrestrial life and of specialization and competitive interactions (Bouché, 1972). This does not exclude a diversification of communities nor adaptation of their structure to macroclimatic conditions and consequent availability of food.

There are nevertheless various difficulties in interpretation, in particular, dyssynchronism of families in the taxonomic hierarchy although these anomalies will doubtless be resolved as taxonomy improves. On the broad time and space scales used in this study a coherent pattern can be seen which is consistent with the independent studies of Jamieson (1974).

We can conclude that the vermiform coelomates became established very early in the development of the Metazoa and that the Annelida have played a dominant role in the porosphere since the Precambrian.

## 38.5 ACKNOWLEDGEMENT

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