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Journal

Biogeographia – The Journal of Integrative Biogeography, 20(1)

ISSN

1594-7629

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Publication Date

1999

DOI

10.21426/B6110025

Peer reviewed

Biogeographia - vol. XX - 1999
(Pubblicato il 31 ottobre 1999)
Biogeografia dell'Anatolia

Biogeographical patterns of terricolous oligochaetes in Turkey (Annelida: Clitellata: Lumbricidae, Enchytraeidae)[1]

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Key words: Anatolia, biogeography, Lumbricidae, *Spermophorodrilus*, *Healyella*, Enchytraeidae.

SUMMARY

Recent surveys of terricolous oligochaetes in Turkey have led to the discovery of a taxon of Lumbricidae endemic to Anatolia, northern Greece and Epirus, which undoubtedly deserves subfamilial rank. The institution of the Spermophorodrilinae not only has produced a more rational classification (particularly with regard to the genus *Bimastos*) but is determinant for reconstructing the phylogeny of part of the order Lumbricina. On the basis of palaeogeographical evidence and of the diversity of adaptive types observed, it is possible to envision Anatolia as an area that provided a variety of ecological niches for a colonising, evolutionarily dynamic, earthworm fauna, originally formed by the Spermophorodrilinae and a stock of the genus *Dendrobaena*. It is plausible to date the indigenous stocks of Spermophorodrilinae and *Dendrobaena* to the Palaeogene, or an earlier time, when Turkey and the Rhodopean area formed together an insular or semi-insular system. Isolation and the absence of competition from other megadriles favoured diversification within the two taxa. A more remote timing is preferable for the Spermophorodrilinae, because these should be contemporary, or older, as morphologically more archaic, than the Sardo-Corsican Diporodrilinae. Turkey and Transcaucasia represented indeed the major centre of diffusion of the genus *Dendrobaena*, and some species spread from there both in an eastward and northwestward direction. For *D. attemsi*, an accurate morphological and distributional study has made possible to trace the possible postglacial migratory routes towards the western Alps, the British Isles and Sweden. Other notable results concern some typical Carpatho-Balkan genera and species (*Cernosvitovia, Fitzingeria, Allolobophora smaragdina, A. leoni*, etc.) which have penetrated into the northern or northwestern Anatolian districts. Previous views of the history of the Turkish lumbricofaunal components must be corrected, as the traditional subdivision into a northern and a southern Aegeid is not supported by modern palaeogeographical reconstructions. On the contrary, the new faunistic data confirm some curious absences of Holarctic species in Turkey (*Lumbricus terrestris, Dendrobaena octaedra, Allolobophora chlorotica, Octolasion cyaneum*, etc.). The southern limits of distribution of these species in the Mediterranean area must be only slightly retouched. Much work has to be done before a thorough biogeographical analysis of the Turkish enchytraeid fauna becomes feasible, but there seem to be significant differences in species composition between the northern and southern zones: strictly Mediterranean species appear to be restricted to the south.

INTRODUCTION

In earlier discussions of the zoogeography of terricolous Oligochaeta, Omodeo (1952a, 1961) observed that some distribution patterns involving the regions extending to the east of the Alpine arc as far as the Caucasus could be referred

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[1] Zoological researches in the Near East by the Universities of Rome: 187.

to the palaeogeography of the Miocene. He recognized: (1) an Alpine-Illyric-Carpathian pattern, proper to the northern Aegeid; (2) a Syrian-Anatolian-Aegean pattern, referable to the southern Aegeid; and (3) a mixed pattern, referable to the period of maximum sea regression occurring toward the end of Miocene. He also noted that the distribution areas of many Lumbricidae show a distinct southern border, which for some species lies to the south, for others to the north of the Anatolian peninsula, and in any case continues to the south of Spain. These ideas were embraced by Avel (1959) and Zaionc (1965) and, with some reservations, by Perel (1979). With the subsequent advancement of palaeogeography, the causes and extension of the Miocenic regression (Messinian salinity crisis) were clarified, and the trans-Aegean transgression separating the two Aegeids *sensu* Jeannel (1942), which was previously deemed so important, came to be viewed as a transitory, not very significant episode. The history of the Western Mediterranean lands was reconstructed and related to the drift apart of the Alboran block, the Greater and Lesser Kabylia, the Peloritan and Calabrian massifs and the Sardo-Corsican plate. On the other hand, the earthworm faunas of Turkey (Omodeo, 1988; Omodeo and Rota, 1989, 1991), Greece (Zicsi, 1973; Zicsi and Michalis, 1981), Caucasus (Kvavadze, 1985), Iran (Omrani, 1973) and Maghreb (Omodeo and Martinucci, 1987; Baha, 1997) were thoroughly investigated and became much better characterized. By integrating the new faunistic data with the available palaeogeographical evidence, we attempt here a historical reappraisal of the distribution patterns of Anatolian earthworms.

THE COLLECTIONS (Fig. 1)

Prior to our studies, the available information on the oligochaetes of Turkey (Rosa, 1893, 1905; Michaelsen, 1907, 1910; Cognetti De Martiis, 1913; Pop, 1943; Omodeo, 1952b, 1955a, 1956; Zicsi, 1973, 1981, 1985) was still very limited and fragmentary. In 1987 and 1990, in the framework of two Italian expeditions organized by Augusto Vigna Taglianti and Achille Casale, respectively, we had the opportunity of performing samplings at 62 Turkish localities (involving 26 vilayets), thus gathering more than 3000 oligochaete specimens. Additional smaller collections were obtained by colleagues and friends during different trips to Turkey: to the slopes of Caucasus by Emilio Balletto, to the east and south of the country by Maria Grazia Filippucci and Shimon Simson, and to various other locations, particularly cave sites, by Marco Bologna, Achille Casale, Saverio Forestiero, Mauro Giachino, Valerio Sbordoni and Augusto Vigna Taglianti. The taxonomy and faunistics of these collections were described in detail in four papers (Omodeo, 1988; Omodeo and Rota, 1989, 1991; Rota, 1994a); on this basis it is possible to build a synthetic picture of the faunal components inhabiting this vast country and attempt a reconstruction of their history.

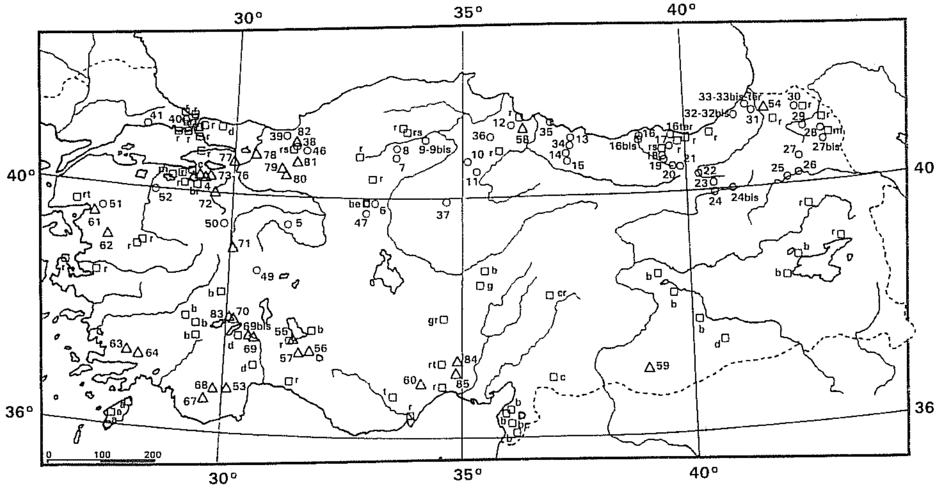

Fig. 1 - Collecting sites of terricolous oligochaetes in Turkey from 1893 to 1991. The richer collections are those from numbered sites: 4 to 52 (Omodeo, 1988; Omodeo and Rota, 1989) and 53 to 86 (Omodeo and Rota, 1991; Rota, 1994a). a: Cognetti De Martiis (1913); b: Omodeo (1952b); c: Omodeo (1955a); d: Omodeo (1956); e: Pop (1943); f: Rosa (1893); g: Rosa (1905); m: Michaelsen (1910); r: Zicsi (1973); s: Zicsi (1981); t: Zicsi (1985).

AGE OF EARTHWORM TAXA

Before going into the question, we believe it worthwhile to consider some points concerning the chronology of evolution of these sedentary animals, which are hardly subject to natural passive dispersal, *i.e.*, one not caused by human activities, but which evidently can rapidly populate climatically favourable areas and become evolutionarily dynamic when competition is scarce and a variety of ecological niches for a colonising fauna is provided. At the species level, we know that: (1) Mediterranean populations of some Lumbricoidea, *e.g.*, *Nicodrilus caliginosus* (Savigny, 1826) and *Hormogaster redii* Rosa, 1887, that remained isolated following the Messinian crisis (5-6 Myr ago), show no significant morphological differentiation and only a weak molecular divergence (Cobolli et al., 1987; Cobolli et al., 1992); besides, (2) populations of *Hormogaster pretiosa* Michaelsen, 1900 (s.l.) that became separate with the detachment of the Sardo-Corsican system from the Alboran plate (24-30 Myr ago) show a wide molecular divergence (Cobolli et al., 1992) but only a slight, almost cryptic, morphological differentiation (Rota, 1994b). Based on these data, we assume that speciation in Lumbricoidea may take more than 20 Myr to become detectable at the phenotypic level. There are other numerous, although less precise, pieces of evidence that support this minimum time estimate. For instance, populations of the aquatic *Criodrilus lacuum* Hoffmeister, 1845 living in now widely separated locations such as Turkey, the Italian peninsula, Sicily and Maghreb, appear morphologically indistinguishable on the subspecific level; however, the caryotype of the Turkish population is slightly different from that of the Sicilian population (Rota and Omodeo, 1992). For a taxon like this, which is supposed to spread only within the boundaries of inland water systems, it is likely that the last opportunity for an effective gene exchange between populations was during the Messinian crisis (5-6 Myr ago).

Concerning the genera (as recognized in current megadrile taxonomy), origins can be assumed at about 100 Myr ago (Omodeo, 1963, 2000). Various populations living in South America and Guinea, thus geographically separated since the Atlantic Ocean began to form, have not diverged beyond the specific level, whereas others have become differentiated at generic level (*Wegeneriella* Michaelsen, 1933 and *Wegeneriona* Cernosvitov, 1939; *Drilocrius* Michaelsen, 1917 and *Callidrilus* Michaelsen, 1890). The most southerly populations, that is, those inhabiting Patagonia and South Africa, have evolved as closely related genera (*Chilota* Michaelsen, 1899 and *Parachilota* Pickford, 1937); one major exception is the genus *Microscolex* Rosa, 1887 which is represented by endemic species on the two continents as well as on circumantarctic islands. Palaeogeographical scenarios (see Omodeo, 2000) suggest estimated ages of 80 Myr, or more, for those genera which are represented by different endemic species in India and Madagascar (*e.g.*, *Howascolex* Michaelsen, 1901), or in India, Ceylon, [Antarctica] and New Zealand (*e.g.*, *Megascolex* Templeton, 1844). Within some of the families, the morphological differences – and the corresponding taxonomic differentiation – seem to have accumulated more rapidly than in others, but the estimated ages can confidently be accepted within the ranges reported above (Omodeo, 2000).

Coming to the highest categories of Lumbricida, *i.e.*, the three superfamilies Lumbricoidea, Megascolecoidea and Eudriloidea, it is important to note that the former two are distributed over more than one continent, which implies that they already existed at the time of Pangaea. Palaeoecological evidence suggests they might have originated towards the end of Palaeozoic, when humic soils began to form (Wilcke, 1955, 1960).

THE SPERMOPHORODRILINAE

Let us begin with the Spermophorodrilinae, the lumbricid subfamily whose discovery constitutes the most exciting result of our research in Turkey. This is undoubtedly the most archaic among the earthworm taxa inhabiting Anatolia: a consistent set of features makes its members different from any other group of Lumbricidae, while showing resemblances to the Hormogastridae (Omodeo and Rota, 1989). Most remarkably, Spermophorodrilinae and Hormogastridae share the location of the clasping organs (used in copulation; Fig. 2) above the sexual pores (segments XIV and XV) rather than in the clitellar region (behind segment XX). By comparing the mating modalities and the morphology of the digestive apparati, Rota and Omodeo (1992) argued that Spermophorodrilinae and

Hormogastridae may have arisen from a common ancestor, a semiaquatic *Archihormogaster* (Fig. 3). The two taxa could indeed be the same age as the Diporodrilinae, another lumbricid subfamily, endemic of Corsica and Gallura (northeastern Sardinia) (cf. Rota, 1992). As mentioned above, the molecular divergence of three cryptic species of the complex *Hormogaster pretiosa* living in Iglesiente (southwestern Sardinia), Catalonia and the southeastern coast of France suggests that the split of the parent population took place 24-30 Myr ago (Cobolli et al., 1992). It follows that the time of the phylogenetic split of Hormogastridae and Spermophorodrilinae must be more than twice that and extend back to the beginning of Cenozoic, if not to the end of Mesozoic (65 Myr ago).

Of the two genera of Spermophorodrilinae, *Spermophorodrilus* Bouché, 1975 (Fig. 4) inhabits northern Greece, Albany, Macedonia, southern Bulgaria

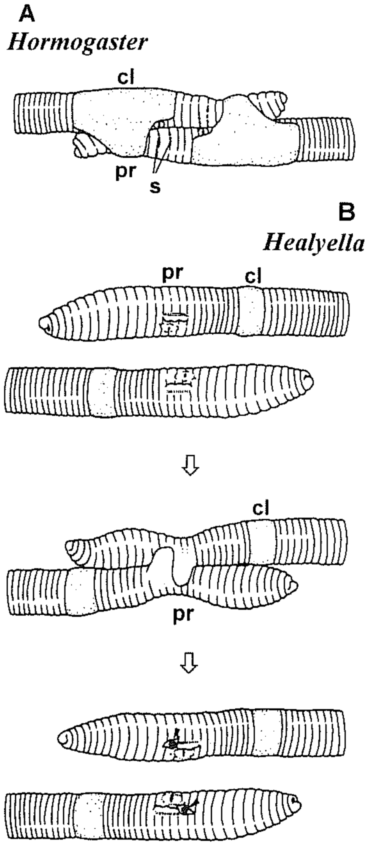

Fig. 2 - Clitellum (cl), erectile pubertal ridges (pr) and mating modalities in the Hormogastridae (*Hormogaster*) and Spermophorodrilinae (*Healyella*). Note that in *Hormogaster* the clitellum is long and connected to the pubertal ridges, whereas in *Healyella* the clitellum is short and cylindrical and the pubertal ridges are confined above the male openings. s: spermathecal pores.

[*S. antiquus* (Cernosvitov, 1938)], as well as northern Anatolia (*S. vignai* and *S. simsoni* Omodeo and Rota, 1989). The genus *Healyella* Omodeo and Rota, 1989 is instead distributed throughout Anatolia, in Syria, Lebanon, Israel and Iran. In all probability, the distribution centre of *Healyella* was also a center for the whole subfamily and was located in the central part of northern Anatolia, as seven of the *Healyella* species are concentrated there and only *H. syriaca* (Rosa, 1893) inhabits the other areas (Fig. 5). It is worth noting that the sole member of Spermophorodrilinae inhabiting the Balkan peninsula, *S. antiquus*, lacks some plesiomorphic characteristics that are typical of the other species.

A comparative examination confirms the old age of the lineage leading to the Spermophorodrilinae. The subfamily includes: (1) two large-sized geophagous species, *H. syriaca* and *H. schweigeri* (Zicsi, 1981), which fill a niche similar to that of the Hormogastridae of Sardinia, Catalonia and Provence; (2) a few middle-sized geophagous species [*H. zapparolii* Omodeo and Rota, 1989, *H. boluana* Omodeo and Rota, 1989, *H. michaelseni* Omodeo and Rota, 1989, *H. kosswigi* (Omodeo, 1952), *S. simsoni* and *S. vignai*] which in the European countries have their ecological analogs in *Nicodrilus caliginosus* and *Lumbricus terrestris* Linnaeus, 1758; and (3) *H. naja* Omodeo and Rota, 1989 and *H. mariae* Omodeo and Rota, 1989, two litter-dwelling species of small or even minute body size (*H. naja* is at most 22 mm long). Such an adaptive radiation (Fig. 6) implies that these animals had both sufficient time and the opportunities to develop the adaptations for fitting into a variety of presumably empty niches.

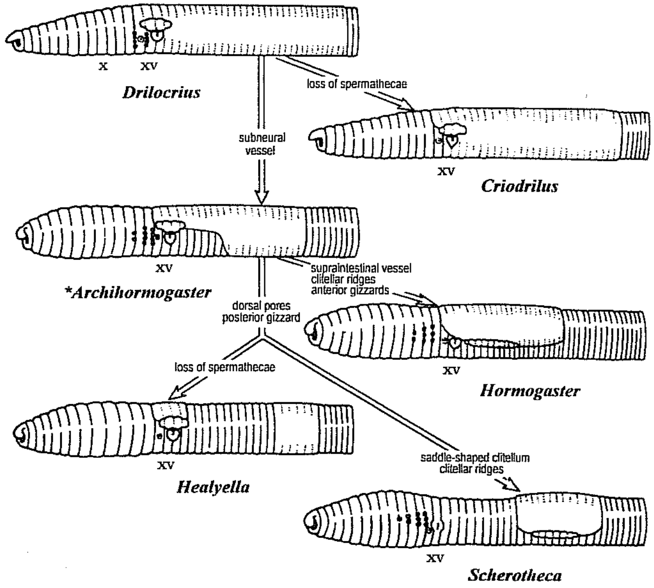

Fig. 3 - Phylogeny of aquatic and terrestrial Lumbricoidea according to Rota and Omodeo (1992).

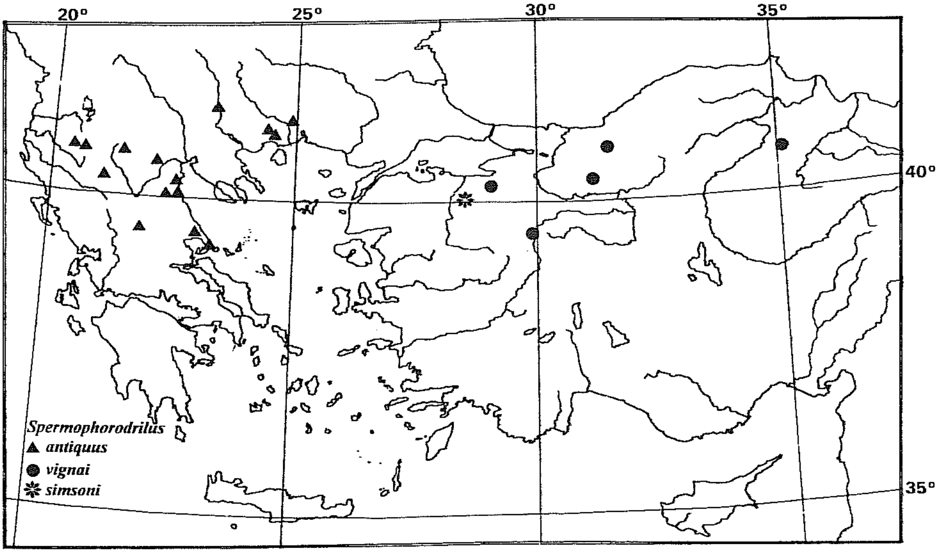

Fig. 4 - Records of *Spermophorodrilus* species.

EOPHILA, CERNOSVITOVIA AND *FITZINGERIA*

In chronological order, the lumbricid genera *Eophila* Rosa, 1894, *Cernosvitovia* Omodeo, 1956 and *Fitzingeria* Zicsi, 1978 seem to have made their appearance in Turkey after the Spermophorodrilinae.

Like the related genus *Scherotheca* Bouché, 1972, *Eophila* comprises an array of palaeoendemic species, with small, sometimes very restricted distribution areas (Fig. 7), ranging linearly from the Pyreneés to the central part of southern Siberia. The name of the genus was coined by Rosa (1894) precisely to indicate the propensity of its species for the eastern countries. *Eophila* is a much debated genus that other authors tend to split into as many genera as the species assigned to it. The reason for this is that its species, by remaining isolated for a considerable time, have often remarkably diverged. However, we believe it convenient to maintain the genus, and at most to identify some subgenera or species groups, not to lose the overall picture.

Eophila cavazzutii Omodeo, 1988 lives in northeastern Turkey (vilayet Trabzon) and comprises two subspecies, one associated with woodland habitats (*E. c. cavazzutii*), the other with mountain pastures (*E. c. pascuorum*). Their overall range of distribution is about the size of Cyprus, a rather small area for a lumbricid species. *Eophila grandis* (Michaelsen, 1907), another polytypic species, occurs in Turkey further east, from the southern foot of the Caucasus to nearly as far as Lake Van. It was recorded by us during the 1987 expedition, in the Artvin and Kars vilayets. The subspecies *E. g. ebneri* (Michaelsen, 1914), possibly deserving species rank, inhabits southern Greece (Fig. 7).

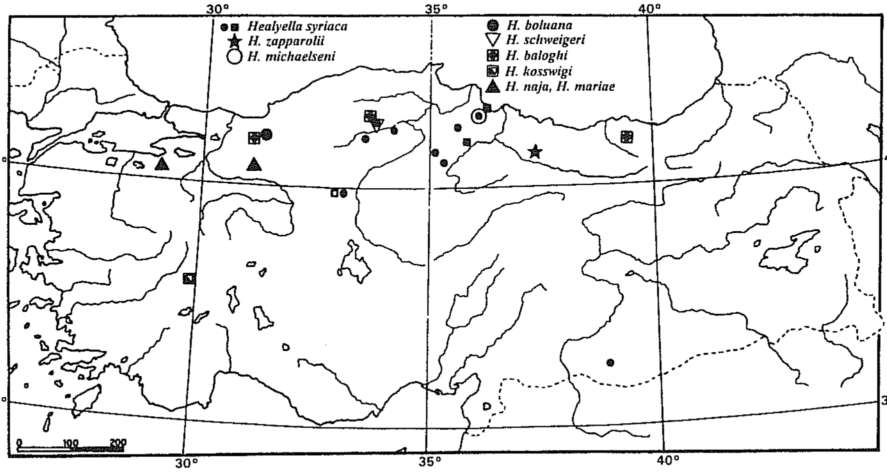

Fig. 5 - Records in Turkey of *Healyella* species.

Cernosvitovia is a genus with archaic features: the male pores are located in the region of the clitellar bands, and the spermathecae, whose size decreases anteriorly or posteriorly, are located at least partly in postgonadic segments. Eight species are endemic to the Balkans, one species inhabits western Spain (*C. bertae* Diaz Cosin, Mato and Mascato, 1985) but was possibly introduced from Romania, and a last species, *C. schweigeri* (Zicsi, 1973), is endemic to northwestern Turkey and has been recorded so far only from two localities south of the Marmara Sea (Fig. 8).

Fitzingeria is another genus with Carpatho-Balkan distribution. It is well characterized and includes four species, of which one, *F. loeblii* Zicsi, 1985, has been described from a locality south of the Marmara Sea (Fig. 8).

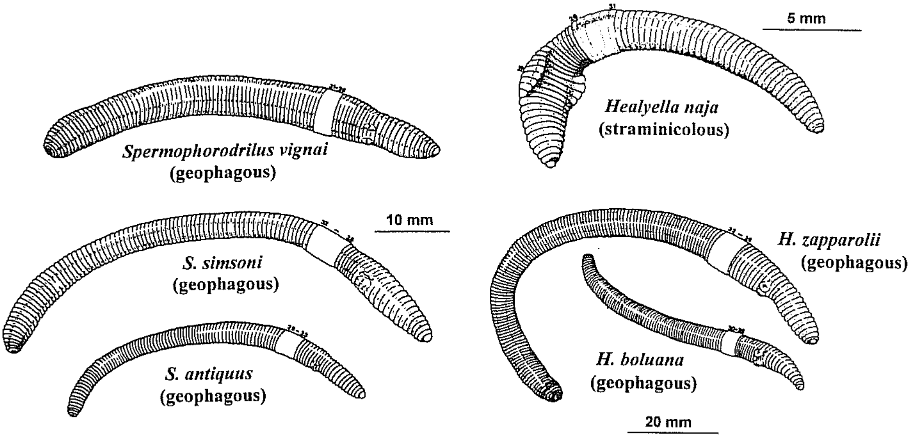

Fig. 6 - Facies and ecological roles of six species of Spermophorodrilinae.

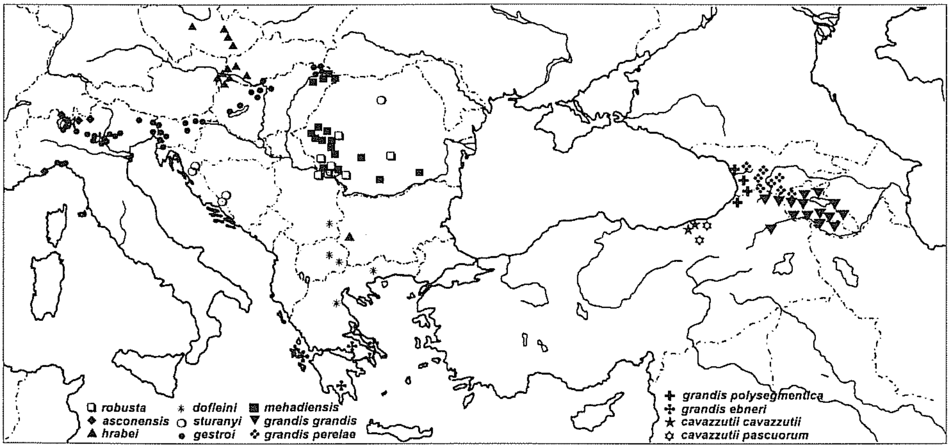

Fig. 7 - Geographical distribution of some *Eophila* s. l. species and subspecies.

The fact that two Carpatho-Balkan genera occur in nothwestern Anatolia would not be so remarkable, except that the species dwelling in Anatolia are endemic and exclusive to Turkey: these constitute further examples of an ancient Balkan earthworm taxon infiltrating into northwestern Anatolia.

THE MODERN FAUNA

Among the taxa possessing modern traits, the genus *Allolobophora* Eisen, 1873 probably represents one of the more recent acquisitions of the Turkish fauna. Unfortunately, the taxonomy of this genus still awaits clarification, so it is convenient to specify that in the present work we adopt the generic definition and classification of species proposed by Bouché (1972) for *Allolobophora* + *Allolobophora* sensu lato.

Allolobophora dubiosa Örley, 1881 is a member of the group of semiaquatic 'green earthworms' inhabiting Maghreb, the southern part of the Iberian peninsula and the Macaronesian islands. The distribution area of *A. dubiosa* corresponds largely to those of the genera *Cernosvitovia* and *Fitzingeria*, as it involves the Carpatho-Balkan region and some territories northeast of Ankara (Fig. 9a); *A. dubiosa*, however, is also found in Moldavia and Transcaucasia (Perel, 1979). Thus, the 'green earthworm' group can be classified as 'escatomediterranean' (cf. Zilli, 1998).

Allolobophora leoni Michaelsen, 1891, *A. smaragdina* Rosa, 1892 and *A. bellicosa* (Ude, 1922) belong to a different taxonomic group than *A. dubiosa* and are terricolous species. Their distribution areas overlap with that of *A. dubiosa*, but the former two species extend further west and southeast: *A. leoni* reaches the hills and plains of northeastern Italy and the coast and mountains of northern Anatolia, as far as Samsun, while *A. smaragdina* occurs through the Alpine Arc (except for a gap in the central Alps), the northern part of the Balkan region and northern Turkey up to the slopes of Caucasus (Fig. 9b,c). In the eastern part of the range these worms do not show the green body colour their specific name refers to; the same was observed for some specimens from Montenegro and Bosnia (Mrsic, 1991). *Allolobophora bellicosa* is a rare species known from only three localities, one in Hungary, one in Macedonia and one in central Anatolia (Fig. 9b).

Let us speak now of the genus *Dendrobaena* Eisen, 1874. With about 60 species described to date, this is the most speciose genus in the family Lumbricidae and also constitutes the dominant faunal component of the Turkish earthworms. Among the 22 species recorded in the country, some are very abundant, to the point that at many sites they formed the bulk of the collection: *e.g.*, *D. veneta* (Rosa, 1886), *D. hortensis* (Michaelsen, 1890) and *D. pentheri* Rosa, 1905.

As observed for the Spermophorodrilinae, the Turkish stock of *Dendrobaena* also shows evidence of an adaptive radiation (Fig. 10). While in other countries species of this genus are typically associated with decaying logs, wood and leaf litter (the name *Dendrobaena* refers to the association with a woodland habitat) and manure heaps, in Turkey geophagous species are found in the deeper soil layers, even in cultivated land. Among these, *D. pentheri*, *D. nivalis* Omodeo and Rota, 1989, *D. bruna* Omodeo and Rota, 1989 and *D. kurashvilii* Kvavadze, 1971 have anatomical adaptations for digging in compact soil, adaptations that are not observed in species living outside Turkey and the Caucasus. The adaptive radiation also led to the evolution of three small-sized species: *D. perula* Omodeo and Rota,

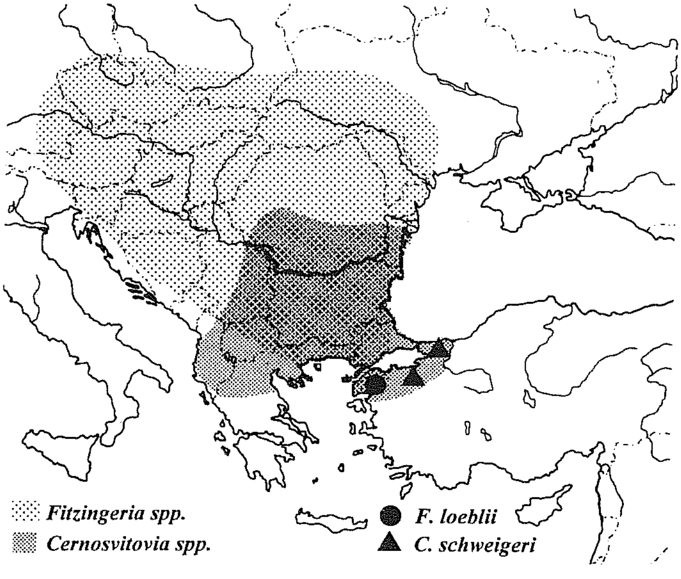

Fig. 8 - Geographical range of two Carpatho-Balkan genera of Lumbricidae (*Cernosvitovia* also occurs in Spain; see text).

1989, *D. fridericae* Omodeo and Rota, 1989 and *D. pantaleonis* (Chinaglia, 1913): the former two, only known from Turkey, have an unusual chaetal arrangement, unique for the family (Fig. 10). The third species lives also on many islands of central Mediterranean and on Cyprus; in Turkey it is amphigonic, elsewhere it is parthenogenetic (pentaploid or subhexaploid) and straminicolous. In Turkey, *D. pantaleonis euytpica* and *D. fridericae* have been collected under moss.

The genus *Dendrobaena* apparently had three distant centres of diffusion. The major centre involved Turkey and Transcaucasia; two other less important extensions occupied the Carpatho-Balkan and the Franco-Iberian regions. The most widespread species seem to have stemmed from the major centre: *e.g.*, *D. veneta* and *D. hortensis*, which reach the British Isles; *D. attemsi* (Michaelsen, 1902), which stretches as far northwards as Scandinavia (Rota and Erséus, 1997) (Fig. 11); and the circum-Mediterranean *D. byblica* (Rosa, 1893).

THE ABSENTEES AND COMPARISON WITH THE TURANIC FAUNA

Before drawing any conclusions, it is important to mention the absentees. The genus *Octodrilus* Omodeo, 1956, which comprises about 50 species living in the Carpatho-Balkan-Alpine region and also two species living in the Italian Apennines and another two in Tunisia and Algeria, is underrepresented in Turkey. Of this genus only the circum-Mediterranean *O. complanatus* (Dugès, 1828) and *O. transpadanus* (Rosa, 1884) have been found in Anatolia, where they are typically restricted to the humid meadows. An analogous situation is that of the genus *Lumbricus* Linnaeus, 1758, which comprises many widespread species with Palaearctic or Holarctic distribution, but is represented in Turkey by the sole *L. rubellus* Hoffmeister, 1843.

At the specific level, the major absentees are the Holarctic *Octolasion cyaneum* (Savigny, 1826) and *Allobophoridella (=Bimastos) eiseni* (Levinsen, 1884), as well as *Allolobophora chlorotica* (Savigny, 1826), all widely distributed through the Palaearctic. Noteworthy is also the absence of *Dendrobaena octaedra* (Savigny, 1826), which is reported from throughout Europe and eastern Siberia up to Greenland and Novaja Zemlja, but comes to a sudden stop in the Alps and Caucasus, being lacking in Italy (Alpine regions excepted), Greece and Turkey (Fig. 12). For this species, it is possible that the area of origin was in France, where the diploid amphigonic strains are still recovered; populations of this species living elsewhere are hexaploid and parthenogenetic apomictic (Omodeo, 1952c, 1955b).

It must be noted that all the specific absences reported for Turkey are shared by Sardinia, and the genera *Octodrilus*, *Octolasion* and *Lumbricus*, poorly represented in Turkey, are completely missing on this island (cf. Omodeo, 1954, 1984). This fact can be useful for dating the faunal components.

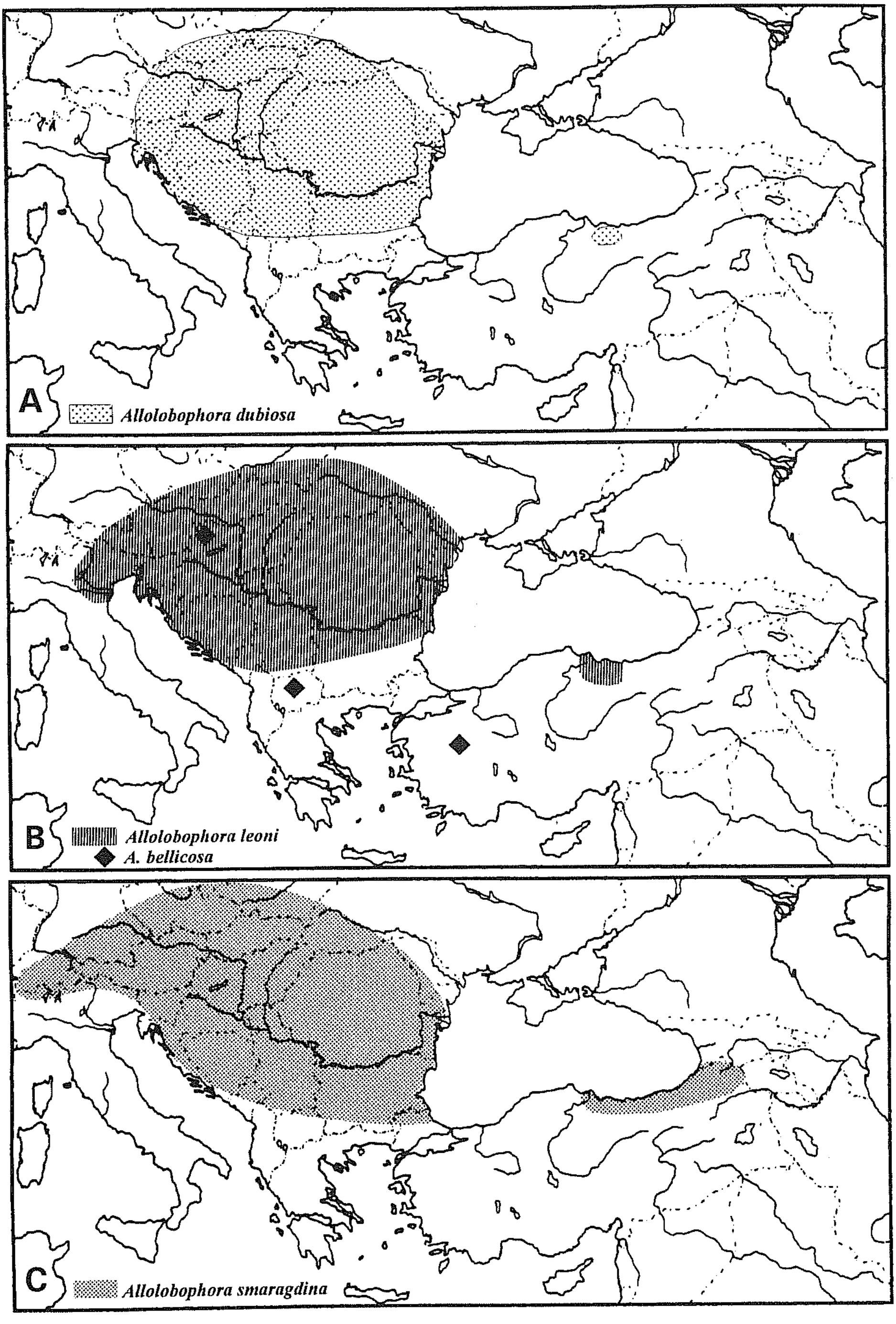

Fig. 9 - Geographical ranges of four *Allolobophora* species which have penetrated into northern Anatolia.

Regarding the relationships between the Turkish and the Turanic fauna, the affinities only concern widely distributed Lumbricinae (*e.g.*, *Dendrobaena veneta, D. hortensis, D. byblica, Allolobophora jassyensis* Michaelsen, 1891) and *Healyella syriaca*, the latter stretching into Iran presumably along the valley of Euphrates (Fig. 13). *Dendrobaena schmidti* (Michaelsen, 1907) s.l., which occurs on the northern shores of the Black Sea and through the Caucasus, and the widespread Palaearctic *D. octaedra* are present in Iran (Omrani, 1973) but absent in Turkey. For the latter species, the route of migration probably curved north of the Caspian Sea and did not cross the Caucasus. The same can be suggested for *Allolobophora kaznakovi* (Michaelsen, 1910) and *A. sotschiensis* (Michaelsen, 1902), also present in Iran and in Transcaucasian territories but absent in Turkey. Peculiar as well is the absence in Turkey of the semiaquatic species *Helodrilus patriarchalis* Rosa, 1893 which occurs in northeastern Italy, Greece, Palestine, Israel, Syria, Iran, Transcaucasia, and the

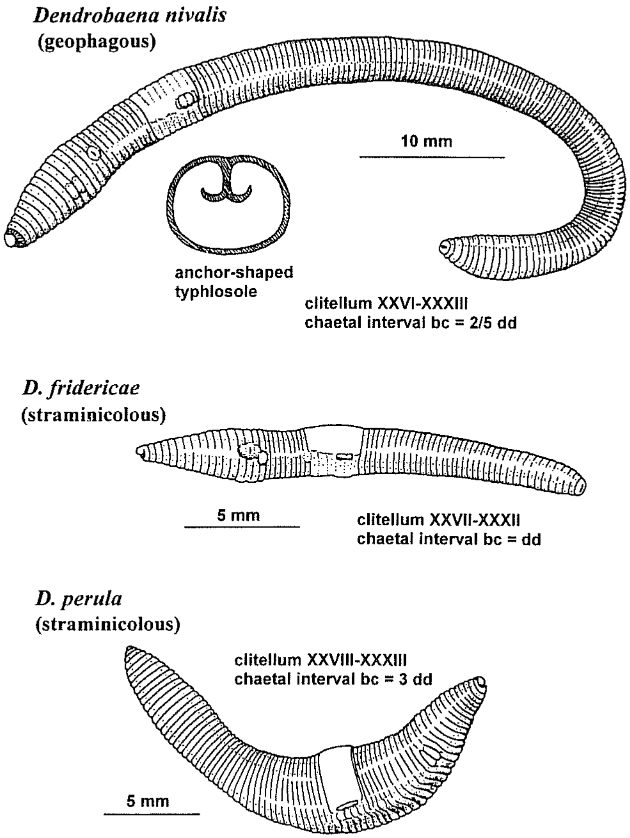

Fig. 10 - Facies and ecological roles of three *Dendrobaena* species endemic to Turkey. Note that geophagous representatives in this genus are only known from lands bordering the Black Sea.

northern shore of the Black Sea. Finally, *Eisenia parva* (Eisen, 1874) is a southern species frequently encountered at the foot of Himalayas, in Iran, the Carpathians and across North Africa, but still unknown from Turkey.

CONCLUSIONS

The occurrence of an endemic subfamily (the Spermophorodrilinae) showing evidence of an evolutionary radiation supports the view that the Turkish earthworm fauna had very ancient origins, more or less contemporary to those of the Franco-Iberian fauna, but largely independent from it. The situation seems to parallel the composition of the Sardo-Corsican fauna, which comprises an indigenous subfamily (the Diporodrilinae) and a stock from the Alboran plate represented by *Hormogaster* and some Lumbricinae (*Prosellodrilus*, *Eophila*).

The Anatolian plate, formerly a piece of Gondwana, does not harbour any oligochaete taxon of Gondwanian affinities (peregrine species excluded). That agrees with geological data which suggest that some portions of this plate had emerged above the sea level during the Jurassic (Zonenshain and Le Pichon, 1986; Dercourt et al., 1986). The northern part of present-day Anatolia, *i.e.*, the western and eastern Pontides, which is the most interesting from the biogeographical point of view, seems to have established at least temporary land

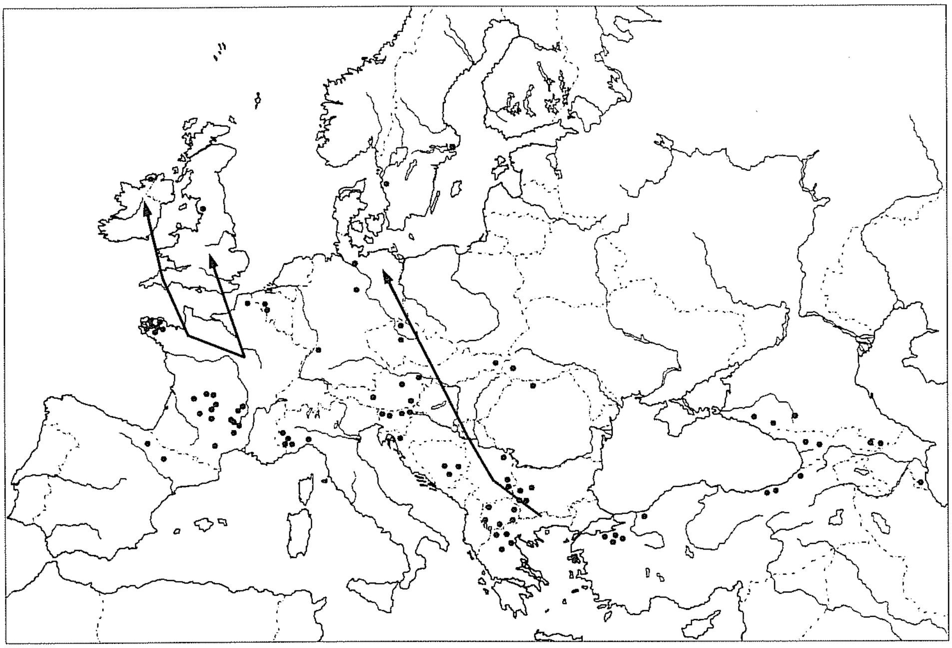

Fig. 11 - Geographical range of *Dendrobaena attemsi* showing some possible postglacial migratory routes.

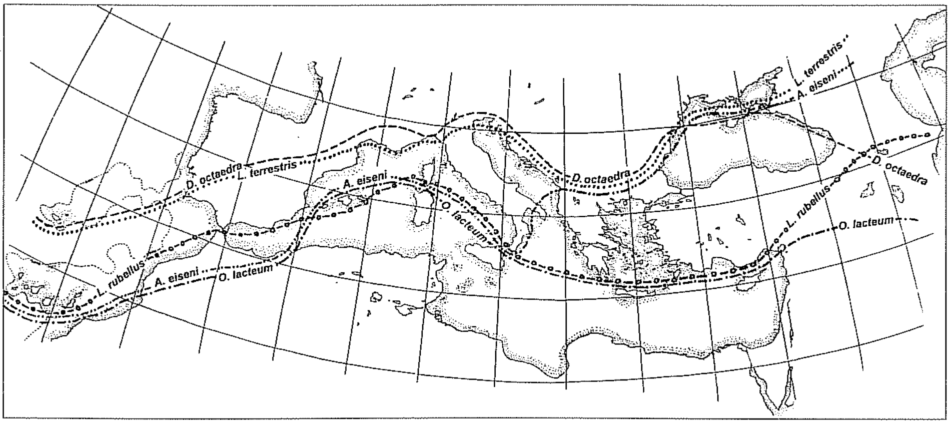

Fig. 12 - Southern limits of distribution of *Dendrobaena octaedra, Lumbricus terrestris, L. rubellus, Allolobophoridella* (= *Bimastos*) *eiseni* and *Octolasion lacteum*.

connections with the Rhodopean and Apulian plates since the Cretaceous (Alvarez-Ramiz et al., 1981). It is from this westerly route, when the country was in a semi-insular condition, that Turkey received the ancestors of its autochthonus lumbricid fauna (Fig. 14).

The large endemic stock of *Dendrobaena*, which also shows signs of an adaptive radiation, arrived during the Palaeogene, a time when the merging of the Anatolian plate with the Rhodopean plate became complete (Rögl and Steininger, 1983) and Europe and Asia were separated by the Turgai Strait. This must have been an important phase for the evolution of the old lumbricid faunas of the Palaearctic, as the fauna to the east of the Ural Mountains is much poorer than that to the west and poorer than the Turanic fauna, too.

The excellent palaeogeographical scenarios provided by Rögl and Steininger (1983) show that from the Oligocene onwards Turkey remained connected to the Balkans, the Dinaric system and the Alps, except for a break during the middle Miocene. Such a situation suggests that the typical Anatolian-Carpatho-Illyric-Alpine distribution patterns arose in the Chattian (ca. 30 Myr ago), or in a somewhat later period. Because the western and eastern populations of *Dendrobaena alpina* show a more marked (subspecific) differentiation than the respective populations of *Allolobophora smaragdina*, for the former species separation must have started earlier.

In the lower Miocene, the Carpathians became connected to more southerly territories. This may explain the infiltration of the genera *Cernosvitovia* and *Fitzingeria* and of *Allolobophora dubiosa* to the south of the Marmara Sea, whereas the bulk of the genus *Octodrilus* (whose overall distribution ranged from the Alps to the Carpathians) would not have had enough time to stretch into Rhodope or Anatolia, because during the middle Miocene these regions were separated from the mainland by a wide transgression involving present-day Tracia and Macedonia.

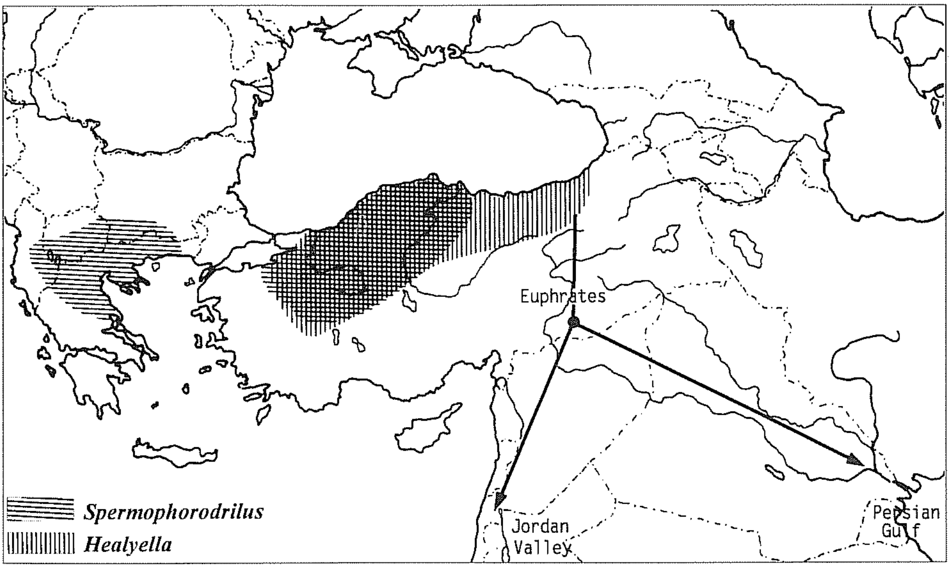

Fig. 13 - Geographical range of the Spermophorodrilinae. Only *Healyella syriaca* has expanded its area, presumably along the Euphrates valley, to reach the Persian Gulf and the valley of Jordan.

It is very likely that the final setup of the Turkish megadrile fauna took place at the end of Miocene, when the fall of sea level facilitated the connections among the countries bordering the Mediterranean and made possible faunal exchanges between the Caucasus (formerly isolated) and Armenia.

During the Messinian salinity crisis, however, not all routes across the emerged sea bottom were transitable by animals, particularly by those that do not tolerate

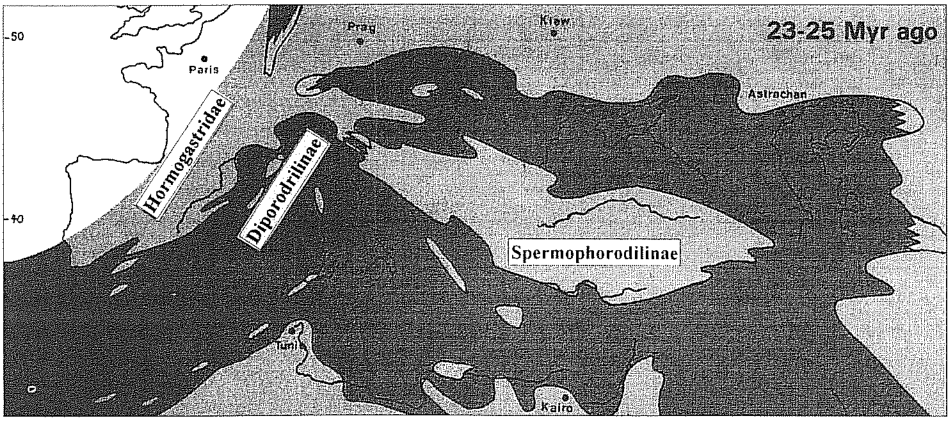

Fig. 14 - Present location of three higher taxa of Lumbricoidea endemic to the Mediterranean region projected on an upper Oligocene map (acc. to Rögl and Steininger, 1983).

arid and salty substrates. This notwithstanding, the parthenogenetic strains of *Dendrobaena byblica*, a species inhabiting the Caucasus, Armenia and the Near East, succeeded in reaching Sicily, Sardinia, Corsica, the Pyrenées and Maghreb. Likewise, the parthenogenetic strains of *D. pantaleonis* from northeastern Turkey colonized all the mentioned islands plus those of the Tuscan archipelago and Cyprus, the only continental record being on the coast of Tuscany in a 'fossil island' (Argentario Promontory; Omodeo, unpublished).

One unchanged conclusion with respect to previous studies (Omodeo, 1952a, 1961) is that the present state of the Turkish earthworm fauna is strictly linked to the geological events of Miocene. Moreover, in spite of the abundant new collections, the southern limits of many Holarctic and Palaearctic species appear confirmed (with only *Allolobophoridella eiseni* occurring in Maghreb; Omodeo and Martinucci, 1987), corroborating the view that there must have been a strong opposition to their migration southwards (Fig. 12). The factors determining some disjunct ranges such as that of *Helodrilus patriarchalis*, involving the Near East, the Balkans and northeastern Italy, still need to be understood.

The first extensive study of the enchytraeids of Turkey (Rota, 1994a), as well as furnishing a preliminary view of the fauna (27 species and 2 subspecies recorded, all but *Enchytraeus buchholzi* Vejdovský 1878 s.l. new for the country), has revealed a clear differentiation between the northern (Pontic) and southern (Mediterranean) portions of the Anatolian peninsula. Owing to the lack of investigations in the neighbouring countries, any comment on the origin of the Turkish enchytraeid fauna appears premature. The majority of the species, including several European species, are concentrated in the north, particularly in the area of Ulu Dag (where 60% of the species were recorded). This may be not merely a result of a higher climatic and edaphic variety in the northern zone but also due to a better preservation of habitats, only a few strictly Mediterranean species (*e.g.*, *Fridericia caprensis* Bell, 1947) being adapted to thrive in the poor soils of the south.

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