Earthworm Diversity and Land Evolution in Three Mediterranean Districts

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The collection and description of terrestrial oligochaetes in the Mediterranean began during Napoleon's campaign to Egypt. Many other collections were made during the 1800s, so that at the turn of the century it was already possible to draw a faunistic picture and make biogeographic considerations on this animal group. However, more methodical and focused investigations were needed to identify boundaries and gaps in the distribution patterns. Thus, starting in 1980, a number of expeditions to the countries bordering the Mediterranean took place in the framework of a joint faunistic program by the Universities of Padua, Catania, Siena, Rome "La Sapienza", and Rome "Tor Vergata". In this paper we report on the Oligochaeta Megadrili and Enchytraeidae collected by the authors and coworkers in Maghreb, Anatolia and the Sardo-Corsican system. We then discuss the biogeographical hypotheses that emerge from the elaboration of the gathered material.

Concerning the fauna of Maghreb, little was known prior to our collections. The fauna of this vast and ecologically varied territory has turned out to be rather poor and largely derived from the fauna inhabiting the Betico-Rifan region plus elements of Balkan origin.

Knowledge of the Anatolian megadrile fauna was much better but still limited. Our extensive surveys have revealed that this large peninsula harbours a rich autochthonous fauna comprised of the subfamily Spermophorodrilinae, with ten species exclusive to Turkey, and fourteen endemic species of *Dendrobaena*, some of which may have originated by adaptive radiation. During the Pleistocene, other species of megadriles arrived in Anatolia from the Balkan Peninsula, but they remained confined to the northern coastal zone.

The Sardo-Corsican fauna was already well documented, but its complexity has been appreciated only after careful research in Gallura, the northeastern corner of Sardinia, where the endemicity rate is high and the faunistic connections with Corsica and the Tuscan archipelago are evident. But this is only a part of the story. The autochthonous fauna of the Sardo-Corsican system originates with certainty from Catalonia and, to a lesser extent, from Provence. This peculiarity fits the palaeogeographical reconstructions proposed by geologists, starting with Alvarez and coworkers: the Sardo-Corsican system, formerly part of the European foreland and contiguous to the Pyrenees, became an independent microplate in the late Oligocene, which drifted until it reached the present position, carrying on itself a sample of Palaeogene fauna. At some later stage, a land bridge connected Provence with Corsica and, thus, indirectly with Sardinia. Other massive faunal exchanges must have occurred during the Messinian salinity crisis and the sea level regression caused by the Pleistocene Ice Age, when Corsica and Sardinia were connected to other districts of the central Mediterraean.

1. Exploration and Descriptive Work

1.1. Historical Collections

The first collection of earthworms in a Mediterranean country was carried out in Egypt by M. Jules César Savigny (1777–1851), a young French naturalist accompanying Napoleon's Egyptian campaign of 1798–1802. Subsequent early collections were made mainly by gentlemen fond of natural history and exploration, who travelled on behalf of scientific museums: Henri Gadeau de Kerville (1858–1940) collected specimens in the Near East and in Maghreb; Dr. Enrico Festa (1868–1939) collected in Anatolia and Sardinia (as well as in South America and the Far East); Fritz Haas (1886–1969) collected in Spain, France and the Pyrenees; Marquis Saverio Patrizi (1902–1957) explored the caves of Sardinia and Africa; and Dr. Knut Lindberg (1892–1962) from Lund collected in Greece, Anatolia, and Afghanistan, also mainly in caves. Naturalists and curators of Vienna Hofmuseum, such as Emil von Marenzeller (1845–1918), Ludwig Ganglbauer (1856–1912), and Arnold Penther (1865–1931), collected interesting material in Veneto, Dalmatia, and Turkey.

Many zoologists, specialists in Oligochaeta, collected material in the surroundings of their own institutions, or entrusted correspondents or friends with the task of digging out specimens during their field trips. Wilhelm Michaelsen (1860–1937), director of the Zoological Institute and Museum in Hamburg, obtained rich oligochaete material from scientific expeditions from all around the world and also through the efforts of navy officers calling at that important Hanseatic port. Kurt Kosswig (1903–1982), who succeeded Michaelsen in the chair and as director of the Hamburg Museum, had himself assembled an earthworm collection while in exile in Turkey.

However, around the middle of the 20th century, the inadequacy of the collecting made in the Mediterranean became evident, especially in the light of the synopses compiled on the earthworm faunas of northern and central European countries (Cernosvitov 1935; Cernosvitov and Evans 1947; Pop 1948; Julin 1949; Graff 1953; Stöp-Bowitz 1969; Perel 1979). Particularly informative and influential was the monograph by Bouché (1972) on the *Lombriciens de France*, a work that revealed an unsuspected species richness in the Pyrenean departments and contained a useful systematic revision of the western European megadriles.

1.2. Recent Collections

Owing to their physiological aptitudes, ecological constraints, and limited dispersal capability (individuals cannot move actively over long distances), earthworm populations tend to remain in the same places during very long periods of time, following the destiny of their habitat and geographic area. Moreover, because genetic evolutionary changes occur very slowly in earthworms, events of allopatric speciation must require a time scale measured by millions of years (see Cobolli et al. 1992; Omodeo 2000), i.e., the same time scale of geological events. Thus the history of an earthworm species can be correlated with the geological transformation of its geographic range. Such a correlation was noticed and exploited in biogeographical studies since long ago: for instance, Michaelsen (1902, 1903) interpreted the absence or presence of endemic lumbricid species at various latitudes with the extension of the ice sheets covering part of Europe and Asia during the last glaciation. Cernosvitov (1932a, b, 1935) followed the same trail to explain the distribution patterns of Czech lumbricids. Michaelsen (1922) and Cernosvitov (1936) were also the first to adopt Wegener's theory of continental drift to reconstruct the phylogeny and explain some geographical patterns of oligochaetes, with hypotheses that seemed heretical at the time (see Benham 1922). In the longer run, Omodeo (1952) linked the present distribution of some southern

European species to the Miocene palaeogeography of the Aegean region, and adopted Michaelsen's views in interpreting the amphiatlantic distribution of some megadrile genera (Omodeo 1954, 1963, 2000).

That considered, and stimulated by the available faunistic evidence and the novelties emerging from the geological surveying of the Mediterranean basin (Alvarez et al. 1974), in the late 1970s a research program was launched by the senior author (P.O.) in Padua to methodically prospect the terrestrial oligochaete fauna of the Mediterranean countries and gain some insight into its origins and evolution.

1.3. The Program

The program, coordinated with similar research programs by other Universities focusing on different animal groups, was approved and soberly financed by the Italian National Research Council and the Ministry for the University and Scientific Research. The sampling of terrestrial oligochaetes started in May 1980 in Sardinia and, within the span of twenty years, covered territories from the Iberian Peninsula and Morocco to Anatolia and the Levant, but it was in fact in the Sardo-Corsican system that the efforts were concentrated, as these islands showed many interesting peculiarities. The visits to Sardinia and adjacent lesser islands implied some logistic difficulties, which were overcome thanks to the aid from colleagues working at Sardinian Universities and the backup to the senior author by the CNR oceanographic vessel *Minerva*. In the period 1980–1999, the archipelago was visited 12 times and about 5000 specimens were collected.

In all five expeditions to Maghreb, the major organizing work was carried out by the Zoology Department of Catania University and, to a lesser extent, by the Biology Departments of Padua and Siena Universities. The teams always travelled by off-road vehicles equipped with roof top tents, which made it possible to venture into remote or uninhabited regions such as the semidesert basin of Hodna and the Djurdjura Massif in Algeria. A total of 135 collecting sites were visited and several groups of arthropods and other invertebrates were collected, including 4900 megadrile specimens. The latter were preserved in ethanol or in liquid nitrogen or kept alive according to the planned studies. During the 1989 expedition, a survey of the terrestrial Enchytraeidae of Tunisia and Algeria was also performed. Additional 1500 oligochaete specimens were sampled and studied by Mounia Baha, a Ph.D. student of the Ecole Normale Supérieure d'Algiers; this material included three new records for Algeria and one species new to science.

The two journeys to Turkey were organized in 1987 and 1990 within the frame "Zoological Researches in the Near East by La Sapienza and Tor Vergata Universities of Rome" and represented the first extensive surveys of the Turkish drilofauna. Much information was available on the megadriles of this vast country, but no methodical study had been carried out which could reveal a general picture and the main geographic patterns of the fauna. Travelling by utility cars and minibus on a good road system and benefiting from the friendly hospitality of the Turkish people, we visited 62 localities (involving 26 vilayets), thus gathering more than 3000 oligochaete specimens. Additional material was obtained from colleagues and friends who visited the country to investigate other animal groups of interest.

1.4. Results of the Research Journeys to Maghreb

The Maghreb (Tunisia, Algeria and Morocco) collections yielded a total of 31 megadrile species, 18 of which were new for the territory and four new to science (Omodeo et al. 2003). The megadrile fauna of this vast and ecologically various territory is scanty in comparison with those of Spain and Italy (~ 100 species in either country). [With one exception, *Helodrilus rifensis*, all

the new taxa described from Algeria and Morocco by Qiu and Bouché (1998a, b) must be considered *species inquirendae*, because their descriptions differ in trifling details — or do not differ at all — from one another or from long known species]. Moreover, its composition changes from West to East: the Moroccan species are almost the same as those inhabiting the south of the Iberian peninsula and the Canary Islands, with the interesting exception of *Allolobophora borellii* (Cognetti, 1904) which is widespread in Morocco and western Algeria and is recorded in Spain only from the Pyrenees. The Algerian fauna lacks two species living in Morocco (*Lumbricus friendi* Cognetti, 1904 and *Helodrilus rifensis* Qiu and Bouché, 1998) but counts four endemic species, two of which surprisingly belong to an Alpine-Balkan genus, *Octodrilus kabylianus* Omodeo and Martinucci, 1987 and *O. maghrebinus* Omodeo and Martinucci, 1987; the third species, *Eisenia xylophila* Omodeo and Martinucci, 1987, also has eastern affinities, while the fourth belongs to the Pyrenean genus *Prosellodrilus* Bouché, 1972 (*P. doumandjii* Baha and Berra, 2001). On the Edough promontory and in adjacent areas lives a population of *Hormogaster redii* Rosa, 1887, possibly arrived there from Tunisia (it is found abundantly on Mt. Zaghouan) or directly from Sardinia (see below). In Tunisia, no other endemics than *O. maghrebinus* and *E. xylophila* are reported, and the *Allolobophora molleri* (Rosa, 1889) complex (= *Heraclescolex* Qiu and Bouché, 1998), so common in the mud of ouadies in Algeria and Morocco, disappears; it is replaced by a vicariant species still undescribed belonging to the *Nicodrilus* Bouché, 1972 group. The most important absentees in Maghreb are the archaic megadrile genera which form such a large part of Pyrenean and Iberian fauna: *Orodrilus* Bouché, 1972*, Scherotheca* Bouché, 1972*, Postandrilus* Qiu and Bouché, 1998 and *Ethnodrilus* Bouché, 1972. *Prosellodrilus* is represented by only one or two localized populations (*P. doumandjii* near Algiers, *P. festai* (Rosa, 1892) near Tunis) and the family Hormogastridae is represented only by its most widespread species. The time of the arrival of *H. redii* in Tunisia has been dated by molecular clock methods (Cobolli et al. 1992) to the Messinian salinity crisis (5.33–5.96 Mya), when possibly also *Dendrobaena byblica* (Rosa, 1893), *Proctodrilus antipai* (Michaelsen, 1891) and modern type taxa such as *Allolobophoridella eiseni* (Levinsen, 1884) and *Murchieona minuscula* (Rosa, 1906) reached the west of the Mediterranean basin.

From soil samples collected in 1989 in Tunisia and Algeria, 20 species of terrestrial Enchytraeidae were also recognized, 17 of which were new for Maghreb and one new to science (Rota and Healy 1994; Rota 1995). These results, unprecedented for North Africa, were made possible by developing adequate methods and devices for collecting, field extracting and maintaining these delicate animals alive until the return to laboratory (Healy and Rota 1992). However, despite the variety of habitats explored, the species list is short compared with similar sized regions in temperate Europe and is dominated by some widespread European elements and a few strictly Mediterranean entities (*Fridericia caprensis* Bell, 1947, *F. sardorum* Cognetti, 1901, *Enchytraeus christenseni bisetosus* Rota and Healy, 1994), apparently the only taxa tolerant of the aridity of soils and the degradation of the landscape affecting most coastal Mediterranean territories.

1.5. Results of the Research Journeys to Turkey

The 1987 and 1990 Turkish megadrile collections yielded 54 species and three subspecies, of which 16 were new to science, and increased the total number of earthworms known from the country to 70 species and six subspecies (Omodeo and Rota 1989, 1991, 1999). The data collected so far document only a part of the Turkish fauna and surely much work remains to be done; these data, however, hint at a peculiar situation: the earthworm genus *Dendrobaena* Eisen, 1874, dominates, counting 23 species (one-third of the total described worldwide), of which 14 are endemic. In other faunistic regions, *Dendrobaena* is strictly an inhabitant of woody habitats, typically

dwelling in the litter and top humic layers or in decaying logs, but in Anatolia — where the genus forms the largest portion of the soil communities — it apparently experienced an adaptive radiation: some species are specialized to live in pasture soils and cultivated fields and have relatively large body size (e.g., *D. pentheri* Rosa, 1905 and *D. bruna* Omodeo and Rota, 1989), whereas others live under moss or stones and show a much reduced body size, less than an inch in length, and other unusual morphological traits (e.g., *D. perula* Omodeo and Rota, 1989 and *D. fridericae* Omodeo and Rota, 1989).

More extraordinary appears the presence in this country of two lumbricid genera attributed by Omodeo and Rota (1989) to a new subfamily, the Spermophorodrilinae. This taxon includes so far 13 species, ten of which are restricted to Turkey, thus constituting the second largest portion of the autochthonous fauna. The Spermophorodrilinae are interesting because their peculiar morphology testifies to the lumbricid kinship to the Hormogastridae, which live in the western Mediterranean. Another two species, *Eophila cavazzutii* Omodeo, 1988 and *Eisenia grandis* Michaelsen, 1907, whose generic attribution is still a matter of inquiry (see proposals by Qiu and Bouché 1998c and Kvavdze 2000, respectively), complete the list of the autochthonous earthworms.

Beside the autochthonous biota, there is evidence that Anatolia hosts several species of Balkan origin. The following taxa, instead, appear to be absent or poorly represented, even though they are well represented in the Balkan Peninsula: the whole genera *Allolobophoridella* Mršić, 1990 and *Proctodrilus* Zicsi, 1985; the genus *Lumbricus* L., 1758, *L. rubellus* Hoffmeister, 1843 excepted; the genus *Octodrilus*, which is represented by its two most common species, *O. complanatus* (Dugès, 1828) and *O. transpadanus* (Rosa, 1884).

From soil samples collected during the 1990 campaign in western Anatolia, 27 species of enchytraeids have been identified and described, all but one new for the country and three new to science (Rota 1994a). The bulk of the collection was obtained from four well-preserved forest sites on the northern massif of Ulu Dag, while at most other localities the fauna was strikingly poorer. On the basis of the present records, beside the preservation of habitats, it would seem that the climatic and edaphic differences between the Black Sea coastland and the Aegean and Mediterranean sides of the country significantly affect the richness and distribution of enchytraeid species.

1.6. Results of the Research Trips to the Sardo-Corsican Archipelago

The results of the faunistic campaigns in Maghreb and Turkey are certainly interesting, but those obtained from the prospecting of the Sardo-Corsican system are more exciting. That was not perceived at once, because early studies had revealed the existence of endemic species in these islands (e.g., Michaelsen 1903); yet, as years went by, some of those species were found also in other parts of the Mediterranean and even in central Europe and the Canary Islands, so the interest went down and only later discoveries promoted it again.

Some twenty years ago, the megadrile species reported from Sardinia could be divided into three groups: (1) seven autochthonous species belonging to archaic lineages; (2) seven species of modern type; (3) six exotic invasive species, introduced by man in the last few centuries (Omodeo 1984). By that time, it was already apparent that the autochthonous fauna of the Sardo-Corsican system was akin to the Pyrenean fauna, and that Sardinia was richer in archaic species and poorer in modern species than Corsica (Omodeo and Rota 1987). The situation became more clearcut as the ongoing collections in Sardinia and lesser islands raised the number of old autochthonous species and subspecies to 14 (Rota 1992), whereas Corsica was shown to host 8 such taxa (Qiu and Bouché 1998d, e). Furthermore, a multivariate analysis of the abundant material collected in various areas of Sardinia, Corsica, Provence and the Tuscan Archipelago (Rota 1992) revealed that Sar-

dinia is faunistically fragmented, as if constituting an archipelago in itself; the isolation of Gallura (the northeastern corner of Sardinia) appeared particularly dramatic, as testified by an endemicity rate as high as 84% (the exotic peregrine species were excluded from the total), i.e. higher than for any area of similar size in the whole Palaearctic.

1.7. Analysis of the Autochthonous Fauna of the Sardo-Corsican System

The old autochthonous megadriles of the Sardo-Corsican system comprise three species of *Hormogaster* Rosa, 1887; the endemic subfamily Diporodrilinae Bouché, 1970; the endemic genus *Eumenescolex* Qiu and Bouché, 1998; some endemic species of *Scherotheca* and *Prosellodrilus*.

Earthworms of the genus *Hormogaster* are large or very large animals measuring up to 90 cm in length and weighing up to 100 g. The most remarkable aspect of their physiology is their tolerance of prolonged periods of drought thanks to a long diapause. *H. redii* combines this aptitude with an exceptionally wide ecological valence: it can inhabit sclerophyll woods, overgrazed pastures, stony lands, coarse granite sand, and even sandy beaches above the shoreline. This species, along with *Nicodrilus caliginosus* (Savigny, 1826), dominates the earthworm communities of Sardinia and lesser islands. In Corsica it is rare, occurring only on the northern tip of the island, whereas it is frequent in the eastern Tyrrhenian islands, Elba and Capraia excepted, and on the Tyrrhenian side of Italy from south of River Arno to 40°S. It appears again in Sicily and is well represented in North Africa — from Tunisia to the Edough promontory and adjacent lands of northeastern Algeria (Fig. 1). *Hormogaster pretiosa* Michael-sen, 1899 is endemic to the southwestern corner of Sardinia (Fig. 2), where it lives in damp clayey soils; the species was believed to occur in Spanish and French Catalonia as well, but

FIGURE 1. Geographical range of *Hormogaster redii*.

Cobolli et al. (1992) and Rota (1994b) have provided genetic and morphological evidence for assigning the Catalan populations to the sister species *H. hispanica* Michaelsen, 1925 and *H. gallica* Rota, 1994. *Hormogaster samnitica* Cognetti, 1914, a close relative of the *H. pretiosa* complex, is widespread in Corsica, Elba and Capraia and in the Tuscan mainland to the south of River Arno (Fig. 2). Together with *H. redii*, it also inhabits the smaller islands of the Tuscan Archipelago and the Maddalena Archipelago (NE of Sardinia), whereas in Sardinia it is restricted to the coastland of Gallura. One isolated station in the Abruzzi gave this species its name.

When first described, the endemic genus *Diporodrilus* Bouché, 1970, was allocated to a new family, the Diporodrilidae. Such classification was not accepted by other specialists, some of whom
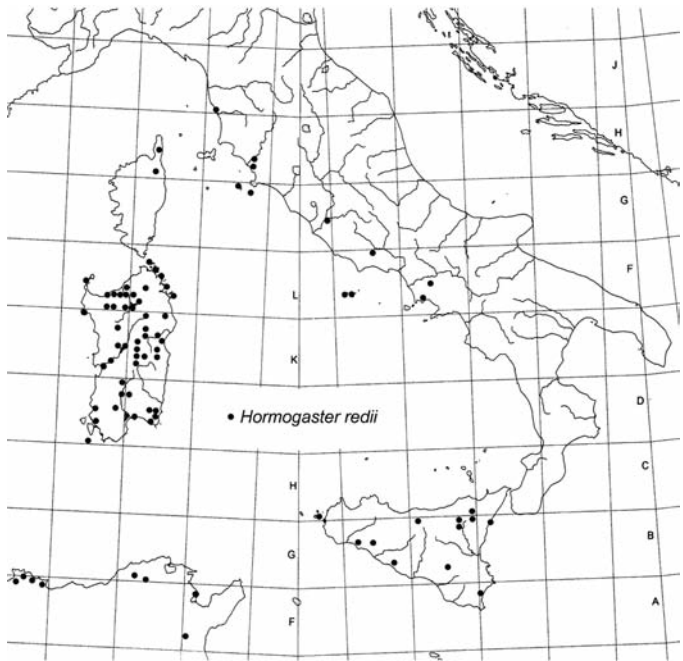
(Sims 1980; Omodeo 1984) preferred to rank the taxon as a subfamily (Diporodrilinae) within the Lumbricidae; the same criterion is adopted here, in accordance with the peculiar anatomy of these animals. *Diporodrilus* comprises four species (Fig. 3): the largest in size, *D. pilosus* Bouché, 1970, is dominant in Gallura and adjacent small islands both by biomass and by number of specimens (290 in 21 sampling stations). *Diporodrilus omodeoi* Bouché, 1970 has a smaller size and is frequent in Corsica (Bouché 1970) but absent from Sardinia, where it is replaced by *D. bouchei* Omodeo, 1984, a closely related but less frequent species (52 specimens from three stations). The fourth species, still undescribed, is known through a single specimen found along the Tirso river near Oristano.

The genus *Eumenescolex* has a conspicuously fragmentary distribution (Fig. 4), its species surviving in restricted areas of the north-western Mediterranean: *E. heideti* Qiu and Bouché, 1998 and *E. emiliae* Qiu and Bouché, 1998 are known each from one station in Corsica, the first from two specimens, the second from three specimens. *Eumenescolex gabriellae gabriellae* (Omodeo, 1984) is known through 32 specimens collected from six stations on the Gennargentu Massif, whereas *E. gabriellae gallurae* (Omodeo, 1984) through 141 specimens from stations ranging from Gallura to Sarcidano (central western Sardinia). The fourth species, *E. pereli* (Bouché, 1972), is known from 24 specimens collected at one station near St. Tropez on the Maures Massif, Provence. Qiu and Bouché (1998d) classified in *Eumenescolex* a fifth taxon, *Allolobophora corsicana simplex* Zicsi, 1981 from Central Italy, that, however, fits only partially the diagnosis of the genus.
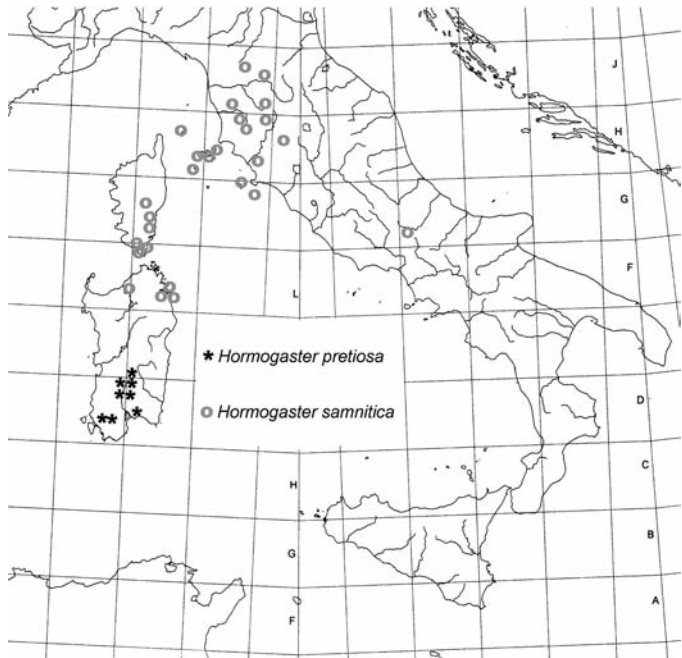

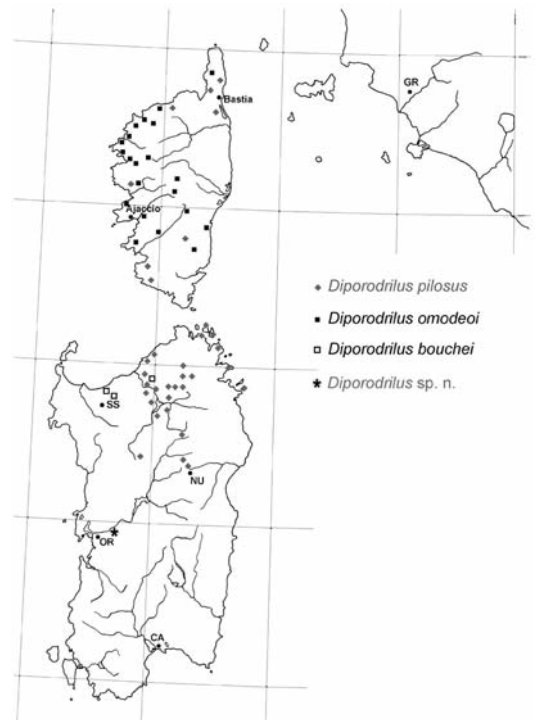FIGURE 2. Geographical range of *Hormogaster pretiosa* and *H. samnitica*.

FIGURE 3. Geographical range of the Diporodrilinae.

Prosellodrilus inhabits Catalonia and the Pyrenees, with the exception of *P. doumandjii* and *P. festai*. The latter, originally described from the neighbourhood of Tunis, was shortly afterwards recorded in Sardinia near Cagliari (Rosa 1893). Later researches showed that *P. festai*, with its four subspecies, is very common in the centre and south of the island (Fig. 5; 330 specimens from 23 stations), almost as much as *H. redii* and *N. caliginosus*. This rather small earthworm bears a superficial resemblance to *Aporrectodea rosea* (Savigny, 1826), with which it also shares the habitat (mainly pastures with trees). In Sardinia lives also another, still unnamed, *Prosellodrilus* species discovered by us at the base of Mount Sette Fratelli (in prep.).

The distribution of the genus *Scherotheca* covers a wide area, which extends from the Pyrenees through Provence to the Western Alps. Throughout Corsica the genus is represented by *S. corsicana* (Pop, 1947), which also populates the Maddalena archipelago (northeastern Sardinia), but not the Sardinian mainland (Fig. 6). Interestingly, *S. targionii* (Baldasseroni, 1906), a species strictly akin to *S. corsicana*, is common on Elba Island and also in the Tuscan Maremma (Fig. 6). In the northern tip of Corsica lives *S. dugesi brevisella* Bouché, 1972, a subspecies of a polymorphic taxon endemic to Provence and western Liguria, *S. dugesi* (Rosa, 1896) (Fig. 7).

Pietromodeona januaeargenti (Cognetti, 1903) is common in central and southern Sardinia (159 specimens from 19 stations), but is absent from the northern part of the island. In the Italian peninsula this species has been found south of 42°20'N latitude, excluding the portion of Calabria south of the Pollino Massif; it is also common on the Tremiti Islands in the Adriatic Sea (Fig. 8). *Pietromodeona januaeargenti* is a polymorphic species, but it is difficult to divide it into subspecies; thus it appears all the more wrong to divide it into many species, as some specialists — who never saw these animals — suggest (see Omodeo and Rota 2004).
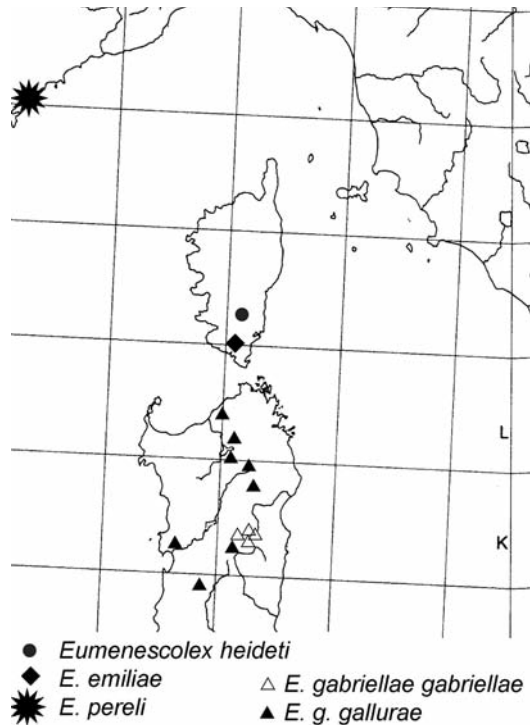

● *Eumenescolex heideti*
◆ *E. emiliae*   △ *E. gabriellae gabriellae*
✳ *E. pereli*   ▲ *E. g. gallurae*

FIGURE 4. Geographical range of *Eumenescolex* species.

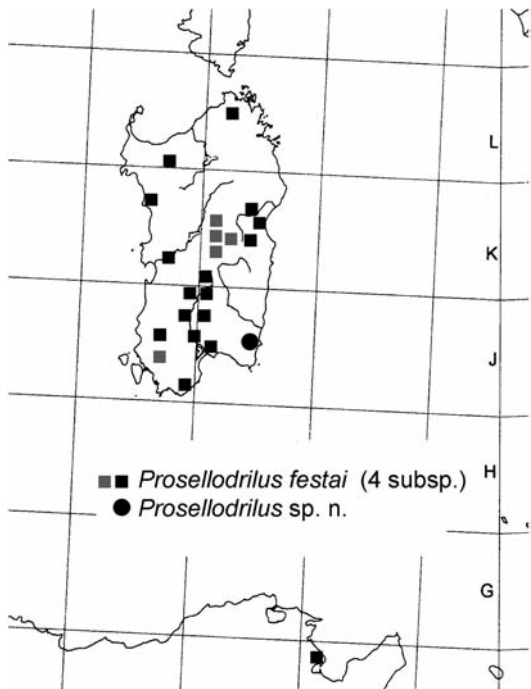■ ■ *Prosellodrilus festai* (4 subsp.)
● *Prosellodrilus* sp. n.

FIGURE 5. Geographical range of two Sardinian species of *Prosellodrilus*.

To the autochthonous fauna of Sardinia may also belong *Helodrilus massiliensis* Bartoli, 1962 and *Dendrobaena cognettii* Michaelsen, 1903. The former is an aquatic worm described from Provence and the Maritime Alps and recently found in Sardinia (unpublished data) but unknown from Corsica, an absence that should be viewed cautiously because aquatic earthworms are often overlooked (Fig. 7). The latter is a small straminicolous species belonging to the western branch of *Dendrobaena*, occurring in woods and scrublands of central and western Europe and Macharonesia. The subspecies, *D. cognettii gallurensis* Rota, 1992, is endemic of Gallura and southern Tuscany.

The absentees in Sardinia are conspicuous: the whole of the genera *Octodrilus, Octolasion* Örley, 1885, *Lumbricus, Allolobophora* Eisen, 1874 *s.s.*, *Allolobophoridella, Proctodrilus,* and *Eisenia*, all well represented on the Italian mainland, and most of the species ascribed to *Aporrectodea* and *Dendrobaena*. In Corsica, *Octolasion* and *Eisenia* are represented each by one species, and *Lumbricus* by three species. Other common genera are similarly absent.

2. ORIGINS AND HISTORY OF THE FAUNAS OF THE THREE DISTRICTS

2.1. Correlation Between the Evolution of Megadrili and the Evolution of Their Homeland

The chronology of the separation of two landmasses provided by geologists and palaeogeographers can be a useful instrument to infer the divergence times of the populations that inhabited those landmasses. In reconstructing the history of the earthworm peopling of a territory, however, it must be considered that the genetic evolutionary rate of oligochaetes is much slower than that of many other animal groups (see Omodeo 1955; Wilcke 1955). The origin of the Lumbricoidea families according to Bouché (1972:485) may be dated to the Cretaceous or before, when Europe was isolated
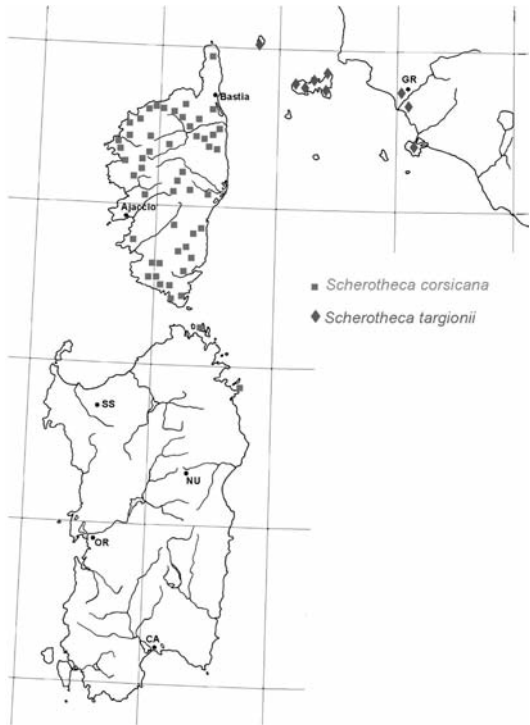

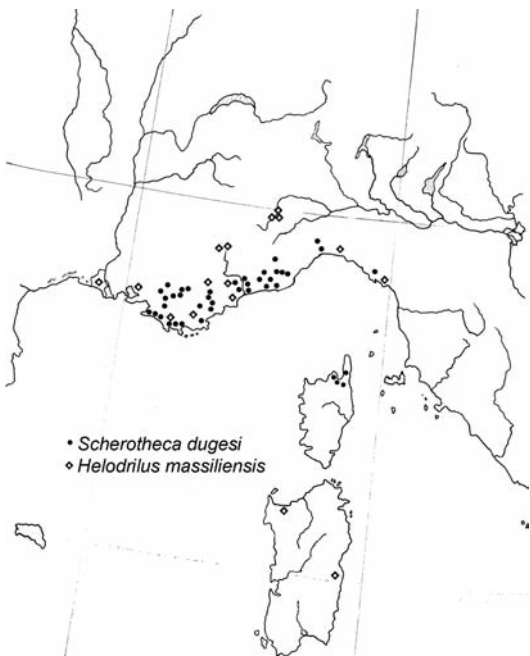FIGURE 6. Geographical range of two *Scherotheca* species.

FIGURE 7. Geographical range of *Scherotheca dugesi* and *Helodrilus massiliensis*.

from Asia by a long sea arm. An earlier date would be preferable, as the modal amount of time required for the splitting of a megadrile genus is reliably estimated at 180 Myr; such an estimate is based on the divergence timings for endemic congeneric species occurring on the two shores of the Atlantic (see Omodeo 2000). That means that most, if not all, the megadrile genera here considered were already differentiated in the early Cenozoic.

The duration of allopatric speciation for earthworms, which

FIGURE 8. Geographical range of *Pietromodeona januaeargenti*.

came to be segregated on different fragments of the West-European landmass, has been investigated in the Hormogastridae; an allozyme analysis was conducted by Cobolli et al. (1992) to assess the genetic distance between populations of the *Hormogaster pretiosa* complex living in SW Sardinia, Spanish Catalonia and Roussillon (Pyrenées Orientales), as well as to compare the divergence time of these populations with the timing of the splitting of the Sardo-Corsican system from Catalonia. One result was that the sampled populations proved to be so genetically differentiated to justify their recognition at species level: *H. pretiosa, H. hispanica* and *H. gallica* (Cobolli et al. 1992; Rota 1994b). A second result was that the divergence timing between the Sardinian and the mainland populations — recalibrated according to Sarich (1977) — was 13–17.5 Myr, a time span quite short compared with the isolation times based on geological events (the most recent calculations place the detachment of the Corsica-Sardinia microplate at 24 Mya; see Andeweg 2002). Such inconsistency with geological data could only be explained by invoking slow molecular evolution in the taxon (Cobolli et al. 1992). That study also revealed an unsuspected high genetic divergence between the Spanish and French populations (which live only 60 km apart), even higher than that between the Sardinian and the two Catalan populations. Interestingly, palaeogeographic maps of the western Mediterranean at late Eocene (Fig. 9) show that the Spanish and French areas of the *H. pretiosa* complex were separated by the Ebro Basin.

2.2. Origins and History of Megadrile Populations in Western Mediterranean Countries

The territories of the Iberian Peninsula, Pyrenees, Maghreb and Sardo-Corsican system went through tormented geological history during the Cenozoic, subsequent to the closing of Neo-Tethys. These vicissitudes have been carefully reconstructed by geologists, so that today we have at our disposal detailed information on the changing palaeogeography of the last 60 Ma (see Andeweg 2002). To attempt to reconstruct the history of the megadriles of the western Mediterranean lands, it is good to start from the late Eocene (36 Mya), when Iberia was attached to Aquitania (France); the Sardo-Corsican block was attached to the Pyrenees; the Betico-Rifan system was a large island comprising the present-day Kabylias (Fig. 9). At this time all the extant genera of Lumbricidae were differentiated.

Based on the present distribution of the autochthonous earthworm fauna, we can hypothesize that the Pyrenees were the homeland of the genera *Orodrilus*, *Etnodrilus* and *Prosellodrilus*, while the more southern Sardo-Corsican system was the homeland of *Diporodrilus* and part of *Prosel-*
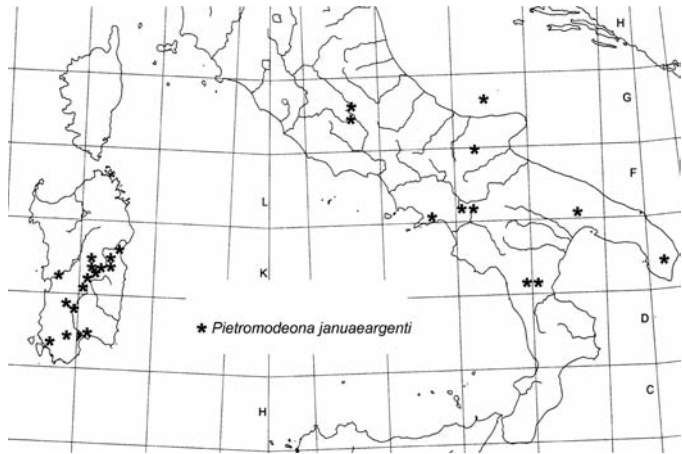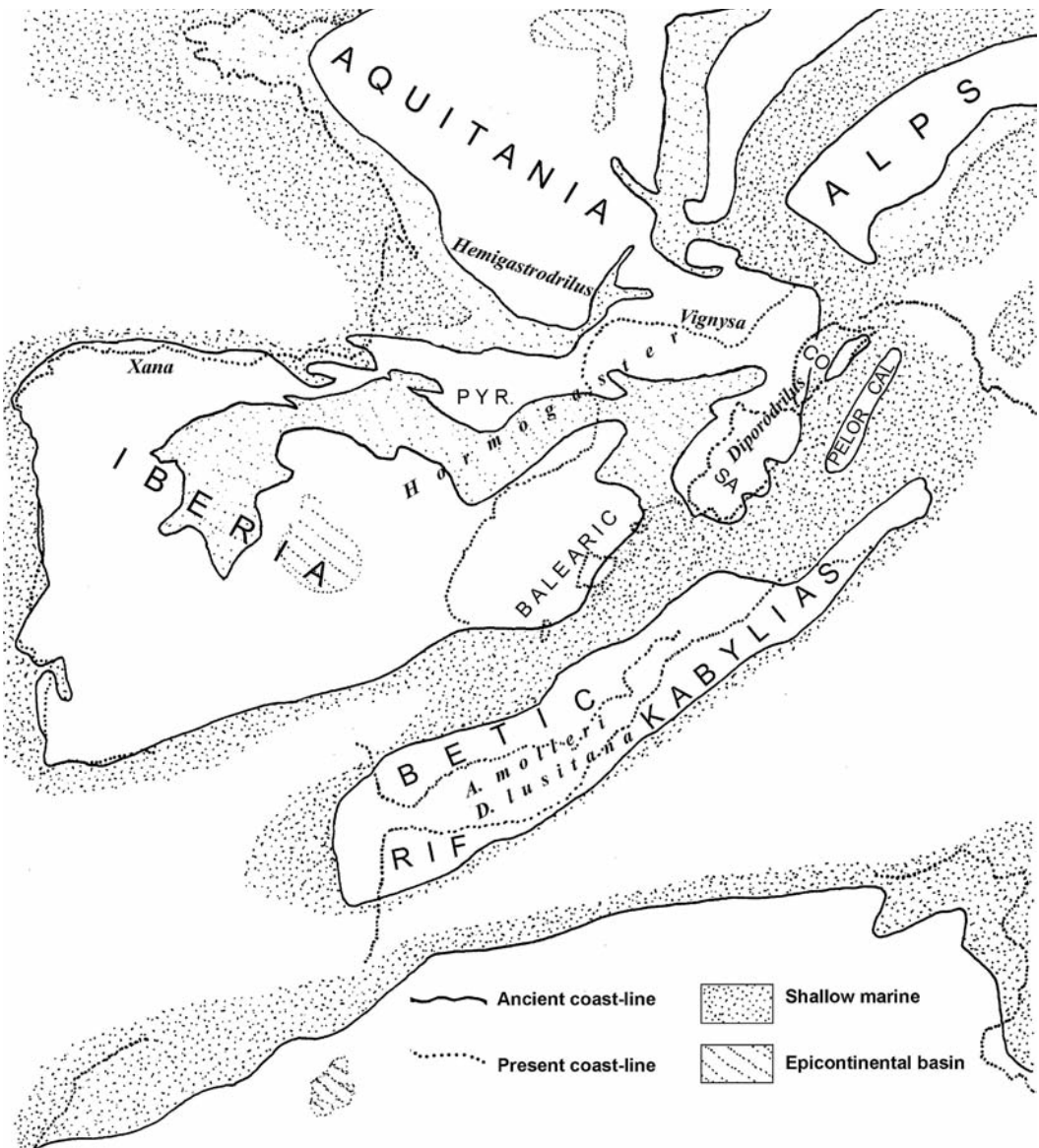
FIGURE 9. Palaeogeographic map of Western Mediterranean at Late Eocene (36 Mya). The Betico-Rifan system, including the two Kabylias, is detached from Iberia, whereas the Sardo-Corsican system is connected to the Pyrénées and further north to southern France — Aquitania (redrawn and modified from Andeweg 2002). CAL, Calabria; CO, Corsica; PELOR, Peloritani Massif; PYR, Pyrénées; SA, Sardinia.

lodrilus and *Eumenescolex*, the latter two genera being closely related. The Betico-Rifan system was instead the homeland of the *A. molleri* complex and *D. lusitana* Graff, 1961. We can also hypothesize that the complete set of the emerged western lands, the Betico-Rifan excluded, was the homeland of the Hormogastridae and of *Scherotheca* (Fig. 9).

During the Miocene and Pliocene, the tectonic setting of the Western Mediterranean changed and so did the topography and reciprocal connections between the above mentioned geographic territories and their earthworm populations.

2.3. History of the Earthworm Fauna of the Sardo-Corsican System

The autochthonous megadriles of Sardinia and Corsica form together an assemblage of 15 to 17 species: a level of biodiversity that is normal for a territory of 33,000 km^2 in the Mediterranean region. The ecological aptitudes represented in this assemblage were complementary and warranted the building and maintenance of stable communities, so that no adaptive radiation occurred. It is reasonable to believe that the present-day assemblage still represents a comprehensive sample of the megadrile lineages populating the south-western edge of Europe at the time of its detachment as a microplate in the late Oligocene, 27 Mya (Fig. 10). Most species dwelling in Sardinia had a Pyrenean origin, while most Corsican species originated from Provence or from Western Alpine territories that were already above sea level and close to northeastern (Alpine) Corsica. A land connection between Corsica and the mainland is herein hypothesized at 24 Mya (Fig. 11; Andeweg 2002), but later land bridges preceding the Messinian salinity crisis have also been suggested (Fig. 12; Orsag-Sperber et al. 1993; Meulenkamp and Sissingh 2003).

After breaking away from the continent, the Sardo-Corsican block became fragmented in a manner that has not entirely been clarified: during much of the time the southwestern corner of Sardinia was separated from the main body of the island by a sea arm, which would be filled later by alluvial deposits to form the Campidano Plain; *H. pretiosa* is endemic to that region (Fig. 2). The northeastern corner of Sardinia, i.e., Gallura, was connected to Corsica at times of low sea level, and, at least as a result of the degradation and loss of pristine forest habitats in adjacent parts of Sardinia, it became ecologically isolated from the rest of the island (Rota 1992): there live *D. pilosus* and *H. samnitica*, two species that are absent elsewhere in Sardinia but are common in Corsica (Figs 2, 3).

During the Messinian desiccation of the Mediterranean, a few species that could withstand the harsh conditions created by the high salinity levels of the former seafloor, expanded their ranges by following the forests to the east or southeast of Corsica and Sardinia. *H. samnitica*, starting from Corsica, spread along the Elban ridge separating Corsican and Montecristo basins, to colonize a vast area including present-day Elba and coastal Tuscany. Its relict populations inhabit today the small Tuscan islands that represent the summits of submarine mountains, in Messinian time rising like pinnacles over the dried up sea bottom (Fig. 2). *Scherotheca corsicana* used the same path and colonized the same land, evolving into a similar but distinct species, *S. targionii* (Baldasseroni, 1906) (see Omodeo and Rota 2005). Its main population lives today on Elba, while smaller populations live on the hills bordering western Tuscany. It has not been found so far in the lesser islands of the Tuscan Archipelago (Fig. 6).

Hormogaster redii outmigrated southwards from Sardinia to populate Tunisia and northwestern Algeria and eastwards to populate the western side of the Italian peninsula and Sicily (Fig. 1). The populations surviving today on the smaller islets rising out of the Tyrrhenian sea (but absent from Capraia and Elba) attest the route that was taken during this second migration. The two epochs of this spreading were placed by allozyme genetic studies at 8 Mya and 3 Mya, respectively (Cobolli et al. 1992). *Pietromodeona januaeargenti* followed, perhaps, the second path, populating southern Italy and the Tremiti Islands in the Adriatic Sea (Fig. 8). Both *H. redii* and *P. januaeargenti* are absent in Calabria south of the Pollino Massif.

It is possible that *Helodrilus massiliensis* found so far only in northern and western Sardinia arrived from the north (Fig. 7), even though it is not recorded in Corsica (aquatic megadriles are very often overlooked).

The last main geological event which affected the faunal composition of the northern Tyrrhenian lands was the lowering of the sea level during the Pleistocene Ice Age, when Corsica and Sar-
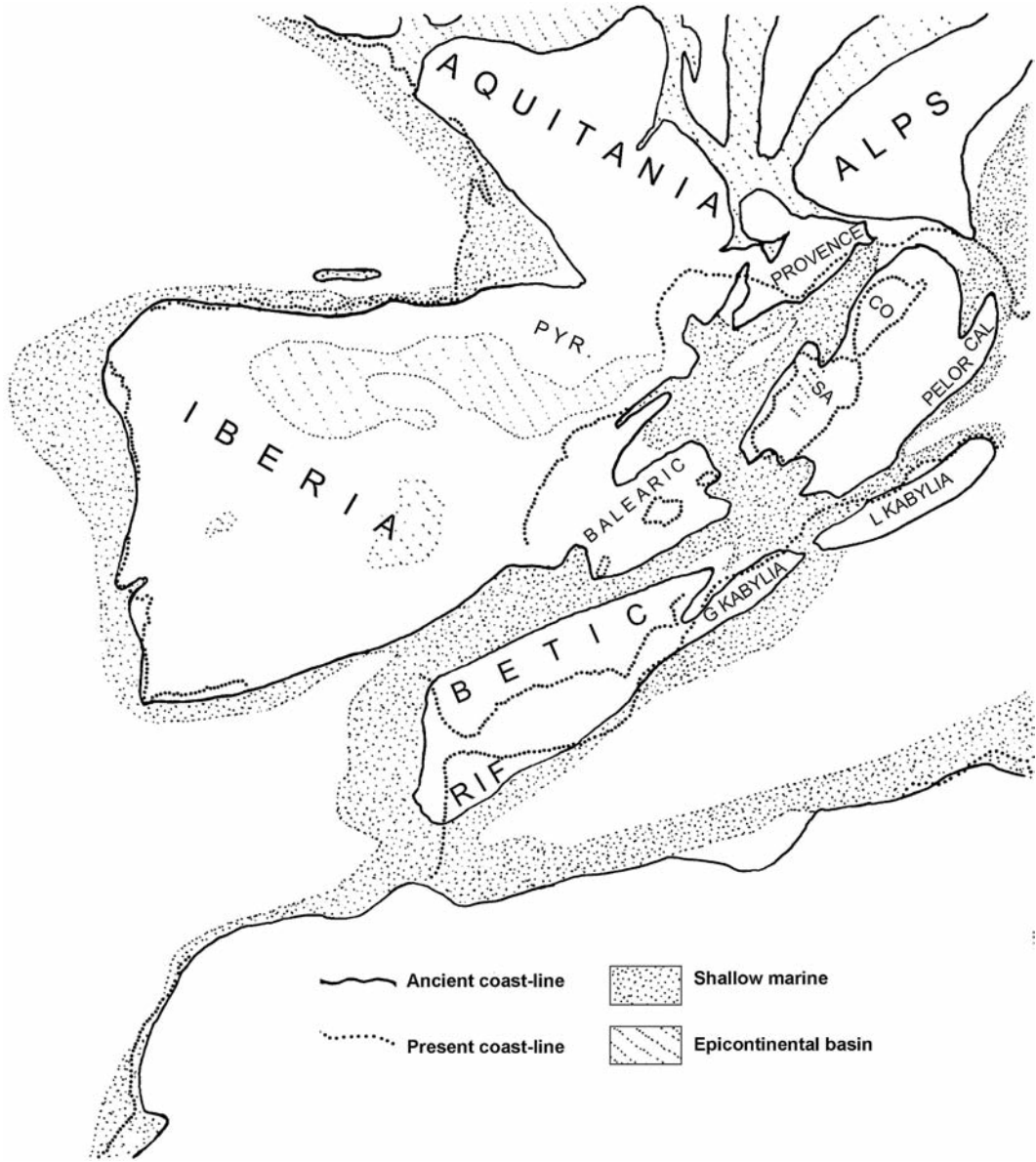
FIGURE 10. Palaeogeographic map of Western Mediterranean at Late Oligocene (27 Mya). The Sardo-Corsican system is completely separated from the Pyrenean region, but northern Corsica remains in close proximity to the Alps and Provence (redrawn and modified from Andeweg 2002). CAL, Calabria; CO, Corsica; PELOR, Peloritani Massif; PYR, Pyrenées; SA, Sardinia.

dinia were joined again by narrow tongues of land to Italy and possibly to Provence, too. This time the net migration direction was toward, not from, the Sardo-Corsican system. Sardinia received three parthenogenetic strains*, respectively of *N. caliginosus trapezoides*, *A. rosea bimastoides* and *Eiseniella tetraedra* (Savigny, 1826), but the two latter did not become so frequent as on the European continent. In Corsica, five more species arrived and thrived: *Allolobophora chlorotica* (Savi-
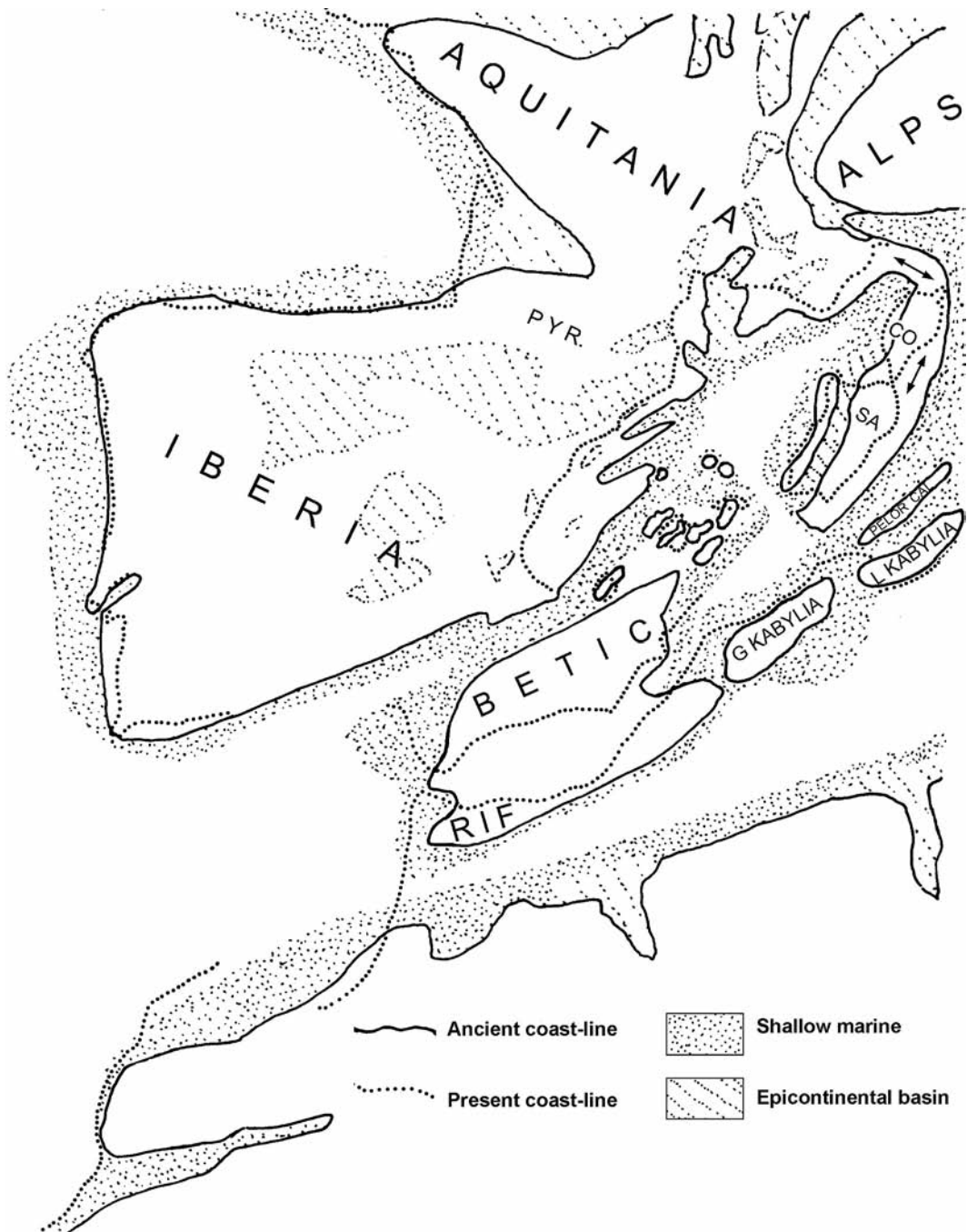
FIGURE 11. Palaeogeographic map of Western Mediterranean at Early Miocene (24 Mya). Corsica is connected to Provence and the Alps. The Calabro-Peloritani massif has broken away from the Sardo-Corsican block. The Betico-Rifan block is fragmented and migrates eastwards (redrawn and modified from Andeweg 2002). Double arrows indicate the possible migration routes of Eumenescolex, Scherotheca and Helodrilus. CAL, Calabria; CO, Corsica; PELOR, Peloritani Massif; PYR, Pyrenées; SA, Sardinia.
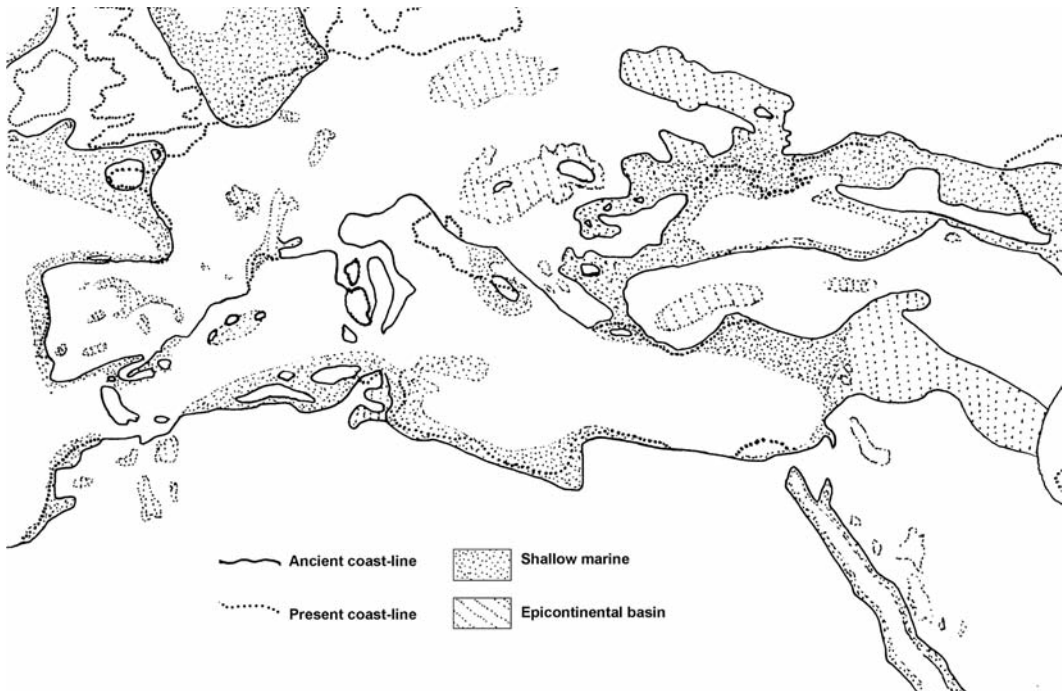
FIGURE 12. Palaeogeography of the Mediterranean at Late Miocene (Tortonian, 7–8 Mya) according to Meulenkamp and Sissingh (2003). The isolation of Turkey from Greece and the Balkans is evident. Note also the hypothetical relationships of the Sardo-Corsican system.

gny, 1826)*, Lumbricus castaneus* (Savigny, 1826)*, O. complanatus, Octolasion lacteum* (Örley, 1885) and *Proctodrilus antipai.* It is possible that such a large contingent of modern species caused the disappearance of some archaic species from this island.

2.4. History of the Earthworm Fauna of Maghreb

The autochthonous species presently living in Maghreb are not numerous and belong to three groups. The first comprises the *A. molleri* complex and *Dendrobaena lusitana*. Both live in the south of Iberia, in the two Kabylias and on the Canary Islands, whereas they are absent in Tunisia; thus it can be assumed that they belong to the old fauna of the Betico-Rifan system, and that their present distribution reflects that of late Eocene (Fig. 9). It is noteworthy that *Allolobophora dubiosa* (Örley, 1881), a species close to *A. molleri*, lives in the Balkan Peninsula and in northern Anatolia and that *A. molleri* is replaced in Tunisia by a vicariant form related to *Nicodrilus*. The second group comprises two archaic species: *P. doumandjii* and *P. festai* (Fig. 5), living respectively in the environs of Algiers and Tunis, but belonging to two different lineages whose paleohistories are not yet understood. The same may be said of *A. borellii,* which was described from one site in the Pyrenees and is rather frequent in Morocco and eastern Algeria. The third group includes three endemic species: *Octodrilus kabilianus* and *O. maghrebinus* from central and eastern Algeria and Tunisia, together with *E. xylophila*, which inhabits the decaying logs of cork oak; these species have their nearest relatives in the Balkan Peninsula. *Dendrobaena byblica* and *H. redii* came to Maghreb from Anatolia and Sardinia, respectively, during the salinity crisis of 5.96–5.33 Mya, possibly together with modern type species such as *A. eiseni, M. minuscula* and *P. antipai* (see above).

2.5. History of the Anatolian Earthworm Fauna

The story of the Anatolian earthworm fauna has been outlined by Omodeo and Rota (1999) on the basis of the 1987 and 1990 collections. Later records (Misirlioğlu 2004; Csuzdi et al. 2006) increase local definition but do not change the faunistic scenario. However, the results emerging from the analyses of the other Mediterranean districts suggest a better organization of the conclusions reached in the 1999 paper. It is possible to recognize three successive episodes in the peopling of Anatolia by the megadriles, all of them connected with main geological events.

The first episode involved the Spermophorodrilinae, a taxon showing affinity with the Hormogastridae, inhabiting southwestern Europe, and with the Diporodrilinae, inhabiting the Sardo-Corsican system. All three taxa, along with the older Criodrilidae, are the relict of a remote fauna which lived on the northern coasts of Palaeotethys and populated Anatolia when this Gondwanian plate emerged as terra firma and collided with Eurasia during the Cretaceous as asserted by Stampfli et al. (2002). The palaeogeographic scenarios provided by these authors and by Meulenkamp and Sissingh (2003) show that from the Oligocene onwards Turkey remained connected to the Balkans, the Dinaric system and the Alps, except for a break during the upper Miocene, when a sea-arm separated two continental masses once called North- and South-Aegeid (Fig. 12). This scenario aids us to interpret the peopling of Anatolia by the European genus *Dendrobaena*, which is so rich in species in both Anatolia and the Balkan peninsula.

The last episode occurred during the Pleistocene, when a wider connection between Tracia and Anatolia was established. In such a circumstance many species migrated southward and populated the northern coastal strip of Anatolia. This strip was wider then, because during the Ice Age the Black Sea was separated from the Mediterranean and its level lowered by about 100 m because of evaporation. When 7150 years ago (date *fide* Ryan et al. 1997), the connection between the two seas was re-established, these species remained confined in the area between Cape Ince and the Lazistan, the Colchis, or in the area south of Marmara Sea.

Conclusions

The evidence gained from the study of old and recent earthworm collections in the Mediterranean, together with earlier interpretative efforts about the history of the populations of particular areas, allowed us to correlate the present distribution of old autochthonous species with the geological and climatic vicissitudes of the Mediterranean basin. Using such correlation, we have formulated hypotheses concerning some aspects of the phylogeny of an animal group which leaves very few fossil remains.

The above reconstructions of the history and relationships of the megadrile fauna of three Mediterranean districts represents a consistent, durable result. Much work, however, remains to be done. First, the inference of a well supported phylogeny based on both morphological and molecular data. Second, the temporal calibration of phylogenetic trees. Third, a thorough investigation of the ongoing or completed processes of differentiation at subspecific and specific levels, as revealed by morphological research.

Acknowledgments

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