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Geophilomorph centipedes in the Mediterranean region: revisiting taxonomy opens new evolutionary vistas

Lucio Bonato* **& Alessandro Minelli**

Dipartimento di Biologia, Università di Padova, via U. Bassi 58b, 35131 Padova, Italy;

e-mail: lucio.bonato@unipd.it; alessandro.minelli@unipd.it

* *Corresponding author*

Abstract

Geophilomorph centipedes (Geophilomorpha) are represented in the Mediterranean region by almost 200 species, 77 % of which are exclusive. Taxonomy and nomenclature are still inadequate, but recent investigations are contributing to a better understanding of the evolutionary differentiation of this group in the region. Since 2000, identity has been clarified for ca. 40 nominal taxa, and unexpected evidence has emerged for the existence of three well-distinct lineages that had remained unrecognised before. Of these, *Eurygeophilus* has evolved an unusually stout body and needle-like forcipules, and the vicariant pattern of its two species is peculiar in encompassing both the Pyrenees and the Corsica-Sardinia microplate; *Diphyonyx* has evolved unusually pincer-like leg claws, convergent to those originated independently in two different unrelated geophilomorph lineages; *Stenotaenia* has maintained a very uniform gross morphology, while differentiating widely in body size and number of trunk segments. The fauna of the Mediterranean region is representative of most major lineages of the Geophilomorpha, and the almost exclusive Dignathodontidae exhibit a remarkable morpho-ecological radiation in the region. Essential to a better understanding of the regional evolutionary history of these centipedes will be assessing the actual species diversity within many of the already recognised lineages, and reviewing in a phylogenetic perspective the nominal taxa currently referred to the composite genera *Geophilus* and *Schendyla*.

Keywords: Geophilomorpha, diversity, faunal composition, morphological evolution, taxonomic revision

1. Introduction

The Mediterranean region, i.e. all the islands and continental lands around the Mediterranean Sea, is well known as one of the major hotspots of biological diversity in the world. Complex geographic and climatic history, coupled with the persistence of extraordinary environmental diversity, prompted the differentiation and radiation of distinct phyletic lineages, and maintained high levels of species richness and evolutionary diversity in the whole region. This has been documented especially for plants and vertebrates, also informing evaluation of conservation priorities (Blondel & Aronson 1999, Myers et al. 2000), but this obviously holds for other animal groups as well.

The distributional records recently assembled for a complete world catalogue of Chilopoda (Minelli 2006) confirmed that the Mediterranean region is a major hotspot for centipedes too, and for geophilomorphs in particular, in terms of both species richness and percentage of exclusive taxa (Tab. 1). Almost 200 species of geophilomorphs in more than 30 genera are known for the Mediterranean region, these numbers accounting for ca. 15 % of all known species and genera in the world. Seven families are represented in the region, i.e, half of all families recognised in Geophilomorpha. More than three quarters of the species and more than half of the genera occurring in the Mediterranean region live exclusively or almost exclusively in the region. Striking is also the morphological and ecological diversity exhibited by these animals in the soil communities around the Mediterranean basin: the diversity within the region is widely representative of the overall variation estimated throughout the world, in terms of overall habitus (from very elongate and ribbon-like to distinctly stout), body size (from dwarf species only 1 cm long to comparatively giant species reaching 20 cm), habitat (from arid grounds to wet forest litter), and functional structure of the feeding apparatus (from delicate, needle-like to robust, strongly tuberculate pincers). The diversity of geophilomorphs in the Mediterranean region is significant also with respect to other centipedes, as they comprise more than one third of all chilopod species and more than half of the chilopod genera occurring in the region (Tab. 1).

Tab. 1 Estimates of taxa of Geophilomorpha known in the Mediterranean region, based on recent taxonomic and nomenclatural revisions and updates (see under Methods). Abbreviations: Geoph. = Geophilomorpha; Med. = Mediterranean.

	Geoph. in Med. region			Geoph. exclusive [incl. almost exclusive] of Med. region	
	number	% of total Geoph.	% of Chilopoda in Med. region	number	% of Geoph. in Med. region
species	177–200	ca 15 % of ca 1260	ca 35 % of ca. 550	135–158	ca 77 %
genera	34	ca 15 % of ca. 230	ca 60 % of ca. 55	13 [22]	ca 38 % [ca. 65 %]
families	7	ca 50 % of 14–15	ca 60 % of 12	0 [1]	0 % [14 %]

However, our current knowledge of the evolutionary and morpho-functional diversity of geophilomorphs in this region, as well as in the world, is very incomplete and largely inaccurate, not only because new species remain to be discovered, but also because the morphology of most of the described species is only roughly documented, and their ecology often unexplored. Moreover, many nominal taxa at different ranks are of uncertain identity and/or dubious validity, and their phyletic position often unknown and sometimes misunderstood. Classification in use is inadequate in many respects and therefore misleading to estimate the actual phyletic diversity of these animals in the Mediterranean biota, and preventing any confident reconstruction of the evolutionary and biogeographic processes occurred in the region.

Basic taxonomic and faunistic investigations on geophilomorphs in the Mediterranean region were carried out between the end of the XIX century and the first half of the XX century, mainly by C. Attems (e.g., Attems 1903, 1929a, 1952), H.-W. Brölemann (e.g., Brolemann 1930, 1932, Brölemann & Ribaut 1912), F. Silvestri (e.g., Silvestri 1895, 1898) and K.W. Verhoeff (e.g., Verhoeff 1898, 1928, 1938, 1941), within other influential contributions with wide geographic scope (above all, Koch 1847, Latzel 1880, Meinert 1870). Most subsequent contributions (e.g., by R.V. Chamberlin, J.-M. Demange, L.J. Dobroruka, J. Kaczmarek, A. Kanellis, A. Machado, P. Manfredi, Z. Matic, A. Minelli, S. Simaiakis, P. Stoev, M. Zapparoli) were limited to faunistics of narrow areas, whereas comprehensive taxonomic investigations with wider geographic scope were rare. In very recent years, however, renewed efforts devoted to morphological investigations (also through S.E.M.), faunistic recording through new field sampling, and taxonomic revisions were stimulated by two major, collaborative projects aimed to compile consistent taxonomic and faunistic databases, namely 'Fauna Europaea' (begun in 2000 and first released on-line in 2004; Fauna Europaea Web Service 2007, Minelli & Foddai 2007) and 'ChiloBase' (begun in 2004 and first released on-line in 2006; Minelli 2006). Recent investigations have also been favoured by the publication of valuable nomenclatural and taxonomic data sources, including complete genus-level nomenclators of centipedes and catalogues of museum collections (Jeekel 2005, Melzer et al. 2005, Spelda 2005a, Shelley 2006).

Research in progress by us and other students is contributing to a significant revision of our understanding of the actual diversity of geophilomorphs in the Mediterranean region. Aims of this paper are (i) to provide a synthesis of significant advances contributed by recent investigations, (ii) to offer an overview of the known regional diversity of these arthropods, based on newly emerged evidence, and (iii) to highlight major limits in present knowledge and priorities for further investigation.

2. Methods

The Mediterranean region as defined here is basically corresponding to the so-called 'Mediterranean Basin' hotspot, recognised by most major assessments of global biodiversity (Blondel & Aronson 1999, Myers and Cowling in Mittermeier et al. 2000, 2005; Myers et al. 2000), but in a quite inclusive circumscription, to include the Macaronesian islands (the Canaries, Madeira, the Savage islands, and the Azores), the whole Iberian peninsula, all major mountain chains surrounding the strictly Mediterranean coastal regions (i.e., the Atlas, the Pyrenees, the Alps, the Dinarides, and the Balkan Mountains), and the whole Anatolian peninsula roughly corresponding to Turkey.

All primary literature on the Geophilomorpha in the Mediterranean region as defined above was analysed. For comparative purpose, the state of the art of taxonomy and nomenclature up to 2000 (when the 'Fauna Europaea' project was launched; see Introduction) was assumed as a conventional reference to evaluate the advance consequent to recent investigations, either published or still in progress.

3. Results and discussion

Recent advance

Clarification of the identity of nominal taxa: Around the year 2000, ca. 65 nominal taxa (ca. 10 in the genus-group and ca. 55 in the species-group) still remained of uncertain identity. Among these taxa were many nominal species introduced by the earliest authors under some of the oldest generic names (above all, many species described by C. L. Koch and F. Meinert under *Geophilus* Leach, 1814 and *Himantarium* C. L. Koch, 1847), but also some more recently proposed taxa, including small nominal genera introduced by K.W. Verhoeff and C. Attems. As only very brief descriptions were available, lacking characters of diagnostic value, most of these taxa had been maintained as putatively valid, and sometimes cited as such even in recent times, but actually they have been practically ignored in faunistic investigations. On the other hand, some 10 nominal species had remained fully neglected for a long time, as they had been introduced in rather obscure publications and subsequently failed to be registered in the most influential monographs (Latzel 1880, Verhoeff 1902–25, Attems 1929b).

In recent years, critical evaluation of published accounts, sometimes coupled with direct examination of type material (Spelda 2005b, Bonato & Minelli 2008, Minelli & Bonato in prep.), allowed clarifying the taxonomic position of ca. 40 taxa. Only some of these have been found to be obviously or most probably distinct from any other known taxon, and have been therefore maintained as valid, whereas ca. 30 names have been found to be synonyms of other taxa. Particularly impacting on the geophilomorph nomenclature has been the resurrection of *Geophilus alpinus* Meinert, 1870 and *Stenotaenia sorrentina* (Attems, 1903) as the valid names for widespread and commonly found species, hitherto most often called *Geophilus insculptus* Attems, 1895 and *Geophilus linearis abbreviatus* Verhoeff, 1925 respectively (Spelda 2005b, Bonato & Minelli 2008).

Identification of hitherto unrecognised lineages: Morphological investigations on already described taxa and reassessment of their geographic occurrence have disclosed compelling evidence for the existence of phyletic lineages whose distinctness had remained unrecognised in the taxonomy in use. Following current practice, these lineages have been recognised as distinct genera, which have been circumscribed to include taxa hitherto misplaced in vaguely diagnosed, heterogeneous genera or separated in different small genera. Particularly significant for our understanding of the evolutionary differentiation of geophilomorphs in the Mediterranean area are the cases summarised below.

Seven species-group taxa previously split into three distinct genera (namely *Chalandea* Brölemann, 1909, *Eurygeophilus* Verhoeff, 1899, and *Mesogeophilus* Verhoeff, 1901, the latter only vaguely diagnosed when its type species was described and subsequently expanded to include four other species from New Zealand, Japan and tropical Africa) have been found to represent a single, well distinct lineage of geophilids (Bonato et al. 2006). This lineage, which has been recognised as a single genus under the name *Eurygeophilus*, is characterised by very unusual features, most probably derived within the geophilids, including a relatively stout and swollen body, extremely short and needle-like forcipules, and peculiar integumental sculpture and sensilla on the trunk sternites. Limited to western Europe, *Eurygeophilus* is represented by two clearly distinct morphospecies with vicariant distribution, namely *E. multistiliger* (Verhoeff, 1899) in sub-Mediterranean woodlands and *E. pinguis* (Brölemann, 1898) in temperate deciduous forests. Worth noting is that the allopatric distribution of the

species encompasses both the Pyrenees and the Corsica-Sardinia microplate. Moreover, despite morphological uniformity throughout its range, *E. pinguis* reveals a peculiar geographic pattern of variation in the number of trunk segments, the modal value being different in the three major parts of the range, namely (1) the Pyrenees together with other western areas, (2) the western and central Alps, and (3) the eastern Alps (Bonato et al. 2006).

Three species-group taxa that had been originally described in an incomplete, unsatisfactory way and have been hitherto classified in different genera (namely *Geophilus* Leach, 1814, *Brachygeophilus* Brölemann, 1909, and *Clinopodes* C. L. Koch, 1847, all of them polyphyletic in their traditional circumscription) have been recognised as strictly related and to actually represent a single, well distinct lineage (Bonato et al. 2008). This lineage has been described as a new genus *Diphyonyx* Bonato, Zapparoli & Minelli, 2008. It is unique among geophilids for the unusual, derived shape of the claws of several anterior pairs of legs: the hypertrophic anterior spur and the claw are facing each other into a pincer-like device, whose function is unknown. Strikingly, a similar derived morphology is found in two other distantly related lineages of geophilomorphs, the American Neogeophilidae and the south-eastern Asiatic *Eucratonyx* Pocock, 1898 (Bonato et al. 2008).

As many as 20 species, previously included in polyphyletic genera (*Geophilus* or *Clinopodes*) or distributed in small, sometimes monotypic genera of uncertain position (*Simophilus* Silvestri, 1896, *Insigniporus* Attems, 1903, *Bithyniphilus* Verhoeff, 1941 and *Schizopleres* Folkmanova, 1956), turned out to obviously belong to a single lineage, for which the old neglected name *Stenotaenia* C. L. Koch, 1847 has been resurrected (Bonato & Minelli 2008). After a preliminary revision, no more than ca. 15 species resulted morphologically distinct, and their overall geographic range covers a wide area in the central and eastern part of the Mediterranean region. Comparative morphology suggests that, in the evolutionary history of the lineage, all species maintained a very uniform morphology, but diverged remarkably in adult body size and number of trunk segments: at one extreme is *S. romana* (Silvestri, 1895), a dwarf species, less than 2 cm long, with less than 50 pairs of legs, apparently paedomorphic; at the other extreme is *S. sturanyi* (Attems, 1903), a relatively giant species, reaching 8 cm and bearing more than one hundred pairs of legs. Such a wide interspecific variation in size and segment number, coupled with a strongly conserved gross morphology, is unusual in the geophilomorphs as a whole.

Revised overview of the evolutionary diversity

Taxonomical and nomenclatural revisions, as those summarised above, are providing new insights on the evolutionary and biogeographic processes that shaped the geophilomorph fauna in the Mediterranean region. An updated overview on the regional diversity of these animals, admittedly still preliminary as further advances are expected, is given in Tab. 2. Some newly emerging evolutionary vistas are presented below.

Phyletic composition of the fauna: Most of the conventionally recognised families remain to be tested for their monophyly, and their phyletic relations are resolved only partially (Foddai & Minelli 2001, Edgecombe & Giribet 2004, 2007). Nevertheless, taking into account the best current hypothesis of geophilomorph phylogeny (Fig. 1), the fauna of the Mediterranean region appears not only remarkably rich (see Tab. 1) but also very diverse in a evolutionary perspective.

Tab. 2 Number of species and geographic distribution of the genera of Geophilomorpha known in the Mediterranean region, based on recent taxonomic and nomenclatural revisions and updates (see under Methods). Figures followed by '+' are possibly underestimated (some evidence of morphological variation suggesting unrecognised taxonomic diversity), those followed by '–' are possibly overestimated (doubts on the actual distinction between some recognised species). Families are listed following Fig. 1, genera in alphabetical order within each family. Abbreviations: C = central, E = eastern, excl. = excluding, incl. = including, Med. = Mediterranean, N = northern, pen. = peninsula, S = southern, W = western.

Genus	Species in Med. region	Species exclusive of Med. region	Geographic range in Med. region	Geographic range outside Med. region
Mecistocephalidae				
Dicellophilus Cook, 1896	1	0	E Alps, Dinarides	disjunct areas in C Europe, Japan, N America
Oryidae				
Orya Meinert, 1870	3 –	3	NW Africa, ? S Iberian pen.	/
Linotaeniidae				
Strigamia Gray, 1842	8	4	S Europe	N America, N and C Eurasia
Dignathodontidae				
Dignathodon Meinert, 1870	2–3	2–3	whole region	/
Henia C. L. Koch, 1847	15–17	11–13	whole region	NW Europe, E Europe
Zygophilus Chamberlin, 1952	1	1	Anatolian pen.	/
Geophilidae				
Acanthogeophilus Minelli, 1982	2	2	Italian pen., NW Africa	/
Bebekium Verhoeff, 1941	1	1	Balkan pen.	/
Clinopodes C. L. Koch, 1847	5	2	E and C (reaching W Alps, Italian pen., Sicily, Levant)	C and E Europe, W Asia
Diphyonyx Bonato, Zapparoli & Minelli, 2008	1	0	Balkan pen., Anatolian pen.	Black Sea basin
Eurygeophilus Verhoeff, 1899	2	1	Iberian pen., Corsica, Sardinia, Alps	Great Britain
Galliophilus Ribaut & Brölemann, 1927	1	1	Pyrenees	/
Geophilus Leach, 1814	45–54	36–45	whole region	N America, N and C Eurasia

Tab. 2 cont.

Genus	Species in Med. region	Species exclusive of Med. region	Geographic range in Med. region	Geographic range outside Med. region
Gnathoribautia Brölemann, 1909	2–4 –	2–4	W (incl. Macaronesia; reaching Iberian pen., Tunisia, Sicily) and NE (reaching S Balkan pen., Levant)	/
Pachymerium C. L. Koch, 1847	4–8 –	3–7	whole region	almost global
Pleurogeophilus Verhoeff, 1901	3–6 –	3–6	Macaronesia, NW Africa, Ligurian basin, E Alps, Balkan pen., Anatolian pen.	N and C Asia, ? C Africa
Porethus Chamberlin, 1952	1	1	Anatolian pen.	/
Stenotaenia C. L. Koch, 1847	14	12	C and E (reaching W Alps, Corsica, Sardinia, Sicily, NW Africa)	C Europe
Tuoba Chamberlin, 1920	4	3	Macaronesia, S Europe	Coastal regions and islands in Atlantic, Indian, Pacific oceans
Himantariidae				
Bothriogaster Selivanov, 1879	1 +	0	E (reaching S Balkan pen., Tunisia)	W Asia
Haplophilus Cook, 1896	9	7	W (incl. Macaronesia; reaching W Alps,? Corsica, Sardinia, S Italian pen., Sicily, Tunisia)	W Europe
Himantariella Chalande & Ribaut, 1909	3	3	E Pyrenees, Balearic Islands, Morocco	/
Himantarium C. L. Koch, 1847	2–4	2–4	whole region (incl. Macaronesia)	? Indian pen. (introduced?)
Mesocanthus Meinert, 1870	1	1	NW Africa	N Africa, C Asia, Indian pen.

Tab. 2 cont.

Genus	Species in Med. region	Species exclusive of Med. region	Geographic range in Med. region	Geographic range outside Med. Region
Polyporogaster Verhoeff, 1899	1	1	NW Africa	C Asia
Stigmatogaster Latzel, 1880	1 +	1	W and C (excl. Macaronesia; reaching W and S Balkan pen., Tunisia)	/
Thracophilus Verhoeff, 1926	7 –	6	NE (reaching S Balkan pen., Levant)	W and C Asia
Schendylidae				
Espagnella Attems, 1952	1	1	Iberian pen.	/
Haploschendyla Verhoeff, 1900	4 –	4	Madeira, NW Africa, Sicily, Balkan pen.	/
Hydroschendyla Brölemann & Ribaut, 1911	1	0	C and E	N and W Europe
Nannophilus Cook, 1896	4	4	Macaronesia, NW Africa, Sicily, Crete	/
Nyctunguis Chamberlin, 1914	1	1	Anatolian pen.	N and S America
Schendyla Bergsoe & Meinert, 1866	24 –	14	whole region (incl. Macaronesia)	N and C Europe
Schendylops Cook, 1899	2	2	NW Africa	C and S Africa, S America

Most of the major lineages of Geophilomorpha are represented in the Mediterranean region. The Placodesmata (including the single family Mecistocephalidae), one of the two basally splitting branches, are here represented by the single species *Dicellophilus carniolensis* (C. L. Koch, 1847). Actually, the narrow range of the species is restricted to central Europe (almost exclusively from central Alps to the entire Carpathian Mountains, and south to Dinarides), and thus reaches the Mediterranean region only marginally, around the northern Adriatic basin. The distribution of *D. carniolensis* is puzzling, as it is hugely isolated from the geographic range of all remaining mecistocephalids (south of the Sahara and the central Asian highlands), and its closest relatives are restricted to narrow areas in Japan and North America (Bonato et al. 2003, in press).

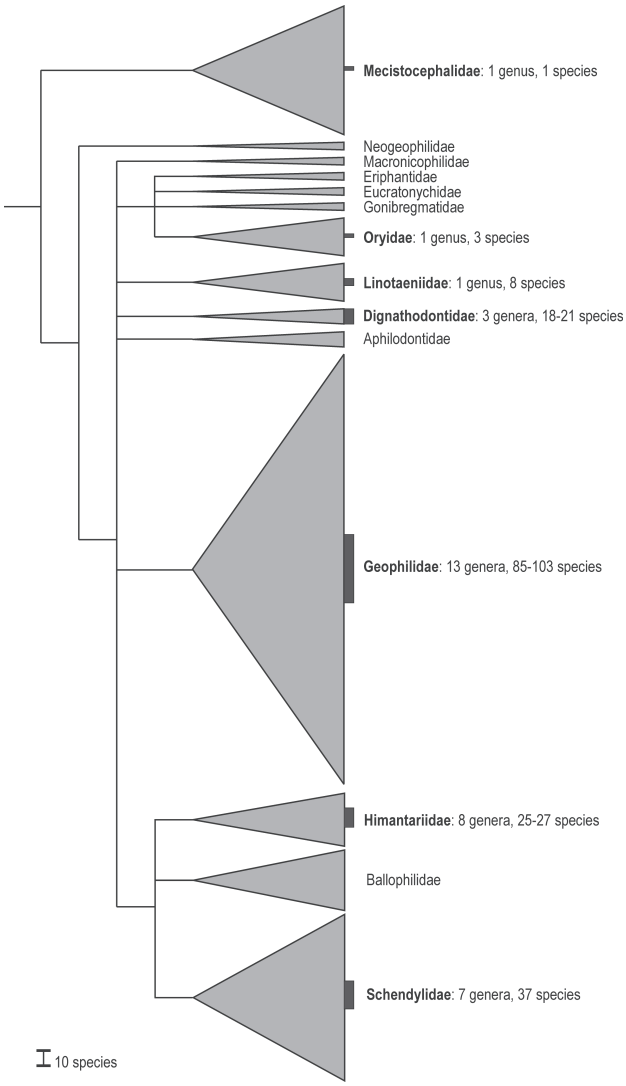

Fig. 1 Phyletic composition of the geophilomorph fauna of the Mediterranean region. For simplicity, each family is accepted as monophyletic and represented by a triangle whose basis is proportional to the number of known species. Relationships are based on the consensus tree compiled by Edgecombe & Giribet (2007), but some less supported branches have been collapsed. Families occurring in the Mediterranean region are highlighted in bold, and accompanied by a bar proportional to the number of species occurring in the region; numbers of genera and species known in the region are also given.

The Adesmata, i.e. the other main branch of the Geophilomorpha, are present in the Mediterranean region with representatives of most major lineages. The lineage including the Oryidae and a few other minor families is represented here by a single, small clade, i.e. the genus *Orya*, apparently comprising very few species. *Orya* is confined to north-western Africa, but also cited from the southernmost part of the Iberian peninsula (Meinert 1870), and is geographically isolated from all other oryids, which are mainly tropical. *Orya* is also morphologically well distinct in respect to the remaining oryids and is probably only distantly related to them.

The Linotaeniidae, Dignathodontidae and Geophilidae have been claimed to comprise a major lineage, but this is still contentious (Edgecombe & Giribet 2004, Edgecombe 2007). Furthermore, at difference with both Linotaeniidae and Dignathodontidae, the monophyly of Geophilidae as currently circumscribed is questionable. Notwithstanding the inadequate phylogenetic framework, it is clear that many, not strictly related lineages belonging to this assemblage are present in the Mediterranean region, suggesting a complex history of colonisation and local diversification.

The Linotaeniidae are represented here only by some species of *Strigamia*, which is a large, quite uniform genus widely distributed in the Holarctics. The core distribution of most of the species occurring in the Mediterranean region is actually centred in more northern European areas. Phyletic relationships among the *Strigamia* species are completely unknown, but it is evident that the differentiation of this lineage in the Mediterranean region has been modest.

Conversely, the Dignathodontidae are almost exclusive of the Mediterranean region, with only a few species extending their range northwards to central and western Europe and eastwards to the Caucasus. This is a well recognised monophyletic group, even though its phyletic origin is still uncertain. It is widespread in the region, with high species richness in the Iberian, Italian, Balkan and Anatolian peninsulas. It represents one of the major radiations of geophilomorphs in the Mediterranean region, with ca. 20 species diverging in morphology, particularly in the shape of the mouth parts and the pattern of sternal glands, and in ecological tolerance, colonising different substrates from arid, rocky grounds to wet, montane forest soils.

The Geophilidae are represented in the region by many lineages morphologically well distinct from each other. A few lineages (above all, *Pachymerium* and *Tuoba*) are widely represented outside the Mediterranean region and the local species are strictly related to other, exotic ones: these lineages probably underwent remarkable intercontinental dispersal but limited local differentiation. Instead, most of the remaining lineages (e.g., *Clinopodes*, *Gnathoribautia*, *Stenotaenia*) live exclusively or almost exclusively in the Mediterranean region. Each of these genera is uniform in general morphology and moderately rich in species. Even though their phyletic relationships are obscure, they most probably originated and differentiated in the region. As for the large genus *Geophilus*, its circumscription and internal taxonomy are still very unsatisfactory. Within *Geophilus*, however, evidence is emerging for the existence of a remarkably differentiated clade characterised by unusually reduced claws of the second maxillae: in the south-western part of Europe extending between the Pyrenees and the whole Italian peninsula, this clade includes both robust and delicately elongate species, ranging from strictly interstitial to troglomorphic cave-dwelling form (Foddai & Minelli 1999, Minelli & Bonato in prep.).

The well-established lineage including Himantariidae+Ballophilidae+Schendylidae is present in the Mediterranean region with many, well-distinct and not strictly related clades, which belong to the traditional families Himantariidae and Schendylidae. Many genera are present exclusively or almost exclusively in the region, but diversified to a different extent. The most spectacular radiations are those of *Haplophilus* and *Schendyla*, involving not only a remarkable variation in adult body size and number of trunk segments, but also the evolution of various sternal markings in the former, and different arrays of tubercles on the forcipules in the latter. Even though no phylogenetic analysis has been performed up to present, comparative morphology suggests that most Mediterranean lineages are more strictly related to other lineages outside the Mediterranean region than to each other. In particular, it is evident that Mediterranean himantariids do not form a monophyletic group, but different Mediterranean lineages are more strictly related to different American lineages.

Biogeographic patterns: Because many accepted supra-specific taxa still need testing for monophyly and a more thorough circumscription, any sound biogeographic analysis is prevented. Nevertheless, a comparative analysis of the known geographic occurrence of the geophilomorphs in the Mediterranean region, based on revised and updated faunistic records and recent taxonomical advance, allows preliminary insight on the evolutionary history of these animals in the geographic scenario of the region. In particular, taking the best known genera as proxies for distinct phyletic lineages, some recurrent patterns emerge in their geographic ranges and the geographic variation of their species diversity (Tab. 2).

Many genera live exclusively or almost exclusively in the Mediterranean region, with only a few species extending beyond its limits, most often to central and northern Europe. Some of these (above all, *Henia*, *Himantarium*, *Schendyla*) are widespread throughout most of the region, with moderate to high species diversity, whereas other genera (above all, *Haploschendyla*, *Hydroschendyla*, *Nannophilus*) are scattered through the region as well, but are apparently not so widespread and only poorly diversified.

Of the other exclusive or almost exclusive genera, some (*Eurygeophilus*, *Haplophilus*, *Himantariella*, *Stigmatogaster*) are limited to the western part of the region, with different eastern limits, only a few species reaching north-western Europe (*E. pinguis* and *Haplophilus subterraneus* (Shaw, 1794)). Conversely, other genera (*Clinopodes*, *Diphyonyx*, *Stenotaenia*, *Bothriogaster*, *Thracophilus*) are limited to the eastern part of the Mediterranean region, with different western limits, only a few species reaching eastern Europe and western Asia (e.g., *B. signata* (Kessler, 1874)).

Widespread and highly diversified in most of the Holarctic region are *Strigamia*, which is mainly diversified in northern, temperate areas, and *Geophilus*, which is quite rich in species also in sub-Mediterranean climates.

Two unrelated genera, *Pachymerium* and *Tuoba*, share a limited diversity in the Mediterranean region coupled with an almost world-wide distribution, most probably associated to their unusual dispersal capacity through sea, and their tolerance or specialisation for littoral habitats.

Puzzling is the occurrence of *Orya*, *Mesocanthus*, *Polyporogaster*, and *Schendylops*. These genera are present in the Mediterranean region with a few species limited to north-western Africa, but the closest relatives of these species live either in central-southern Asia or in tropical areas, with a wide gap in between.

Current limits and priorities for future investigations

Despite the recent advance discussed above, the current taxonomic framework is still inadequate to describe the actual geophilomorph diversity in the Mediterranean region. Therefore, further significant progress in our understanding of the evolutionary differentiation of these animals within this complex eco-geographic scenario is expected to be fuelled not only by the discovery of hitherto undetected species, but also by the on-going revision of the taxonomic system in use. Major limits still persisting in the latter are highlighted below.

Taxa of uncertain identity: Of the currently accepted genera (Tab. 2), the morphological identity and phyletic position of some monotypic genera have not been evaluated adequately, therefore their actual distinction remains dubious. This holds, in particular, for the geophilids *Bebekium* and *Porethus*, and the schendylid *Espagnella*.

Identity and phyletic position need be clarified also for many nominal species, for which only vague morphological accounts are available. Among these are many nominal species described by Chamberlin (1952) from the Anatolian peninsula in the heterogeneous genus *Brachygeophilus* (currently synonymised under *Geophilus*) (*B. ballidagus*, *B. erzurumensis*, *B. eudontus*, *B. honozus*, *B. mundus*, *B. orientis*, *B. pauciporus*, *B. simoporus*), but also some species introduced under *Geophilus* by earlier authors for geophilomorphs from the Balkan peninsula (*G. bosniensis* Verhoeff, 1895, *G. gorizensis* Latzel, 1880, *G. herzegowinensis* Verhoeff, 1901, *G. labrofissus* Verhoeff, 1938, *G. strictus* Latzel, 1880, *G. unguiculatus* Daday, 1889) and some species described more recently from the Iberian peninsula (*Orinophilus pauciporus* Machado, 1952, *Geophilus alzonis* Attems, 1952, *Geophilus nanus* Attems, 1952) (see Minelli & Bonato in prep.).

Species diversity within recognised lineages: Even though other morphologically well distinct species from the Mediterranean region are present in collections and still await description, the number of species currently distinguished within some genera is probably overestimated because many species are so poorly described that they lack effective differential diagnoses (Tab. 2). This can be suspected, for instance, for *Clinopodes* and *Stenotaenia* (7–8 species in each genus have been described from different authors from the Balkan and Anatolian peninsulas, often without unambiguously distinctive diagnoses), *Thracophilus* (a total of 7 species are recognised at present, but almost all described from single localities by different authors), and *Schendyla* (24 species are presently maintained as valid in the Mediterranean region, but many are of uncertain distinctness).

On the other hand, geographic variation has been found in some species, mainly in terms of body size and number of trunk segments, but sometimes also other characters such as pattern of coxal pores, shape of the legs of the last pair, and density of setae (e.g., Bonato & Minelli 2008, Simaiakis 2009). This is suggestive of geographic phylogenetic structure, eventually deserving to be recognised taxonomically. This is a common shortcoming of the traditional taxonomic practice in the whole of the Chilopoda (Edgecombe 2007). Valuable insights are expected to come from in-depth investigations through adequate geographic sampling, and application of techniques other than traditional light microscopy and sources of evidence other than external morphology. Indeed, different subspecies or varieties have been described in the past for some widespread species such as *Strigamia crassipes* (C. L. Koch, 1835), *Clinopodes flavidus* C. L. Koch, 1847, *Geophilus alpinus* Meinert, 1870 (= *Geophilus insculptus* Attems, 1895), *Pachymerium ferrugineum* (C. L. Koch, 1835), *Bothriogaster signata* (Kessler, 1874), *Stigmatogaster gracilis* (Meinert, 1870), and *Schendyla carniolensis*

Verhoeff, 1902, above all by K.W. Verhoeff (e.g., Verhoeff 1934, 1938, 1943). However, those subspecies were most often proposed without an adequate analysis of intraspecific variation for possibly diagnostic characters, and without any effort to provide an exhaustive arrangement into subspecies of all populations known to belong to the species. Therefore, the resulting intraspecific taxonomy proposed for most of the species lacks consistency, and indeed it has been applied only rarely. As a consequence, most of these species have been recently treated, provisionally, as monotypic (e.g., Zapparoli 2002, for *B. signata*; Minelli & Bonato in prep., for *S. gracilis*).

Heterogeneous genera: A few genera, above all *Geophilus* and *Schendyla*, still remain vaguely diagnosed, raising doubts on their monophyly under their current circumscription. Previous proposals to split them into subgenera or distinct genera (above all, Verhoeff 1928, for *Geophilus*; Brölemann & Ribaut 1912, for *Schendyla*) turned out unsatisfactory, and have been dismissed by recent authors. Revisional works on some species previously assigned to *Geophilus* (Bonato & Minelli 2008, Bonato et al. 2008) are contributing to dismantling the traditional, waste-basket concept of this genus, but a comprehensive, satisfactory rearrangement is still a target for future research.

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