


Article

Assessing the Diversity of Ant-Associated Silverfish (Insecta: Zygentoma) in Mediterranean Countries: The Most Important Hotspot for Lepismatidae in Western Palaearctic

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Abstract: The Mediterranean Basin is considered one of the most important hotspots of biodiversity in the European region. Many taxa exhibit high levels of speciation and endemism in this area. This is the case of the myrmecophilous insects of the families Lepismatidae and Nicoletiidae (Insecta: Zygentoma) that are further assessed in this study using unpublished and bibliographic data. A complete checklist of all ant-associated silverfish occurring in the Mediterranean Basin is presented, together with an updated identification key and interesting new records for several countries. Considering all described Zygentoma species, the myrmecophilous silverfish of the Mediterranean area represent 28% of all ant-associated species of the world and about 35% of the studied area. Even with the scarce knowledge of Zygentoma in other biogeographic areas and with insufficient sampling in other continents, we conclude that the Mediterranean region, and neighbouring areas of the Western Palaearctic, represent the most important biodiversity hotspot of ant-associated Lepismatidae (about 30% of the myrmecophilous species of this family described in the world so far), while the highest diversity of myrmecophilous Atelurinae is linked to tropical regions.

Keywords: *Atelura formicaria*; identification key; *Lepismina*; myrmecophilous silverfish; nidicolous insects; *Neoasterolepisma*; soil insects; *Tricholepisma*



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1. Introduction

Biodiversity hotspots are biogeographic regions with significant levels of plant and animal diversity greatly threatened by human alteration [1]. Myers et al. [2] defined a total of 25 hotspots around the world, characterized mainly by a significant number of endemic plants and animal species. One of the most important and complex hotspots is the Mediterranean Basin [3]. Its Mediterranean climate, together with its geography and the geological history of this region, have led to this biodiversity pattern [4]. The Mediterranean Basin has a stunning plant diversity with more than 30,000 plant species, near 40% endemic to this area [2]. In addition, it also has an incredible diversity of terrestrial and marine vertebrates, many of which are also endemic [2,4–6]. However, the diversity of invertebrates, and particularly arthropods, is far from being fully evaluated [4]. Only some taxa, such as Odonata and Decapoda [4,7], have been even slightly well-studied. However, there is still much work to be completed. One of these unstudied groups are soil arthropods. Although they present a high diversity level in many regions, their cryptic habitat, and their morphological resemblance (inside close taxa) have led to a wide knowledge gap [8].

Zygentoma is a primitive wingless insect order composed by soil inhabitants which include about 650 described species distributed worldwide. Most silverfish species are free-living and can be found in several natural habitats but other species live in human buildings as synanthropic [9]. Furthermore, there are a lot of subterranean species usually found in caves, cavities, and the shallow underground environment [10]. However, a great

number of species live as parasites or commensals in ant or termite [11,12]. Ant-associated silverfish tend to live inside ant nests, using ant-collected remains as food resources. Many of these species are considered occasional or facultative myrmecophiles (silverfish not exclusively associated with ants that can occur in other habitats, in some cases more frequently than in ant nests) or generalists (silverfish species associated with more than one genus). However, specialist ant-associated silverfish (species only associated with a single genus of ants) are the most frequent [13]. All myrmecophilous *Zygentoma* are included in two families: Nicoletiidae Escherich and Lepismatidae Latreille. Their worldwide diversity is different, with myrmecophiles Nicoletiidae being more abundant in tropical regions and Lepismatidae in the Western Palearctic [13]. Unfortunately, information on the distribution of most of these species is scarce because of the lack of experts and the difficulty in correctly identifying species or even genera due to the great morphological resemblance of most taxa that makes identifications difficult in the field. In addition, there is a lack of ecological information since many of the records do not provide ecological data or deal with species that have not been heavily sampled. Therefore, the main goals of our work are (a) to prepare an updated checklist and an identification key for the myrmecophilous silverfish of the Mediterranean Basin, (b) to summarize all the available distributional and ecological information of these species, and (c) to evaluate the diversity of ant-associated silverfish in the Mediterranean Basin compared to other regions.

2. Material and Methods

2.1. Study Area

This study focused not only on those countries strictly bordered by the Mediterranean Sea, but also on those of southern Europe and southwestern Asia with a significant Mediterranean influence. For this, the bioclimate classification given in [14] was considered, including other countries such as Bulgaria, Jordan, Saudi Arabia, and Iran. However, the fauna of geographical areas closest to the Caspian Sea and the Caucasus were not examined.

2.2. Studied Species

We have considered as ‘ant-associated silverfish’ all those species which were found with ants in a significant proportion of the records available in the scientific literature, according to the classification of [13]. Moreover, little-studied silverfish species (without habitat information) suspected to be myrmecophilous, were also included and discussed. Free-living species that were found accidentally with ants (xenomyrmecophiles following the nomenclature of [13]) were not contemplated. A particular case is *Lepisma saccharinum*: although its records with ants are low compared to other habitats (natural or synanthropic), its association with ants cannot be considered accidental [15].

2.3. Bibliographic Revision and Sources of Information

An exhaustive bibliographic revision was carried out to locate all the available information on the occurrence of ant-associated silverfish of the Mediterranean area. The literature review on these insects was mainly based on the personal database of the authors, that compiles all the publications with reliable identifications of them. This database is the result of more than three decades of work and collaboration with other *Zygentoma* specialists. Some relevant works on these insects such as [13] or [16] include abundant information for this revision. All the considered records for this work are included in the Supplementary Materials Table S1, together with a list of all the literature references. Web-based repositories and search strategies were used, but they are insufficient. Most of them do not cover many of the old papers authored by specialists and publications that are not indexed in these repositories (especially those that are morphology-based taxonomic and faunistic works, which are considered in recent times to deserve low scientific impact). Regarding biodiversity repositories such as gbif.org, we have not considered them because the inappropriate origin of most of the included records (i.e., based on photographs of insects whose correct identification almost always requires microscopic examination; see

an example in the section of *Lepisma chlorosoma* and a general evaluation in the General Discussion section).

2.4. New Material Studied

In addition to the literature review, some unpublished specimens from occasional samplings were included in this work. All these specimens were hand-collected (sometimes with an entomological aspirator) and then fixed and preserved in ethanol 70%. For identification, they were dissected and mounted on slides (see details below). These specimens were deposited in the entomological collection of the University of Córdoba (UCO), although some of them will be transferred in a few years to the collection of the Museo Nacional de Ciencias Naturales (MNCN) in Madrid.

2.5. Keys to Myrmecophilous *Zygentoma* of the Mediterranean Area

Additional silverfish specimens from previous collections were used to prepare identification keys for ant-associated silverfish species in the Mediterranean region and its surroundings. These specimens were examined with a Nikon SMZ-10 binocular stereomicroscope for preliminary identification and some dissections were made to confirm the identity of several specimens. Dissected insects were mounted on slides using Tendeiro medium [17] and examined with a Nikon Labophot light microscope. For identification illustrations, pencil drawings were prepared using micrographs taken by a Nikon DS-Fi1 and a camera lucida attached to the same microscope. Some drawings were based on previously published designs by in [16,18,19].

2.6. Nomenclature and Authorship of Species

Although most works have cited the genus *Lepisma* and its derivatives *Neoasterolepisma* and *Tricholepisma* as feminine, recent nomenclatural changes have assigned them to neuter gender [20,21]. Therefore, this change will be adopted for the nomenclature used in this work. The authorship of species from the Mediterranean region mentioned in this work has been indicated in the commented checklist and in the identification key; only authors of species occurring outside the Mediterranean region were indicated in other parts of the text of this work.

2.7. Distribution Maps and Analysis

Distribution maps were generated with ArcGis Desktop 10.8.1. In the maps we have tried to include, we considered not only the records of these species in the Mediterranean Basin, but all records even outside the study area, to provide a better idea of their current distribution range. However, records far away from the study area (e.g., America) were not included to improve the visualization of the maps. For the calculations of occurrence and endemism by country, only species with confirmed and not doubtful records have been considered.

3. Results and Taxonomic Discussion

Up to now, a total of 35 species of *Zygentoma* have been found living with ants in the Mediterranean countries. Six of them (17.7%) belong to the family Nicoletiidae and twenty-nine (82.3%) to Lepismatidae. Two of the Nicoletiidae species (belonging to the genus *Coletinia*) are considered as accidental in ant nests and three of the Lepismatidae species (specifically, those belonging to the genus *Lepisma*) are considered as facultative or occasional with ants. The remaining species are classified as obligate myrmecophiles, although the biology of those belonging to the genus *Lepismina* is poorly known. Nine additional species (three of Nicoletiidae and six of Lepismatidae) are probably associated with ant colonies, despite the few records and scarce information on their habitat, because they are very closely related to other species that are clearly myrmecophiles. For a more exact distributional information, see the Supplementary Materials Table S1.

3.1. Commented List of Ant-Associated Silverfish from Mediterranean Countries

Here, we provide a comprehensive and updated checklist of all myrmecophilous silverfish species. For each taxon, the state of knowledge of each species is discussed, as well as their confirmed and updated known distribution. For those species with new unpublished records, the details of this material are included.

Family **Lepismatidae**.

Subfamily **Acrotelsatinae**.

Genus **Lepismina** Gervais, 1844 (Figure 1).

A little-studied genus that requires a deep review. Three myrmecophilous species are distributed throughout North Africa and the most southwestern part of Asia. The original descriptions are old, so the most valuable redescriptions were given in [19,22]. However, several characteristics (especially body shape) are variable enough to discard them from identification keys [23].

Lepismina audouinii (Lucas, 1840) (Figure 1).

This myrmecophilous species was recorded in nests of *Cataglyphis* and with *Anacanthotermes* termites. It is distributed in north Africa (Algeria, Libya, and Egypt). It is important to note that *Lepismina emiliae* Escherich, 1903 (described from Algeria and reported with ants of the genus *Formica*) has been considered by most authors as a synonym [24]. However, Irish [23] considered *L. emiliae* as a separate species. We do not have enough information to decide about this controversy, so for the moment both species are considered synonyms and have been put together in the identification key.

Lepismina aurisetosa Wahlgren, 1906 (Figure 1).

As the previous species, *L. aurisetosa* was found in nests of *Cataglyphis* ants and *Hodotermes* termites. It was described from Egypt (near Cairo). Its current distribution includes north Africa (Egypt, Libya, and Sudan) and Southern Asia (Afghanistan, Turkey, Turkmenistan, Kuwait, and Sudan). This species could be usually confused with other *Lepismina* species such as *L. persica*.

Lepismina persica Escherich, 1905 (Figure 1).

This species was recorded living in ant nests of the genera *Cataglyphis*, *Messor*, *Formica* and *Tetramorium*. Up to now, *L. persica* is present in southwestern Asia (Israel, Syria, and Turkmenistan). In Turkmenistan, the possibility of a misidentification with *L. plurisetosa* should not be ruled out.

Subfamily **Lepismatinae**.

Genus **Lepisma** Linnaeus, 1758 (Figure 2).

This genus includes three species from the Mediterranean region, two from the Caucasian area, and one species from Australia (*Lepisma umbrum* Smith, 2015), which suggest that the ancient distribution of this clade was quite large. The Mediterranean species can be divided into two groups. One of them contains only *Lepisma saccharinum*, the “authentic” silverfish, with dorsal uniform of silvery greyish colour, and a group of two small darker-coloured species bearing some stripes of whitish scales. *L. saccharinum* is mostly a synanthropic species; however, in the Mediterranean region it has been found in other natural environments, including ant nests. The second group of Mediterranean *Lepisma* includes facultative myrmecophilous species and requires an exhaustive and deep revision.

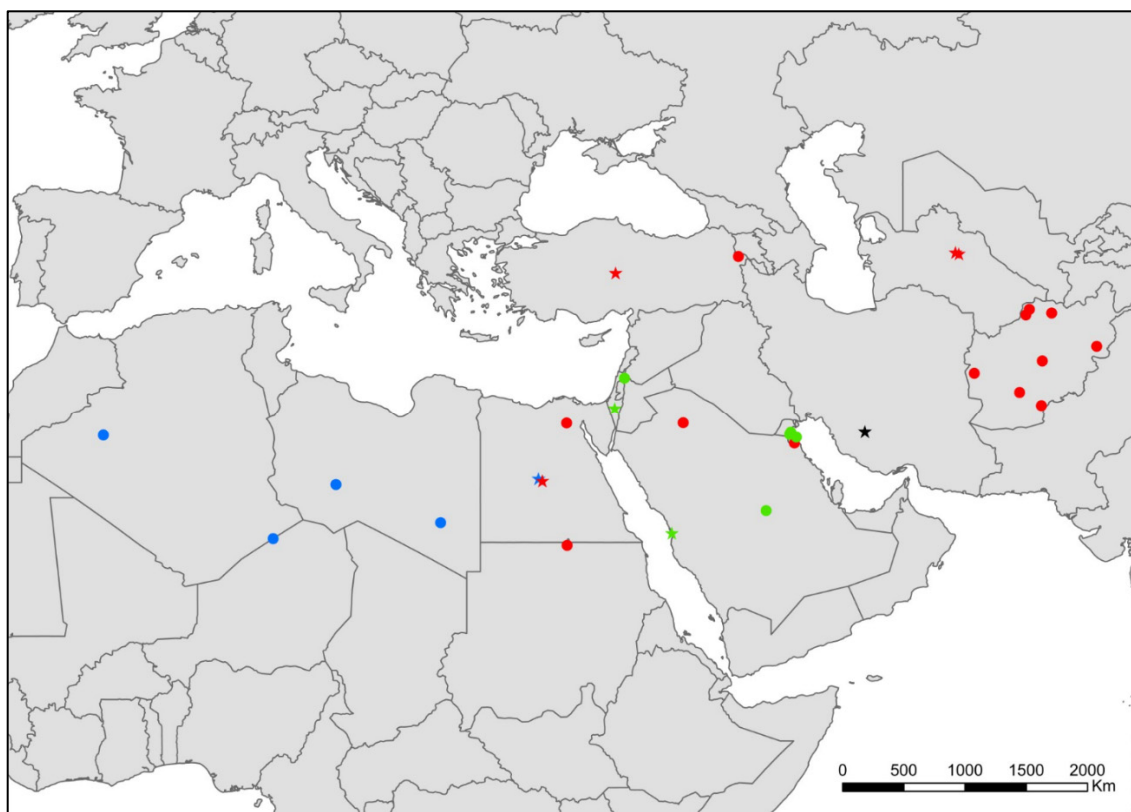


Figure 1. Distribution of species belonging to the genus *Lepisma*. *L. persica* (black), *L. audouinii* (blue), *L. aurisetosa* (red), and *L. plurisetata* (green). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Lepisma chlorosoma Lucas, 1846 (Figure 2).

This is a facultative myrmecophilous species usually found with *Bothriomyrmex*, *Camponotus*, *Crematogaster*, *Pheidole*, *Tapinoma*, or *Tetramorium* ant species. The most updated description is presented in [16]. It is important to note that *L. demissa* Silvestri, 1908 and *L. lucasi* Grassi & Rovelli, 1889 are considered important synonyms of this species. In addition, *L. brachyura* Rafinesque-Schmaltz, 1814 could also be a synonym of this species, but until new taxonomic evaluation, we prefer to consider it as *species inquirenda*. A revision of North African forms identified as *L. chlorosoma* and *L. demissa* should be carried out to unravel their taxonomic status and the possibility of coexistence of different cryptic species. Up to now, *L. chlorosoma* is present in southern Europe (Portugal, Spain, and Italy, including the islands of Sardinia and Sicily) and north Africa (Morocco, Algeria, and Tunisia). In this work we have included the first record for Croatia. Additional material under study from other countries is available, although these unpublished samples suggest that there is an unexpected diversity of forms with a similar colour pattern but probably corresponding to different species. The colour pattern, i.e., dark greyish or blackish with transverse rows of white scales on the posterior margin of the head and the three thoracic nota, is shared with *L. baetica*, although this species is slightly darker and shinier, and has a different urotergal chaetotaxy. In fact, this resemblance of *L. chlorosoma* to *L. baetica* and to other yet undescribed species has led to specimens that most probably do not belong to *L. chlorosoma* being identified by non-specialists as this species. The map of *L. chlorosoma* provided by Gbif includes, for example, a citation in south-eastern Spain (in Almería province) derived from a photograph included in iNaturalist. Our knowledge of the distribution of the genus *Lepisma* in the Iberian Peninsula allows us to be fairly certain that this specimen corresponds in fact to *L. baetica*, although in reality a complete certainty that ratifies this hypothesis could only be obtained by examining characteristics such as the chaetotaxy of the infralateral

groups of abdominal tergites (which is, according to the original description of *L. baetica* and to the key provided here, the most valid characteristic to distinguish both species). The information sources used for these maps is inappropriate regarding *Zygentoma*, since they do not include correct records of the scientific literature such as those of *L. baetica* and *L. chlorosoma* given in [13] and other specialists. Moreover, the record of *L. chlorosoma* from north-eastern continental Greece also included in iNaturalist could correspond to this species or not, since we have examined a few specimens from this country that, despite their poor conditions, deserve to be described as new species when enough well-preserved material will be available for specialists. The records of iNaturalist of *L. chlorosoma* in Croatia are congruent with our new record of this species in this country because the author of the photos sent us some specimens to confirm the identity. This is the correct way to proceed for an accurate record, although the identification should be *Lepisma* sp. before its formal publication in this paper.

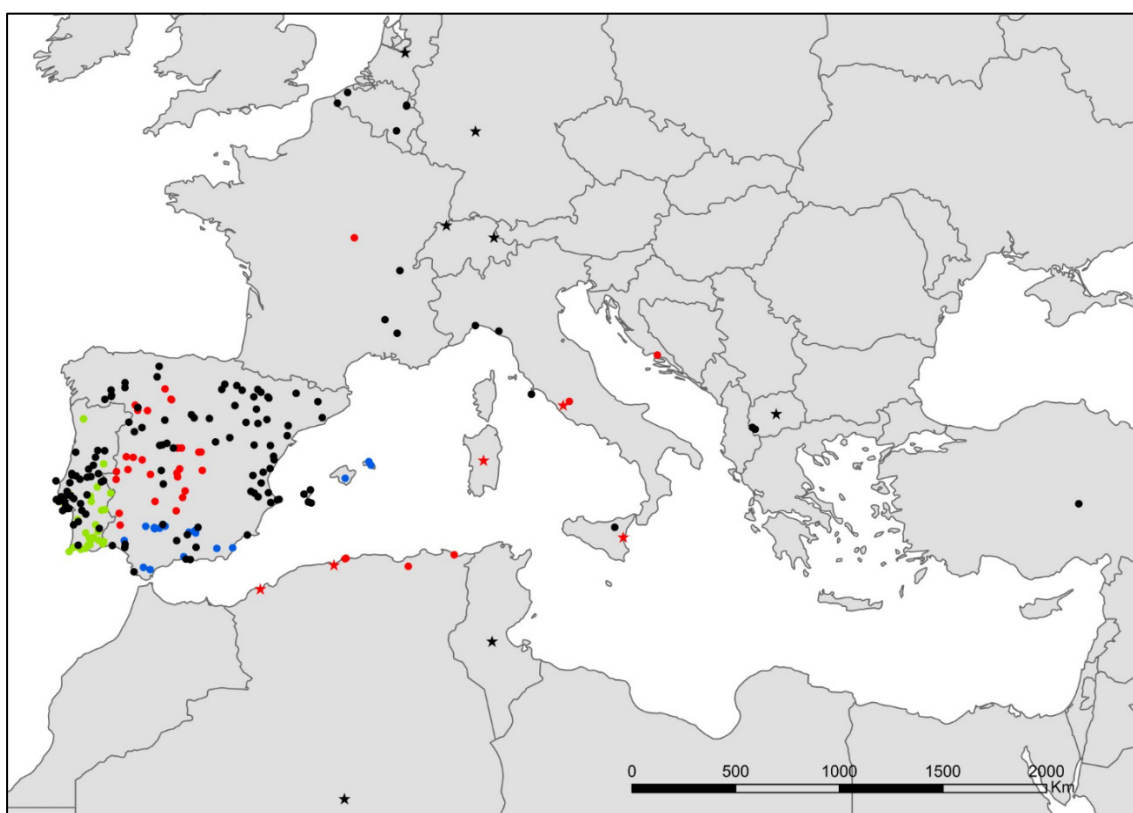


Figure 2. Distribution of species belonging to the genus *Lepisma* in the Mediterranean Region. *L. saccharinum* only occurring in natural habitats (black), *L. baetica* (blue), *L. chlorosoma* (red), and *L. chlorosoma/L. baetica* (green). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

New records. Croatia–Podstrana: near Split, 3♀ (Anton Gjeldum col.), 24-V-2021, with *Crematogaster* sp. (UCO, Ref. Z2758).

Lepisma baetica Molero-Baltanás, Gaju-Ricart, Bach de Roca & Mendes, 1994 (Figure 2).

This species is considered as an occasional or facultative myrmecophilous silverfish [13]. It is commonly reported with ants of the genera *Aphaenogaster*, *Crematogaster*, *Leptothorax*, *Pheidole*, or *Tetramorium*, but also without ants in several natural habitats (probably several records without ants correspond to abandoned nests). Its distribution is limited to southern and eastern Spain, including the Balearic Islands. However, it could be probably present in southern Portugal, so the records of the related species *L. chlorosoma* should be reviewed as both species are virtually identical without microscopic examination of their

chaetotaxy. Mendes [25] admitted that some specimens collected in Portugal by him and attributed to *L. chlorosoma* could be *L. baetica*.

Lepisma saccharinum Linnaeus, 1758 (Figure 2).

The most studied, distributed, and known silverfish species of the world is native to the Mediterranean region, from Portugal to Turkey, with a few records as free-living in Central Europe. This species is mostly found as a synanthropic species in all continents, but it has been occasionally found with ants in those areas where it lives in natural habitats. Although most records of this species do not mention the habitat, some works registered the association of this species with ants in the Iberian Peninsula and particularly to red wood ants in Belgium [15]. In addition, it was reported in nests of swallows or wasps. Figure 2 and Appendix A only consider records where the occurrence of this species in natural habitats (with or without ants) is expressly mentioned.

Genera *Neoasterolepisma* Mendes, 1988 and *Tricholepisma* Paclt, 1967.

These two genera are very related and probably a future revision will prove that the diagnostic characteristics distinguishing both are homoplastic. In this case, we prefer to treat them together. Most species are well described in [16]. As the most diverse group of ant-associated silverfish of the Mediterranean Basin, we present their species clustered in several sets that can be considered more natural groups based on their biology or their distribution patterns.

Group 1. *Messor* specialists with sexually dimorphic metatibiae and bearing some series of strong urosternal spines (Figure 3).

This group includes four species with shared morphological characteristics that suggest their phylogenetic closeness, especially a series of strong pigmented spines in some abdominal sternites (Figure 4e). These ant-associated silverfish are mainly widespread over southwestern Europe and are generally associated with *Messor* ants. However, sometimes they can be found with other ant genera.

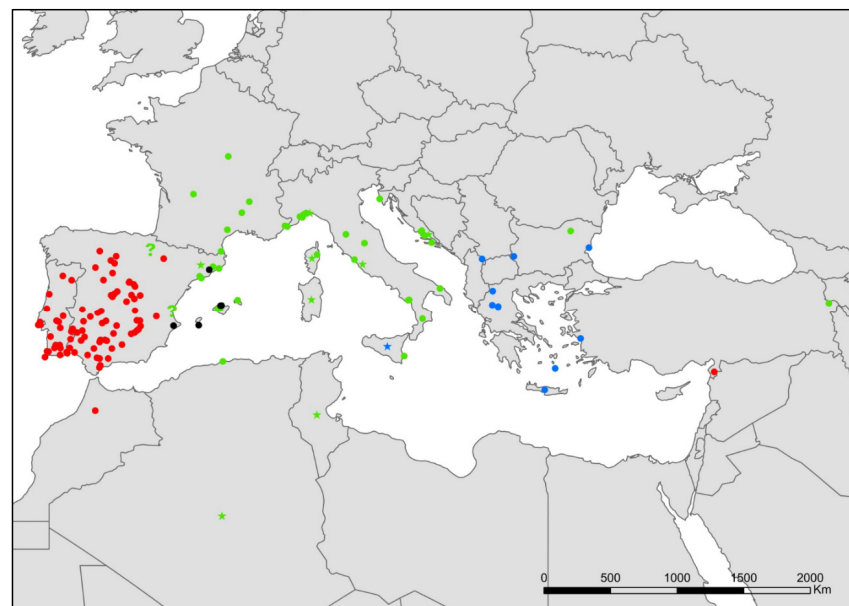


Figure 3. Distribution of species belonging to Group 1 of the genus *Neoasterolepisma*. *N. balearicum* (black), *N. balcanicum* (blue), *N. lusitanum* (red), *Tricholepisma aureum* (green), and doubtful records of *T. aureum* (?). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

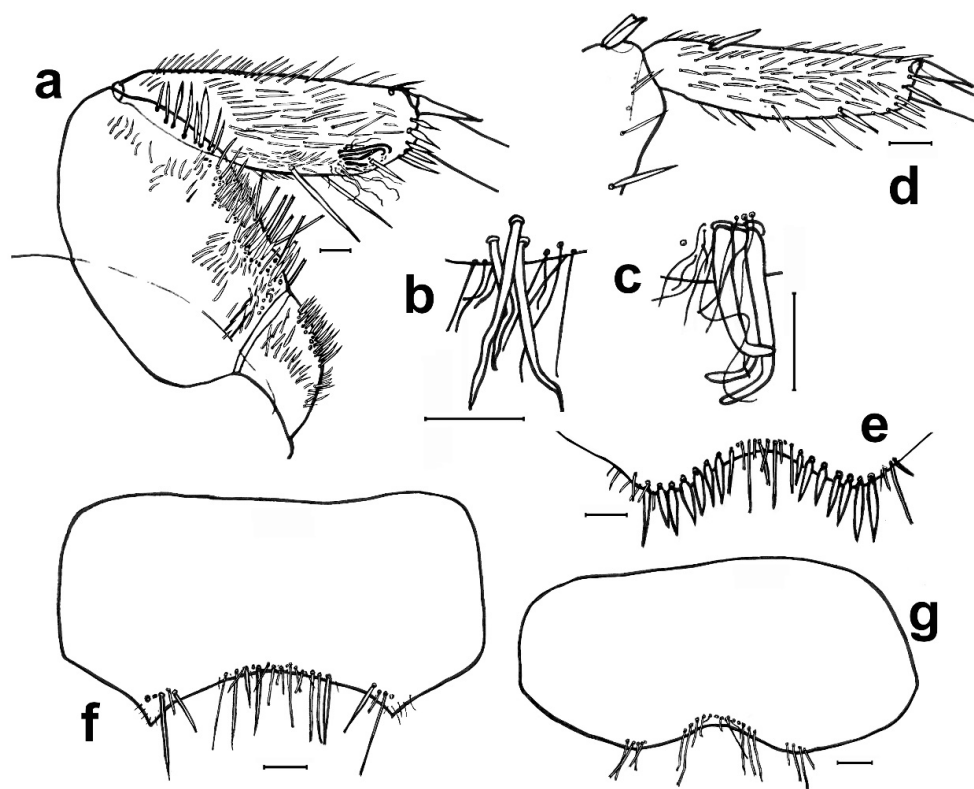


Figure 4. Some characteristics defining groups inside myrmecophilous Lepismatinae. (a): Hind leg of the male of *Tricholepisma aureum*, showing specialized chaetotaxy on tibia, femora, and trochanter. (b,c): group of strong and more or less hooked spines of the apical half of the tibiae of two specimens of *T. aureum*. (d): Metatibiae of the male of *Neoasterolepisma pallidum*, not modified with respect to those of the female. (e): Hind margin of the VII urosternite of *N. lusitanum*, showing strong sclerotized spines. (f): Seventh abdominal sternite (urosternite VII) of *N. crassipes*, showing pseudostyli in its hind margin. (g): Urosternite VII of *N. curtiseta*, with 1 median and 1 + 1 lateral usual bristle-combs, without modified chaetotaxy or shape of the hind margin. Scales: 0.1 mm.

Neoasterolepisma balcanicum (Stach, 1922) (Figure 3).

This species has been found in southern Europe (Albania, Bulgaria, Greece, including Crete and Santorini Islands) and Turkey. Its occurrence in Sicily, reported in [26] should be checked because of the possible confusion with the very similar *N. balearicum*.

Neoasterolepisma balearicum Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1997.

Described from Mallorca (Balearic Islands) and the Eastern areas of Spain. It is morphologically clearly related to *N. balcanicum* and *T. aureum*, sharing with them the same type of modified chaetotaxy in the hind leg of males (Figure 4a,c). Future works should assess the relationship between these species.

Neoasterolepisma lusitanum (Wygodzinsky, 1945) (Figure 3).

It was described from Portugal but also occurs in the south and west of Spain and can be considered vicariant with the remaining three species of this cluster. The modifications of the metatibiae of males are different to the remaining species of the group, suggesting that its relationship with the other species is slightly more distant. *N. lusitanicum* tends to inhabit *Messor* ant nests with other ant-associated silverfish species.

Tricholepisma aureum (Dufour, 1831) (Figure 3).

Lepisma aurea was described in 1831 from Valencia (Spain) [27]. However, this description can correspond to any yellowish ant-associated species. This name was applied to a lot of records from the 19th to 20th centuries that cannot correspond to the originally described species. Escherich [18] updated the description in his work providing additional morpho-

logical data and established the presence of a row of macrochaetae on the posterior margin of each thoracic notum as an important diagnostic characteristic for this species, at that time shared only with *Lepisma gyriniformis*. Curiously, further studies have not found any species with these characteristics in the Valencia region. Escherich [18] also indicated that this species occurs in the north-eastern Iberian Peninsula (Navarra and Catalonia), but after exhaustive samplings it has only been found in Catalonia, but not in Navarra [13,28,29]. Therefore, it is impossible to identify which of the yellowish myrmecophilous Lepismatidae silverfish of Valencia or Navarra is the authentic *Lepisma aurea* found by Dufour. We assume the description presented in [18] and later in [16] as attributable to the name *Tricholepisma aureum*, not considering it impossible (but doubtful) that this species could occur in Valencia region, as presented in the map for this species (Figure 3). Paclt [24] established the subgenus *Tricholepisma* by attributing special importance to the characteristic of the thoracic rows of macrochaetae, and Mendes raised this to the generic level. Considering the inaccurate records of this species in scientific literature and the possible confusions with related species (mainly those included in this Group 1), its geographic distribution remains slightly unknown. It probably ranges from northeastern Spain and the Balearic Islands to Sicily and Croatia, with their occurrence being doubtful in other areas. Some records in eastern regions (e.g., Romania and Turkey) could be confusions with *N. balcanicum* or other related species. Furthermore, its occurrence in Northern Africa (Algeria and Tunisia) should be considered with caution, although it is not impossible because of the proximity of Tunisia to Sicily. It is interesting to note that *Tricholepisma aureum* produces cuticular hydrocarbons resembling those of *Messor* [30]. This strategy is probably shared with other myrmecophilous *Messor* specialists.

Group 2. *Messor* specialists with more or less strong sexual dimorphism in the metatibiae and with-out a series of strong urosternal spines and presenting pseudostyli (Figure 5).

This group includes six species lacking modified spines in their abdominal sternites but some lateral acute expansions in the seventh urosternite, called pseudostyli (Figure 4f).

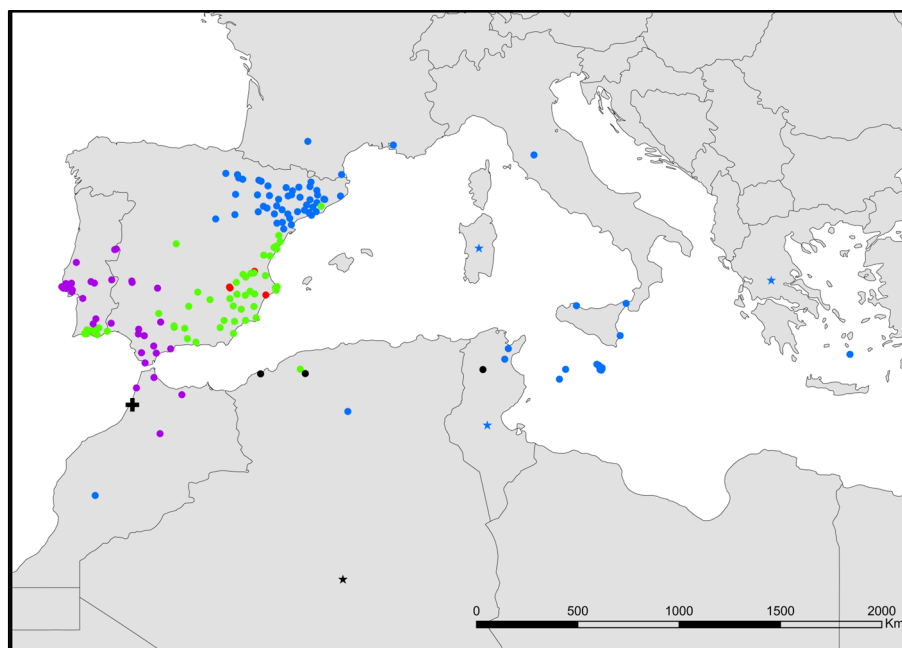


Figure 5. Distribution of species belonging to Group 2 of the genus *Neoasterolepisma*. *N. gauthieri* (black), *N. crassipes* (blue), *N. calvum* (red), *N. foreli* (green), *N. soerenseni* (purple) and *N. imitans* (+). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Neoasterolepisma gauthieri (Wygodzinsky, 1941) (Figure 5).

This species was described from North Africa (Algeria) and then also recorded in Tunisia. A new population initially attributed to this species (with a different subspecific status: *Neoasterolepisma gauthieri calva*) was found in south-eastern Spain. However, in this work we resolve its status. Therefore, up to now this species has not occurred in the Iberian Peninsula and is exclusive to northern Africa.

Neoasterolepisma calvum Molero-Baltanás, Mendes, Gaju-Ricart & Bach de Roca, 1994 *stat. nov.* (Figure 5).

We have considered this taxon with the specific level, although it was described as a subspecies of *Neoasterolepisma gauthieri*. Morphological differences between both taxa are discussed in [28] and highlighted in the identification key. The geographic isolation of both species also supports considering them as separated and independent species. Up to now, it has only been present in southwestern Spain.

Neoasterolepisma crassipes (Escherich, 1905) (Figure 5).

This species has a wide distribution over the Mediterranean Basin. It occurs from the north-eastern Iberian Peninsula to Greece in southern Europe, including several European islands (e.g., Sardinia, Sicily, or Malta). Furthermore, *N. crassipes* has been recorded in North Africa (from Morocco to Tunisia). It is one of the biggest myrmecophilous silverfish (up to 13 mm length), generally associated with *Messor* ants and to other myrmecophilous *Zygentoma*, such as *N. wasmanni* or *T. aureum*. The resemblance of the modified chaetotaxy of the hind legs of males suggests the possibility of a close relationship with species of Group 1.

Neoasterolepisma soerenseni (Silvestri, 1908) (Figure 5).

This species was described from North Africa (Morocco) and it is also found in the southwestern Iberian Peninsula. The species *N. marianeki* (Wygodzinsky, 1945), described from Portugal, resulted in being a synonym of *N. soerenseni* [28].

Neoasterolepisma foreli (Moniez, 1894) (Figure 5).

This species is distributed in North Africa (Morocco and Algeria) and in the southern Iberian Peninsula, reaching Catalonia in the most northern part. *N. foreli* is usually found in *Messor* ant nests with other myrmecophilous silverfish (e.g., *N. spectabile*, *N. lusitanum* and others). Its distribution area is almost vicariant with *N. soerenseni*, although both species have been found together in one nest in Seville (Spain) in the limit of their respective distribution areas [28]. Both species share a special type of dorsal scales that are not found in any other species of the genus, suggesting a close phylogenetic relationship.

Neoasterolepisma imitans (Mendes, 1980) (Figure 5).

This silverfish species was not found after its original description. In the unique available record, it was recorded with unspecified ants. Its morphological similarity with species of this Group 2 suggest that it could be associated with *Messor* colonies.

Group 3. Species that are mainly associated with *Messor* or *Aphaenogaster* ants, with sexual dimorphism in the metatibiae, without a series of strong urosternal spines and lacking pseudostyles (Figure 6).

This group includes six species lacking modified abdominal spines or pseudostyli (Figure 4g) but sharing with Groups 1 and 2 the occurrence of sexual dimorphism related to specialized chaetotaxy and/or shape of the male metatibiae. Although mainly associated with *Messor*, some species are *Aphaenogaster* specialists or can be found occasionally (but more frequently than previous Groups) in nests of other ant genera.

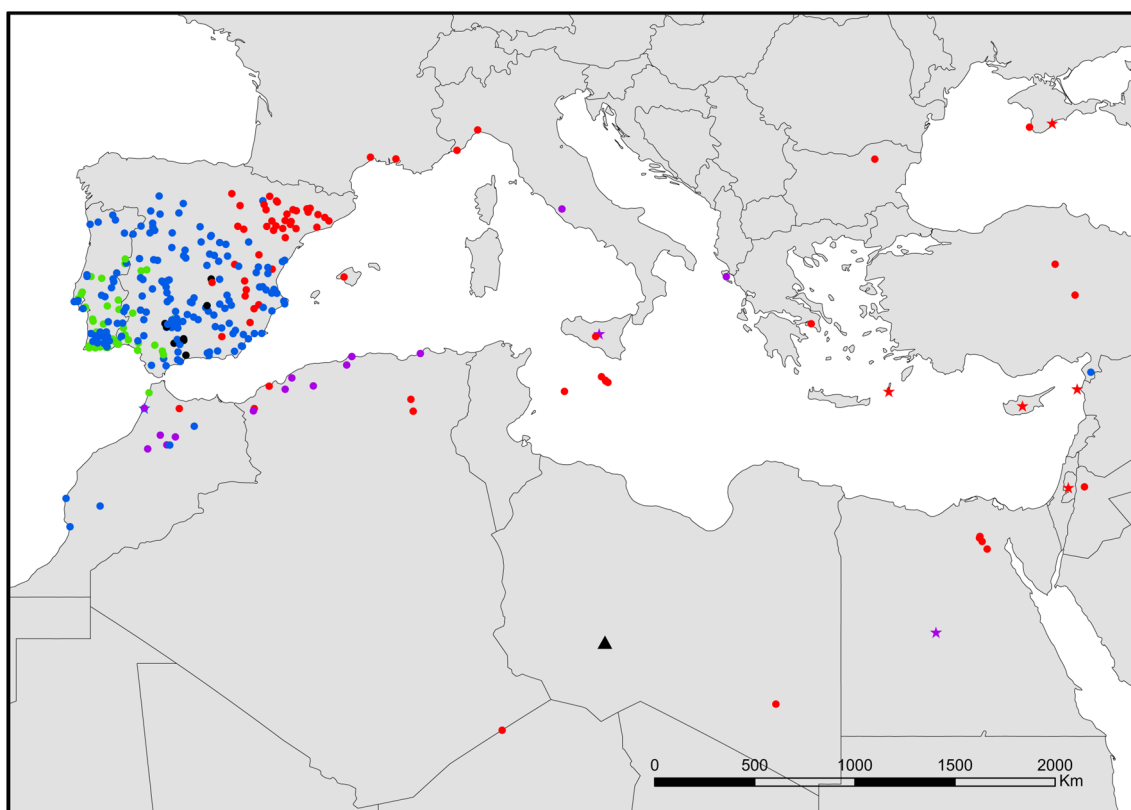


Figure 6. Distribution of species belonging to Group 3 of the genus *Neoasterolepisma*. *N. delator* (black), *N. spectabile* (blue), *N. wasmanni* (red), *N. hespericum* (green), *Tricholepisma gyriniformis* (purple) and *N. spectabiloides* (▲). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Neoasterolepisma delator Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1996 (Figure 6).

This species is endemic to the Iberian Peninsula. It occurs from the centre to southern provinces (from Toledo to Málaga), immediately at the east of the *N. hespericum* distribution. It is found mainly in *Aphaenogaster* nests as a specialist of these ants [13]. It is very closely related to *N. hespericum* and both were previously considered as the same species under the denomination of *N. iberica*: silverfish whose males have metatibia with a relatively rounded and convex hind margin and some ciliary setae (Molero-Baltanás et al., 1996). However, Molero-Baltanás et al. [31] split these silverfish into the two recognisable and different taxa. In addition, they considered that the original description of *N. iberica* was based on *N. wasmanni* juveniles. The distinction between *N. delator* and *N. hespericum* requires microscopic examination of the specialized chaetotaxy of male metatibiae or some details of the coxites VIII of females.

Neoasterolepisma hespericum Molero-Baltanás, Bach de Roca & Gaju-Ricart 1996 (Figure 6).

This species was previously included in *N. iberica* and split as a different species from *N. delator* in [31]. Considering only the silverfish registered as *N. hespericum*, this species is endemic to southern Spain and is mainly associated with *Aphaenogaster* ants. It has an almost vicariant distribution with *N. delator*. Here we present the first reliable record for Africa, concretely in the western coast of Morocco. There is a previous record of *N. iberica* from Morocco [32] that could correspond to *N. hespericum* and could suggest that this species has a Iberic–Moroccan distribution.

New records. Morocco–Asilah: 3 km to Larache, 3♂ (two subadults) + 2♀ (Miquel Gaju col.), 05-V-1993, with *Aphaenogaster* sp. (UCO, (Ref. Z2659).

Neasterolepisma spectabile (Wygodzinsky, 1945) (Figure 6).

This species was first described from Portugal and then found in southern and eastern Spain, being absent in the Balearic Islands. It has also been recorded in Morocco. Therefore, this silverfish species can be defined as Ibero–north African. It appears with several ant species, but mostly with *Messor* colonies [13]. In its distribution area, it tends to be the most frequent *Messor* specialist.

Neasterolepisma spectabiloides Mendes, 1988 (Figure 6).

This species is only known from its original description from Libya where it could be an endemism. It was recorded with unidentified ants, but it could be associated with *Messor* considering the morphological resemblance of abdominal sternites and male metatibiae with species of this group (e.g., *N. spectabile*).

Neasterolepisma wasmanni (Moniez, 1894) (Figure 6).

It was described from northern Africa (Algeria) and this is one of the most recorded myrmecophilous Lepismatidae species in the Mediterranean area and beyond. This species ranges from eastern Iberian Peninsula and Algeria to Tunisia and Black Sea coasts. Significant variability was detected in males metatibiae of different populations [16]. Most of this can be interpreted as intraspecific variability, corresponding to different stages of the postembryonic development of the sexual secondary characteristics associated with male metatibiae. Nevertheless, the populations of different countries should be intensively studied due to the possibility of similar situations occurring to that described in Spain [31]. Due to its ubiquitous distribution, several of the specimens previously studied could correspond to different species. It is important to note that *Lepisma skorikowi* Escherich, 1905 (described from Crimea) has been considered a synonym of this species. Furthermore, Paclt [24] and Mendes [16] considered that *Lepisma escherichi* Karawajew, 1910 (described from Turkmenistan) is probably a synonym of *N. wasmanni*. However, they did not give any reason to justify this statement. Then, Kaplin [33] described two new species of *Neasterolepisma* from Turkmenistan (*N. deserticola* and *N. psammophilum*) that could be related to *L. escherichi* (even being conspecific). Kaplin [34] considered that *N. wasmanni* could occur in Krasnodar (near Crimea), but without providing records. With this situation, we think that *L. escherichi* should be considered as *species inquirenda* and that the eastern limit of the distribution of *N. wasmanni* reaches the Black Sea in Crimea. This species has been recorded as introduced in Peru [35], but a review for an accurate identification is advisable.

Tricholepisma gyiriniforme (Lucas, 1846) (Figure 6).

This species was described from North Africa (Algeria). Afterwards, this silverfish was recorded in Egypt, Italy (Sicily and Roma), and Greece (Corfu). The Italian records were previously identified as a different species (*Lepisma lubbocki* Grassi & Rovelli, 1889) but the synonymy was established in [36]. The number of samples with ants is low but is mainly associated with *Aphaenogaster* and *Messor* ants. It could be a generalist species. A good description of this species was given in [19] and updated in [16]. Although included in the same genus than *T. aureum*, this species is probably more related with the species included in this Group 3 due to the ciliary setae in the modified male metatibiae.

Group 4. Species without sexual dimorphism on metatibiae and without morphological specializations in abdomen such as urosternal spiniform setae or pseudostyli (Figure 7).

Species of this group lack a modified shape or chaetotaxy in male metatibiae (Figure 4d). Most of them could be endemic to a small geographic region. Some species occurring outside the limits of the Mediterranean region (for example, Macaronesian endemisms) can be included in this group. These species are probably facultative or generalist myrmecophiles, but the information on most of them is scarce (a low number of records and lack of ecological information); therefore, for these taxa it is not possible to state which is the current geographic distribution or the nature of the ant-association of most species.

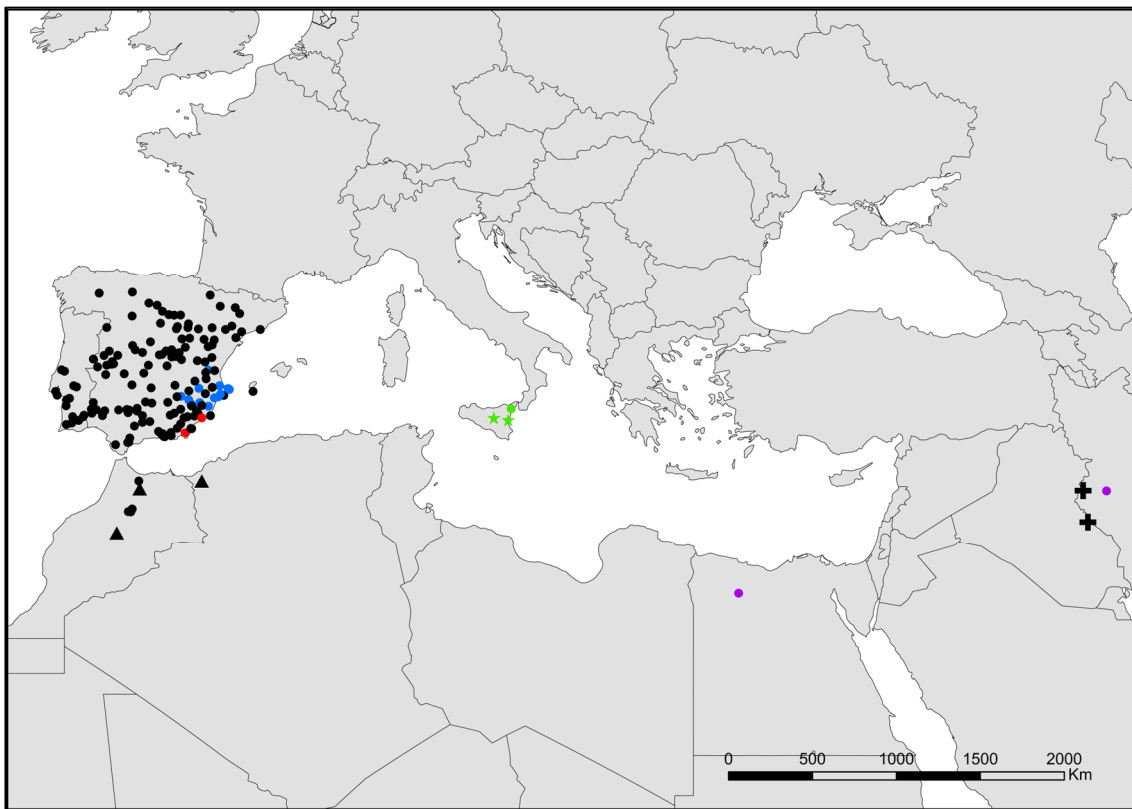


Figure 7. Distribution of species belonging to Group 4 of the genus *Neoasterolepisma*. *N. curtiseta* (black), *N. pallidum* (blue), *Tricholepisma indalicum* (red), *N. angustothoracicum* (green), *N. priesneri* (purple), *N. stachi* (▲), and *N. evansi* (✚). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Neoasterolepisma angustothoracicum (Grassi and Rovelli, 1889) (Figure 7).

This myrmecophilous species found with *Messor* ants was only reported in Sicily (Italy) and is considered as an endemism of this island. However, the possibility of its occurrence in southern continental Italy should not be discarded. The most updated redescription is given in [37].

Neoasterolepisma curtiseta Mendes, 1988 (Figure 7).

This species is endemic to the Iberian Peninsula (Spain and Portugal). It is only absent in the most northern parts of Spain. All silverfish identified previously as *N. myrmecobium* from the Iberian Peninsula resulted in being *N. curtiseta* after the review of Mendes [16]. This is a generalist species of several genera of ants (e.g., *Camponotus*, *Formica*, *Messor*, *Cataglyphis*, *Pheidole*).

Neoasterolepisma pallidum Molero-Baltanás, Gaju-Ricart & Bach de Roca, 1995 (Figure 7).

This silverfish is endemic to south-eastern Spain. It is associated with several ant genera as a generalist, although is more frequent with *Aphaenogaster* ants in its distribution range.

Neoasterolepisma evansi (Silvestri, 1923) (Figure 7).

N. evansi was described from the northwest of Bagdad (Iraq). It was only known from this locality until Kahrarian et al. [38] reported this silverfish again from western Iran, suggesting that its geographic range is broader than presumed. It was found with unidentified ants.

Neoasterolepisma priesneri (Stach, 1946) (Figure 7).

This species was described from the northwest of Egypt with unidentified ants and then found in western Iran [39]. As *N. evansi*, its distribution area is not well known.

Neoasterolepisma stachi (Wygodzinsky, 1941) (Figure 7).

This silverfish was recorded in north-western Africa (Morocco and Algeria) with unidentified ants. It is very close to *N. myrmecobium* and other Macaronesian species.

Tricholepisma indalicum Molero-Baltanás, Bach de Roca & Gaju-Ricart 1995 (Figure 7).

This species is endemic to a small area of south-eastern Spain (Murcia and Almería provinces). It was only recorded with *Camponotus sylvaticus* ants, so this silverfish could be a *Camponotus* specialist, but more samplings are needed to extract proper conclusions. It could be considered as a threatened species giving the size of its distribution area and the specificity of its habitat. It was included in the *Tricholepisma* genus considering its dorsal thoracic chaetotaxy. However, it can be more closely related to other species without sexual dimorphism in metatibiae (e.g., *N. curtiseta* and *N. pallidum*).

Group 5. Uncertain *Neoasterolepisma* spp.

In this group, we have included records of silverfish whose identification can be considered as uncertain.

Neoasterolepisma cf. *myrmecobium* (Silvestri, 1908).

Initially described from the Cape Verde islands, specimens identified as *Neoasterolepisma myrmecobium* in other geographic areas require a deep revision. Most of the collected Mediterranean silverfish attributed to this species have been corrected, reassigned to other species, or have been the basis of the description of new species (e.g., *N. curtiseta* in the Iberian Peninsula or *Afrolepisma wygodzinskyi* Mendes, 1981 in Santa Helena Island). Records of this species from Peru [40], Turkey [41], Sudan [42], and Cameroon [26] have been questioned in [16] and probably correspond to other described or undescribed species. However, records from Morocco (e.g., those presented in [43]), could correspond to the authentic *N. myrmecobium* while others could be *N. stachi*, *N. curtiseta*, *N. spectabile* juveniles, or other undescribed species. In fact, Mendes [16] amended some of his identifications in a previous paper [43]. We think that *N. myrmecobium* is probably a Cape Verde endemism (where this species was originally described) absent in Mediterranean countries. Perhaps it could occur in some additional islands of the Macaronesian region. However, some specimens previously attributed to *N. myrmecobium* from the Canary Islands resulted in being a new species exclusive of one or two islands. Therefore, a deep review and study should be carried out to understand the actual status of all specimens previously considered as belonging to *Neoasterolepisma myrmecobium* out of Cape Verde islands.

Family Nicoletiidae.
Subfamily Atelurinae (Figure 8).
Tribe Atelurini.

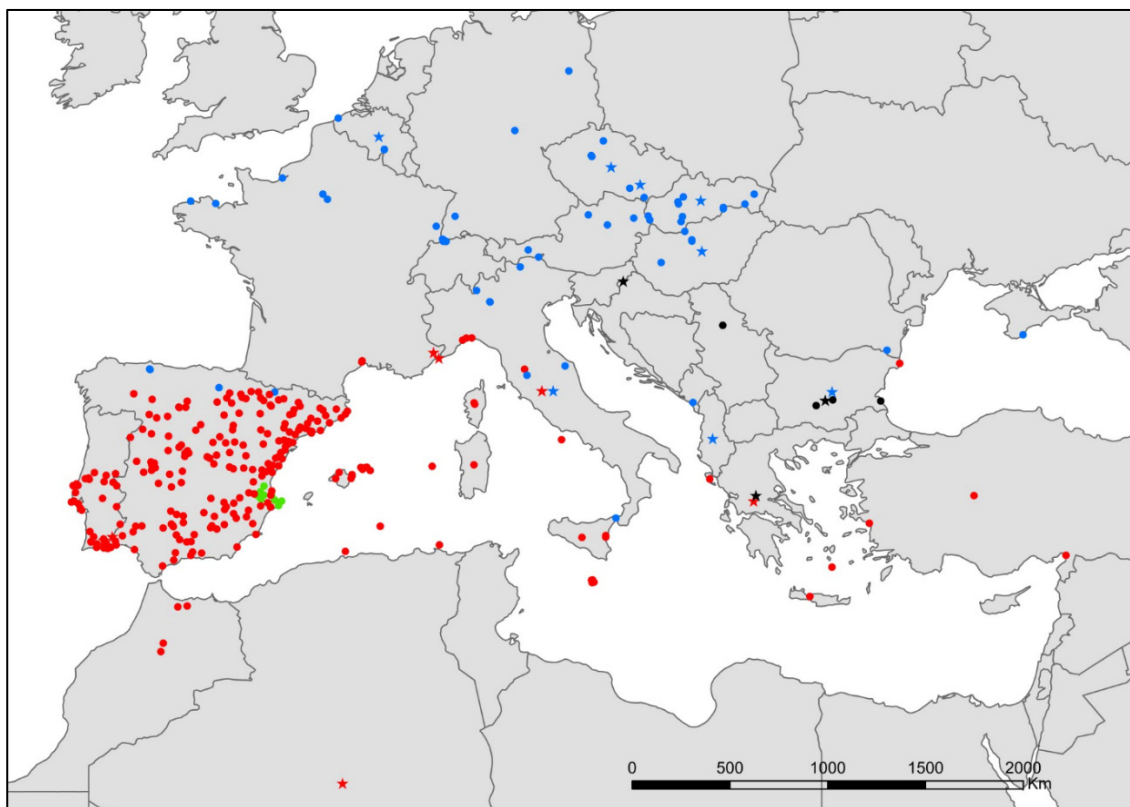


Figure 8. Distribution of species belonging to the genera *Atelura* and *Proatelurina* (subfamily Atelurinae) in the Mediterranean Region. *Atelura montana* (black), *A. formicaria* (blue), *A. valenciana* (green), and *Proatelurina pseudolepisma* (red). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Atelura formicaria Heyden, 1855 (Figure 8).

Described from southwestern Germany [44], this species is widespread over Central Europe. In addition, it is the species of the genus with a wider geographic distribution and the indigenous *Zygentoma* that reaches the highest latitude in natural habitats in Europe. Meineke [45] provides a detailed revision of its geographic distribution in Central Europe and discuss the difficulties of establishing the southern and eastern limits of this distribution. Here, we present the first record for Spain, which represents the westernmost populations of its geographic range. The southernmost reliable citation of this generalist myrmecophile is Sicily. Nevertheless, the eastern limits of this distribution are not clear because it has sometimes been probably confused with other species of the genus (*Atelura montana* in the Balkans or *Atelura abkhazica* in the Caucasus region) and other genera of the subfamily Atelurinae (*Proatelurina* or *Persiatelurina*).

New records. Spain–Asturias: Parque Purificación Tomás (Oviedo), 1♀+ 2 juveniles (Jairo Robla col.), 01-VII-2021, in a nest of *Lasius niger* in an urban park (UCO, Ref. Z2759); 2♂+ 1 juvenile (Jairo Robla col.), 28-VIII-2021 in a nest of *Lasius emarginatus* in an urban park (UCO, Ref. Z2760); **Burgos:** Condado de Treviño, 1♀(Rafa Molero col.), 09-VIII-2017, in a nest of *Lasius* sp. (UCO, Ref. Z2757); **Huesca:** Broto, 1♂(Rafa Molero col.), 26-VIII-2021, riverside forest, in a nest of *Lasius* sp. (UCO, Ref. Z2756).

Atelura montana (Stach, 1946) (Figure 8).

This species was originally recorded and described from Bulgaria and Croatia. It was firstly included in the genus *Lepidoatelura*, but the differences with *A. formicaria* are so reduced that even the specific status is questionable. *Atelura montana* is currently considered as a different species, but the range of variability of some of its characteristics needs to be better established to offer detailed comparisons with its closer species. Most differences are included in [46]. It has been found in Greece [42] and in Serbia [47]. One specimen of the Balkan Peninsula studied in [48] was identified as *A. formicaria* before the description of *A. montana*, and after a review it corresponded to one specimen of *A. montana*. However, there are other records of *A. formicaria* in this area that have not been checked and confirmed (e.g., one from Montenegro in [47]). Thus, the exact geographic range of both species in this area is not clearly delimited. It has been found with ants, but little information has been indicated on these associations.

Atelura valenciana Molero-Baltanás, Gaju-Ricart, Bach de Roca & Mendes, 1998 (Figure 8).

This species is endemic to a reduced area in the Valencian Region of eastern Spain. It has been found with several genera of ants [46], so it can be considered as a generalist.

Proatelurina pseudolepisma (Grassi, 1887) (Figure 8).

This species is strictly Mediterranean. It replaces the *Atelura* species in the southernmost regions of Europe with a clearer Mediterranean climate (from the Iberian Peninsula to Turkey). It has also been recorded in some countries of North Africa. A good description of this species was given in [41]. It is a generalist species that has been found with several genera of ants [13].

Subfamily **Coletiniinae** (Figure 9).

Genus *Coletinia* Wygodzinsky, 1980.

Coletiniinae insects live in subterranean habitats and cannot be considered as myrmecophilous [10]. Nevertheless, some species have been accidentally collected in ant nests. These silverfish have been included in the checklist, considering that the low number of records does not allow a quantitative statement that the association of these species with ants is infrequent.

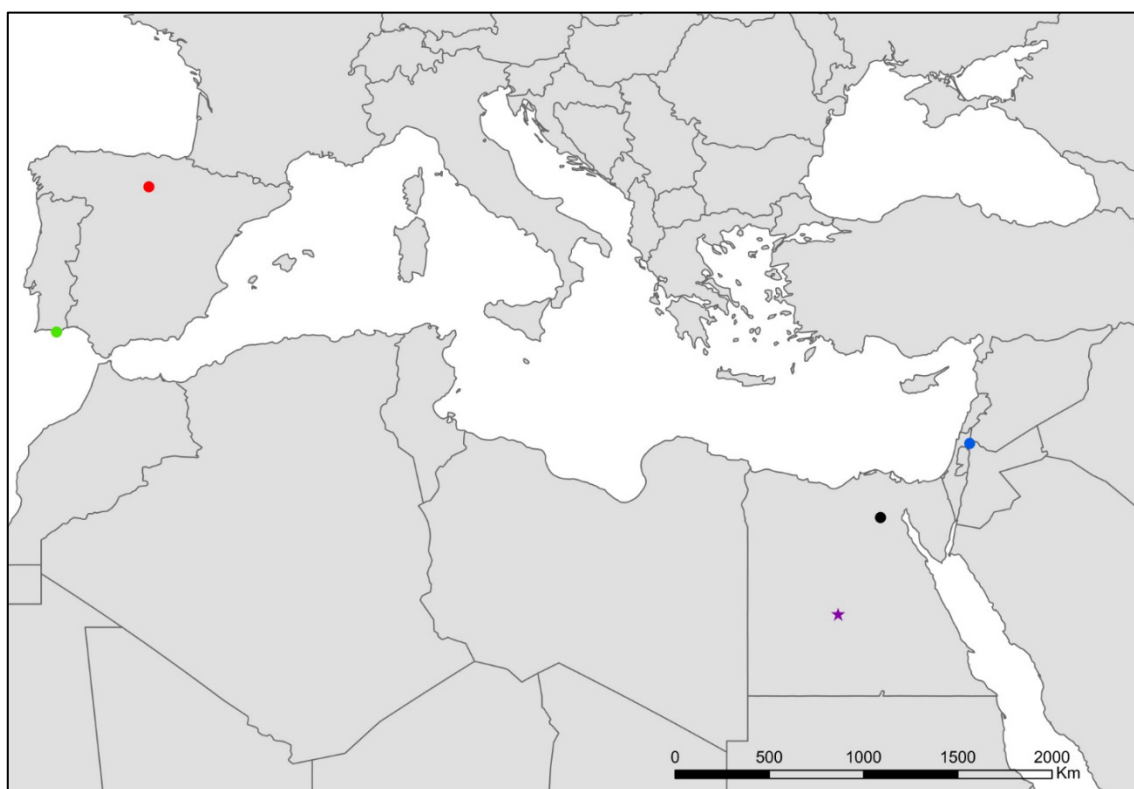


Figure 9. Distribution of species of the genera *Arbiatelura*, *Coletinia*, and *Grasiella* (family Nicoletiidae) in the Mediterranean region. For *Coletinia*, only records where specimens were found with ants are included. For the other two genera, all records are included although their myrmecophilous condition has not been confirmed. *Arbiatelura spinifera* (black), *A. palaestinensis* (blue), *Coletinia* gr. *maggi* (red), *C. mendesi* (green), and *Grasiella leuca* (purple). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Coletinia maggi (Grassi, 1887) (Figure 9).

Described from Italy (Sicily) and found in several countries of southern Europe. However, it is currently under review because of its morphological variability. It was interpreted as intraspecific [49], probably corresponding to a group of related species. One specimen was found in an ant nest of *Messor*, so probably its association with ants is occasional. Figure 9 and Appendix A only consider records where the occurrence of this species in natural habitats expressly mentioned its association with an ant colony.

Coletinia mendesi Wygodzinsky, 1980 (Figure 9).

This species occurs in the southwestern part of the Iberian Peninsula and is one of the most epigeal species of the genus. One specimen was found with *Messor* ants in southern Portugal [50] and it can probably occur accidentally in the deeper chambers of some ant nests. Figure 9 and Appendix A only consider records where the occurrence of this species in natural habitats expressly mentioned its association with an ant colony.

3.2. Possibly Ant-Associated Silverfish without Enough Information

These species probably live with ants due to their close relationship with the previous commented myrmecophilous silverfish. However, there are very few records, and the habitat has not been mentioned.

Lepismina pluriseta Wygodzinsky, 1942. (Figure 1).

Described from Israel and present in Syria. It was also recorded in Kuwait and Saudi Arabia, but confusion with *Lepismina persica* is possible because the insufficient significant differences given for the diagnosis of both species [51] For this reason, both species are

considered together in the identification key. Its occurrence in ant nests is not mentioned, but it is probable considering the ecology of the remaining *Lepismima* species.

Neoasterolepisma necrophilum Mendes, 1992 (Figure 10).

This species was described from Egypt, but it was not recorded again after its original description. It is probably associated with ants, but its habitat was not specified.

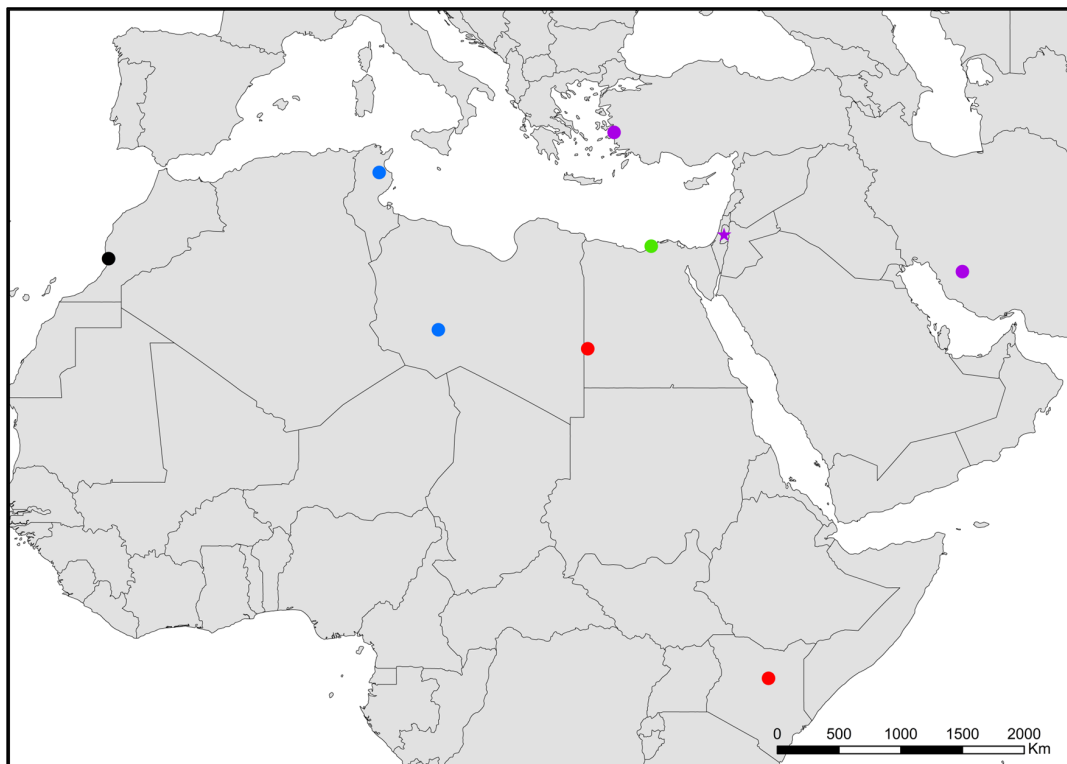


Figure 10. Distribution of species belonging to the genus *Neoasterolepisma* in the Mediterranean region whose association with ants is probable but not confirmed. *N. scorpius* (black), *N. santschii* (blue), *N. paucisetosum* (red), *N. necrophilum* (green), and *N. palmonii* (purple). Circles (●) represent accurate presences and stars (★) presences whose location are not clearly indicated.

Neoasterolepisma palmonii (Wygodzinsky, 1942) (Figure 10).

This species has been found in Iran, Turkey, and Palestine, but without information on its possible association with ants.

Neoasterolepisma paucisetosum (Stach, 1935) (Figure 10).

This species has been recorded in a Mediterranean locality in Egypt and in other locations close to the Indian Ocean in Kenya. The occurrence of this species in Egypt may be accidental, but more samples are needed to extract conclusions about its distribution. However, it is important to note that the special type of labial papillae of this species (called “aufgelöst” when described, i.e., composed of disperse papillae and not compact as in the remaining Palaearctic species) suggests that it could be more related to a group of Afrotropical silverfish of the genus that share this characteristic.

Neoasterolepisma santschii (Silvestri, 1908) (Figure 10).

This species was firstly collected with termites in Tunisia and in an uncommented habitat in Libya [16]. This species could be a facultative termitophile and could also be associated with ants, but more sampling is needed to understand its preferences.

Neoasterolepisma scorpius Mendes, 1993 (Figure 10).

This species is only known from its type locality in North Africa (Morocco), where it was found under a stone close to a scorpion burrow. Although its occurrence with ants has

not been reported, this species is related to other species of the Group 4 (i.e., without sexual dimorphism and provided with a low number of urosternal setae), so its association with ants cannot be discarded.

Arabiatelura palaestinensis Mendes, 1995 and *Arabiatelura spinifera* (Stach, 1935) (Figure 9).

The genus *Arabiatelura* Mendes belongs to the subfamily Atelurinae (Tribe Atopatelurini). It includes three species. *A. perarmata* (Silvestri, 1949) from Ethiopia was reported occurring with ants. However, the other two species are known from the Eastern Mediterranean area, but their habitats have not been commented on and their association with ants has not yet been reported. However, as their closest species, both Mediterranean species could be myrmecophilous. These species are *A. palaestinensis*, described from Israel and *Arabiatelura spinifera* described from a locality close to Cairo in Egypt under a board in a garden.

Grassiella leuca Stach, 1935 (Figure 9).

Grassiella is an enigmatic genus that belongs to the tribe Grassiellini of the subfamily Atelurinae. Curiously, *Grassiella* contains American species [52] except for *G. leuca* described from North Africa (Egypt). Insects of this genus live with ants in several habitats. However, *G. leuca* was found under a stone on the banks of the Nile with no more data about its habitat. Although the description of this species in [19] is extensive, its attribution to the genus *Grassiella* is doubtful. The revision of this species could likely lead to its inclusion in another taxon but, unfortunately, the location of the holotype is unknown and no further record of this species in Egypt has been made.

3.3. Identification Key

This identification key includes all the confirmed ant-associated silverfish of the Mediterranean region. Furthermore, other occasional and accidental myrmecophilous species have been included. All the other potentially myrmecophilous species previously commented have been included in the identification key for facilitating future studies and samplings.

1. Head without eyes. Some abdominal sternites with 1 + 1 vesicles in their hind margin (Figure 11h). Eighth abdominal sternite of females divided in two lateral coxites and a median subgenital plate (Figure 11a) Family **Nicoletiidae** (2).
—Head with black compound eyes. Abdominal sternites without vesicles. Eighth abdominal sternite of females divided in two lateral coxites without a median subgenital plate (Figure 11b) Family **Lepismatidae** (9).
2. Body short, ovoid or limuloid, with thorax wider than abdomen (Figure 11c), covered with scales (Figure 11f,g) Subfamily **Atelurinae** (3).
—Body cylindrical, elongated, with thorax not clearly wider than abdomen (Figure 11d), without scales Subfamily **Coletiniinae**—Genus *Coletinia* Wygodzinsky, 1980.
* For distinguishing all *Coletinia* species see [10].
3. Head with setae restricted to the frontal area. Cephalic capsule covered with scales only. Male antennal pedicellus with an inner distal apophysis (4).
—Head densely setose and without scales (Figure 11e). Antenna of male without pedicellar apophysis. Abdominal vesicles only on urosternite VI, with a medial tuft of long, often deeply cleft robust setae; pseudovesicles on urosternite VII. Seven pairs of abdominal styli, on segments III–IX (Figure 11h) Tribe **Atopatelurini**—Genus *Arabiatelura* Mendes, 1995 (8).
4. Urosternite II without vesicles; these are present on abdominal segments IV–VII or V–VII. Styli on abdominal segments IV–IX (6 pairs) Tribe **Grassiellini**—Genus *Grassiella*—*Grassiella leuca* Stach, 1935.
—Urosternite II with vesicles, that are absent on the remaining abdominal segments (although pseudovesicles occur on urosternite VII) Tribe **Atelurini** (5).
5. Eight pairs of abdominal styli (present on segments II–IX) genus *Atelura* Heyden, 1855 (6).

- Three pairs of abdominal styli (present on segments VII-IX) *Proateturina pseudolepisma* (Grassi, 1887).
6. Pedicellar apophysis of male thumb-shaped and bent, its distal part thinner and forming a more or less right angle with the basal part (Figure 11i). Endemic of eastern Spain *Atelura valenciana* Molero-Baltanás, Gaju-Ricart, Bach de Roca & Mendes, 1998.
- Pedicellar apophysis of male more or less cylindrical or ovoid, slightly narrowed but not bent in its apical part (Figure 11j) (7).
7. In adult males, the pedicellar apophysis is bigger (surpassing the middle of the first flagellomere, sometimes attaining its apex or even the base of the second), the urotergite X has about 30 pegs (or a higher number), and a shallower concavity of its posterior margin. Basal divisions of the cerci with two–three rows of pegs, each division with a higher number of pegs (about 10; Figure 11l) *Atelura montana* (Stach, 1946).
- In adult males, the pedicellar apophysis is smaller (at most reaching the middle of the first flagellomere), the urotergite X has about 20 pegs (or a lower number), and a deeper concavity of its posterior margin. Basal divisions of the cerci with one–two rows of pegs, each division with a lower number of pegs (about six; Figure 11k) *Atelura formicaria* Heyden, 1855.
8. Pedicel longer than wide. Urotergite X with a deep notch in its hind margin, its ventral surface with a rounded little membranous projection in each side of the posterolateral angles (Figure 11m). Paramera about three times longer than wide *Arbiateturina palaestinensis* Mendes, 1955.
- Pedicel wider than long. Urotergite X with a shallower notch in its hind margin, its ventral surface lacking membranous projections. Paramera about 2.5 times longer than wide *Arbiateturina spinifera* (Stach, 1935).
9. Sternal plates of thorax not very developed, not overlapping the base of coxae. Macrochaetae plumose (Figure 11n). Abdominal sternites without combs of macrochaetae. Ovipositor with apical fossorial spines (Figure 12a) Subfamily **Acrotelsatinae**—Genus *Lepismina* Gervais, 1844 (10).
- Sternal plates of thorax well developed, overlapping the bases of coxae. Macrochaetae smooth, bifid apically. Abdominal sternites with combs of macrochaetae. Apex of the ovipositor more or less acute, but without apical fossorial spines (Figure 12b) Subfamily **Lepismatinae** (12).
10. Scales black on dorsal and ventral surfaces . . . *Lepismina audouinii* (Lucas, 1840).
- Scales black on dorsal side, those of the ventral side bright, lighter (11).
11. Urotergite I with submedian macrochaetae *Lepismina persica* Escherich, 1905/*L. plurisetata* Wygodzinsky, 1942.
- Urotergite I without submedian macrochaetae *Lepismina aurisetosa*. Wahlgren, 1906.
12. Antennae with asteriform sensilla (Figure 12c). Posterior trichobothrial areas of the pronotum open, in contact with the lateral margin of the notum (Figure 12f) Genera *Neoasterolepisma* Mendes, 1988 and *Tricholepisma* Paclt, 1967(15).
- Antenna without asteriform sensilla, with Silvestri’s sensilla (globular basiconic; Figure 12d). Posterior trichobothrial areas of the pronotum closed (surrounded by scales and not in contact with the margin of the notum; Figure 12e) Genus *Lepisma* L. 1758 (13).
13. Dorsal scales uniformly greyish. Epidermic pigment absent or light yellowish *Lepisma saccharinum* L. 1758.
- Dorsal scales blackish or greyish, except one row of white scales at the posterior margin of each thoracic notum (14).
14. Infralateral group of the urotergites consisting of only one macrochaeta and an additional thin acute smaller seta (Figure 12g) *Lepisma chlorosoma* Lucas, 1846.
- Infralateral group of the urotergites consisting of two macrochaetae and an additional

- outer thin acute smaller seta (Figure 12h)
- *Lepisma baetica* Molero-Baltanás, Gaju-Ricart, Bach de Roca & Mendes, 1994.
15. Hind margin of thoracic nota with a row of more or less short bifid macrochaetae (Figure 12i) Genus *Tricholepisma* Paclt, 1967 (16).
—Hind margin of thoracic nota without macrochaetae, only with some thin and acute setulae (Figure 12f) or bare Genus *Neoasterolepisma* Mendes, 1988 (18).
16. Infralateral groups of urotergites consisting of two macrochaetae, lacking a thinner outer seta (Figure 12j). Urotergite IX only with infralateral groups of macrochaetae, its hind margin lacking additional setae. Males without modified metatibiae. Endemic of south-eastern Spain
. . . *Tricholepisma indalicum* Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1995.
—Infralateral groups of urotergites at least with two macrochaetae and a thinner outer seta (Figure 12h). Urotergite IX with at least 1 + 1 macrochaetae in its hind margin additional to the infralateral groups. Males with modified metatibiae (17).
17. Transverse row of macrochaetae of the posterior margin of the tergites interrupted in the middle line. Urosternites with combs of numerous setae, some of the more internal of the lateral combs and the more external of the medial combs of segments V–VIII short and spiniform (Figure 4e). Hind leg of the male with modified chaetotaxy on the ventral side of trochanter, femur, and tibiae, with a dense field of straight spines; metatibiae in its apical half with a group of strong and more or less hooked spines (Figure 4a–c) *Tricholepisma aureum* (Dufour, 1831).
—Transverse row of macrochaetae of the posterior margin of the tergites continuous. All urosternal macrochaetae thin. Metatibiae ventrally dilated and with several ciliary setae but lacking a group of strong hooked spines; femora and trochanters not modified *Tricholepisma gyriniforme* (Lucas, 1846).
18. Urosternite VII with pseudostyli (Figure 4f) (19).
—Urosternite VII without pseudostyli (Figure 4g) (24).
19. Dorsal side of the body with abundant scales with its apical part ending in an acute point, as prolongation of central rays (Figure 13e) (20).
—Dorsal side without pointed scales (21).
20. Prosternum about as wide as long, or slightly longer than its width at the base; its lateral margins are slightly or hardly constricted, and its apex is sharp (Figure 13a). Metatibiae of males not ventrally dilated and devoid of ciliary setae, quite similar to that of the female and with a diameter slightly larger in its basal part than in the middle or distal zone (Figure 13b). Parameres very small, straight and slender, almost devoid of glandular area
. *Neoasterolepisma soerenseni* (Silvestri, 1908).
—Prosternum wider at its base than long, usually with a very sharp constriction on its lateral margins; less acutely angled apex (Figure 13c). Metatibiae of adult males convex or slightly ventrally dilated, wider in its middle or distal zone than in its basal part, and usually with some ciliary setae inserted on the dilation (Figure 13d). Parameres more developed of usual size, with curved apex and provided with a distinct glandular area *Neoasterolepisma foreli* (Moniez, 1894).
21. Metatibiae of adult males with parallel sides, ventrally with a row of fine and robust setae and a row parallel to this of short spiniform setae ending in a small button and lacking ciliary setae (Figure 13f,g). Urotergite X as long as wide at its base or slightly shorter, with a deep and semi-circular posterior notch
. *Neoasterolepisma imitans* (Mendes, 1980).
—Metatibiae of adult males with convex ventral side, their specialized chaetotaxy different, provided with ciliary setae. Urotergite X longer than wide at its base, its posterior notch wide and shallow (22).
22. Metatibiae of adult males with a subtriangular expansion on the distal part of its ventral side (Figure 13h). Robust setae of the tibiae acute, not with curved apex . . . (23).
—Metatibiae of adult males ventrally dilated, the expansion is uniformly curved, and

the width of the tibia is higher in the middle area (Figure 13i) Robust setae of the male metatibiae with curved apex. ... *Neoasterolepisma crassipes* (Escherich, 1905).

23. Urotergite I with 1 + 1 infralateral groups of macrochaetae, 1 + 1 lateral isolated lateral macrochaetae and 1 + 1 submedian macrochaetae. Urotergite IX with 1 + 1 infralateral groups of macrochaetae and 1 + 1 isolated submedian macrochaetae (Figure 14a) ... *Neoasterolepisma gauthieri* (Wygodzinsky, 1941).
—Urotergite I with 1 + 1 infralateral groups of macrochaetae and 1 + 1 submedian macrochaetae, lacking lateral macrochaetae. Urotergite IX only with 1 + 1 infralateral groups of macrochaetae, lacking submedian macrochaetae (Figure 14e) ... *Neoasterolepisma calvum* Molero-Baltanás, Mendes, Gaju-Ricart & Bach de Roca, 1994.

24. Posterior urosternites (usually V–VII or V–VIII) with some of the more external setae of medial comb and some of the more internal of lateral combs, short and more robust and sclerotized, spiniform (Figure 4e) ... (25).
—All urosternites with combs of macrochaetae, if some of them spiniform, not sclerotized and thin (Figure 4g) ... (27).

25. Metatibiae of adult males with their ventral side slightly convex, and with a specialized chaetotaxy consisting of abundant fine setae externally and internally and a group of three–four spiniform setae, at the beginning of the ultimate ventral third, accompanied by long, slightly dense cilia. Metafemur of males with a dense field of strong spines (similar to that of *Tricholepisma aureum*, Figure 4a–c) ... (26).
—Metatibiae of adult males not clearly convex, its ventral side more or less parallel to the dorsal side, but with a specialized chaetotaxy completely different, consisting of one–two ventral rows of fine, erect spines and a row of long and strong setae (similar to Figure 13f,g). Metafemur of males not modified, without a dense field of strong spines ... *Neoasterolepisma lusitanum* (Wygodzinsky, 1945).

26. Urotergite I with 1 + 1 infralateral groups of macrochaetae and 1 + 1 submedian macrochaetae, lacking lateral macrochaetae. Apart from infralateral groups, the urotergites II–VIII have only 3 + 3 isolated macrochaetae on their posterior margins (1 + 1 sublateral, 1 + 1 lateral and 1 + 1 submedian, as in Figure 12k) ... *Neoasterolepisma balcanicum* (Stach, 1922).
—Urotergite I with 1 + 1 infralateral groups of macrochaetae, 1 + 1 lateral isolated lateral macrochaetae and 1 + 1 submedian macrochaetae. Apart from infralateral groups, the urotergites II–VIII have a higher number of macrochaetae on their posterior margins, usually 5–6 + 5–6 ... *Neoasterolepisma balearicum* Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1997.

27. Submedian macrochaetae on urotergites I–VIII substituted by groups of setae; urotergite I–IV with 1 + 1 submedian groups of 12–18 setae, clearly isolated on the more anterior tergites, very close on V. On VI and VII, the median groups are merged, constituting a single band (Figure 14b,c). On VIII, the setae of median groups are very dense forming a sagittal brush ... *Neoasterolepisma evansi* (Silvestri, 1923).
—Without these characteristics, i.e., chaetotaxy of urotergites typical, usually with 1 + 1 infralateral groups (of one or two setae), 1 + 1 lateral, 1 + 1 sublateral and 1 + 1 submedian macrochaetae (Figure 12k) ... (28).

28. Labial papillae of type “aufgelöst” (disperse sensilla, such as those of Figure 5j). Median combs of urosternites with only three macrochaetae ... *Neoasterolepisma paucisetosa* (Stach, 1935).
—Labial papillae compact (Figure 14k). Median combs of urosternites with a higher number of macrochaetae ... (29).

29. Median combs of urosternites with 25–34 setae, the lateral combs with 12–14; the distance between them about 0.5 the width of the latter. Inner process of coxite IX of females about five times longer than wide at its base (Figure 14d) ... *Neoasterolepisma priesneri* (Stach, 1946).
—Median combs of urosternites in general with much fewer setae, a maximum of 27

- and the distance separating them from the lateral combs much greater and these with fewer setae. Inner process of coxite IX of females generally less elongate (30).
30. Infralateral group of urotergites with only one isolated macrochaeta or one bifid macrochaeta and an outer tiny, small seta (as in Figure 12g) (31).
—Infralateral group of urotergites with at least two bifid macrochaetae (33).
31. Infralateral group of urotergites with only one isolated macrochaeta, without an outer tiny, small seta. Median combs of urosternites III–VII with 12–15 macrochaetae. Open trichobothrial areas long and narrow
. *Neoasterolepisma santschi* (Silvestri, 1908).
- Infralateral group of urotergites consisting of one macrochaeta and an outer thin acute seta. Median combs of urosternites with four–seven macrochaetae. Open trichobothrial areas shorter and wider (32).
32. Prosternum as long as wide, with a more acute apical region (Figure 14f). Metasternum constrained towards the apical region (Figure 14h). Distance between the subapical combs of the metasternum similar or higher than the width of a comb
. *Neoasterolepisma myrmecobium* (Silvestri, 1908).
- Prosternum wider than long, with a rounded apical region (Figure 14g). Apical part of the metasternum rounded, without a constriction in lateral margins (Figure 14i). Distance between the subapical combs of the metasternum shorter than the width of a comb. Up to now, endemic to Sicily
. *Neoasterolepisma angustothoracicum* (Grassi & Rovelli, 1889).
33. Infralateral group of urotergites II–VIII with two bifid macrochaetae only . . . (34).
—Infralateral group of urotergites II–VIII with two macrochaetae and an outer tiny acute seta, usually shorter than the bifid macrochaetae (35).
34. Median combs of urosternites with four–six macrochaetae. Prosternum slightly wider at its base than long (ratio L/W about 0.9). Hind margin of metanotum not clearly concave. Coxite VIII of females with only one comb consisting of two macrochaetae (Figure 14l). Inner process of the coxite IX of adult females about 2.5 times longer than wide at its base
. *Neoasterolepisma scorpius* Mendes, 1993.
- Median combs of urosternites with a higher number of macrochaetae (9–27). Prosternum about as wide as long. Hind margin of metanotum clearly concave. Coxite VIII of females with two combs of macrochaetae, the lower one with a higher number of macrochaetae (Figure 14m). Inner process of the coxite IX of adult females about 3.5–4 times longer than wide at its base
. *Neoasterolepisma curtiseta* Mendes, 1988.
35. Distance between median and lateral urosternal combs more than four times the width of a lateral comb; these consisting of a low number of macrochaetae (two–four). Metatibiae of males not modified in respect to those of females
. *Neoasterolepisma stachi* (Wygodzinsky, 1941).
- Distance between median and lateral urosternal combs lower, at most four times the width of a lateral comb; these frequently consisting of a higher number of macrochaetae (3–15). Metatibiae of males frequently modified in shape and/or chaetotaxy respect to those of females (36).
36. Metatibiae long in both sexes, more than four times longer than wide (Figures 4d and 14n). Coxites VIII of females with only one comb of setae (37).
—Metatibiae shorter, at most four times longer than wide; frequently, their ratio length/width is lower. Coxites VIII of females with one or (frequently) two combs of setae (38).
37. Metatibiae of males modified in chaetotaxy respect to those of females (Figure 14n,o). Apical article of labial palps similar in both sexes. Urotergite I with 1 + 1 submedian macrochaetae *Neoasterolepisma spectabiloides* Mendes, 1988.
- Metatibiae of males not modified in respect to those of females (Figure 4d). Apical article of labial palps of males with a dense glandular field (Figure 14p). Urotergite I with-

- out submedian macrochaetae
- ... *Neoasterolepisma pallidum* Molero-Baltanás, Gaju-Ricart & Bach de Roca, 1995.
38. Metatibiae of males not modified in respect to those of females (39).
—Metatibiae of males modified in chaetotaxy and shape respect to those of females (40).
39. Lateral urosternal combs with 3–5 macrochaetae; distance between urosternal combs similar to the width of a lateral comb (Figure 15c). Prosternum as long as wide or even a little longer than wide. Males with long and thin cilia in the notch of the hind margin of the tenth urotergite (Figure 14q). Paramera very reduced and glabrous (Figure 15a) *Neoasterolepisma palmonii* (Wygodzinsky, 1942).
—Lateral urosternal combs with 6–11 macrochaetae; distance between urosternal combs more than twice the width of a lateral comb (Figure 15d). Prosternum wider than long (ratio length/width about 0.8–0.85). Hind margin of the tenth urotergite without setae, only with one macrochaeta and one thin seta in each posterolateral corner. Paramera developed and with several thin setae (Figure 15b) *Neoasterolepisma necrophilum* Mendes, 1992.
40. Metatibiae of males with parallel sides and modified chaetotaxy (Figure 15e) consisting of numerous rows of short and robust spiniform setae and with a row of long strong setae, lacking ciliary or hooked setae on its ventral side (Figure 15f). Metasternum with rounded apex, its combs in the antedistal position. Inner process of coxite IX of the female about five times longer than wide at its base, stylus IX not reaching the apex of coxite IX *Neoasterolepisma spectabile* (Wygodzinsky, 1945).
—Metatibiae of males with its ventral side dilated, convex, with specialized chaetotaxy including ciliary and/or hooked setae on its ventral side. Metasternum usually with the distal region truncate, the combs in a terminal or almost apical position. Inner process of coxites IX of the females proportionally shorter, the respective styli always longer (41).
41. Urotergite X as long or longer than its width at the base in adults. Tibia III of males with a subtriangular dilation and its maximum width usually on the apical half of its length; the contour of the apical half of the ventral margin of this article is slightly concave. A large number of ciliary setae are inserted on the dilation, and an oblique row of strong, straight setae is inserted laterally (Figure 15g). Male urotergites often with supernumerary setae. Ovipositor with more than 25 divisions. Dorsal scales usually yellowish *Neoasterolepisma wasmanni* (Moniez, 1894).
—Urotergite X wider at the base than long. Tibia III of males slightly domed ventrally, its maximum width about the middle of its length. With or without ciliary setae, and with an oblique row of strong setae whose apex may be straight, ciliary, or curved. Urotergites of males with the usual chaetotaxy (i.e., 1 + 1 infralateral groups of two macrochaetae and one thin outer seta, and 3 + 3 isolated macrochaetae). Ovipositor with less than 25 divisions. Dorsal scales frequently greyish, although sometimes they can be yellowish (42).
42. Metatibiae of adult males presenting several ciliary setae with curly apex. The most distal strong setae of the oblique series have a straight or ciliary apex (Figure 15h). Coxites VIII— of females with a single comb of macrochaetae. Prosternum less than 0.8 times as long as its maximum width. Head capsule with more or less intense brownish purple epidermic pigment *Neoasterolepisma hespericum* Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1996.
—Metatibiae of males devoid of ciliary setae, at most with some setae with a very fine and almost straight apex. The macrochaetae of the oblique series have a strong, hooked apex (Figure 15i). Coxite VIII of females presenting two combs, sometimes the upper one with only one or two setae. Prosternum 0.9–1.1 times as long as its

maximum width. Epidermic pigment absent or very diffuse
 *Neoasterolepisma delator* Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1996.

3.4. Diversity and Endemicity of Mediterranean Countries

At least one myrmecophilous silverfish species has been reported in twenty-three countries of the Mediterranean Basin, while in seven countries (e.g., Bosnia and Herzegovina, United Kingdom, Lebanon, San Marino, Serbia, Slovenia, and Syria) we have not found any reliable records of myrmecophilous silverfish. The countries with the greatest number of ant-associated silverfish in their fauna are Spain with 21 species, Morocco with 12, Portugal and Algeria with 11, and Italy with 10. However, 70% of the countries considered for this study has none or less than five species (Appendix A). It is interesting to note that about 85% of the confirmed myrmecophilous species are strictly endemic to the Mediterranean Basin. Only five species are more widespread outside this area: *Lepismina aurisetosa*, *L. persica*, *Lepisma saccharinum*, *Neoasterolepisma wasmanni*, and *Atelura formicaria*.

3.5. Diversity Comparison with Other Non-Mediterranean Areas

Although an updated catalogue of nidicolous Zygentoma is not available, our own data (all the literature of described species in which association with social insects is indicated) estimate the world diversity of these insects over 200 species. Approximately, more than 100 species are obligate or facultative myrmecophiles, while at least 75 of them are associated with termites. Most myrmecophiles belong to the family Lepismatidae and most of the termitophiles to the family Nicoletiidae (subfamily Atelurinae). However, there are representatives of both taxa associated with ants and termites. Focusing on ant-associated Lepismatidae, the number of species of silverfish described over the world is about 80. Considering these numbers, the Mediterranean Lepismatidae associated with ant nests are especially diverse, since they represent about 35% of the myrmecophilous silverfish of this family that are known to live with ants in the world. Finally, the knowledge of nidicolous faunas of other biogeographic regions is enough to state that the percentage of myrmecophilous Atelurinae and of termitophile Zygentoma is comparatively low in the Mediterranean region.

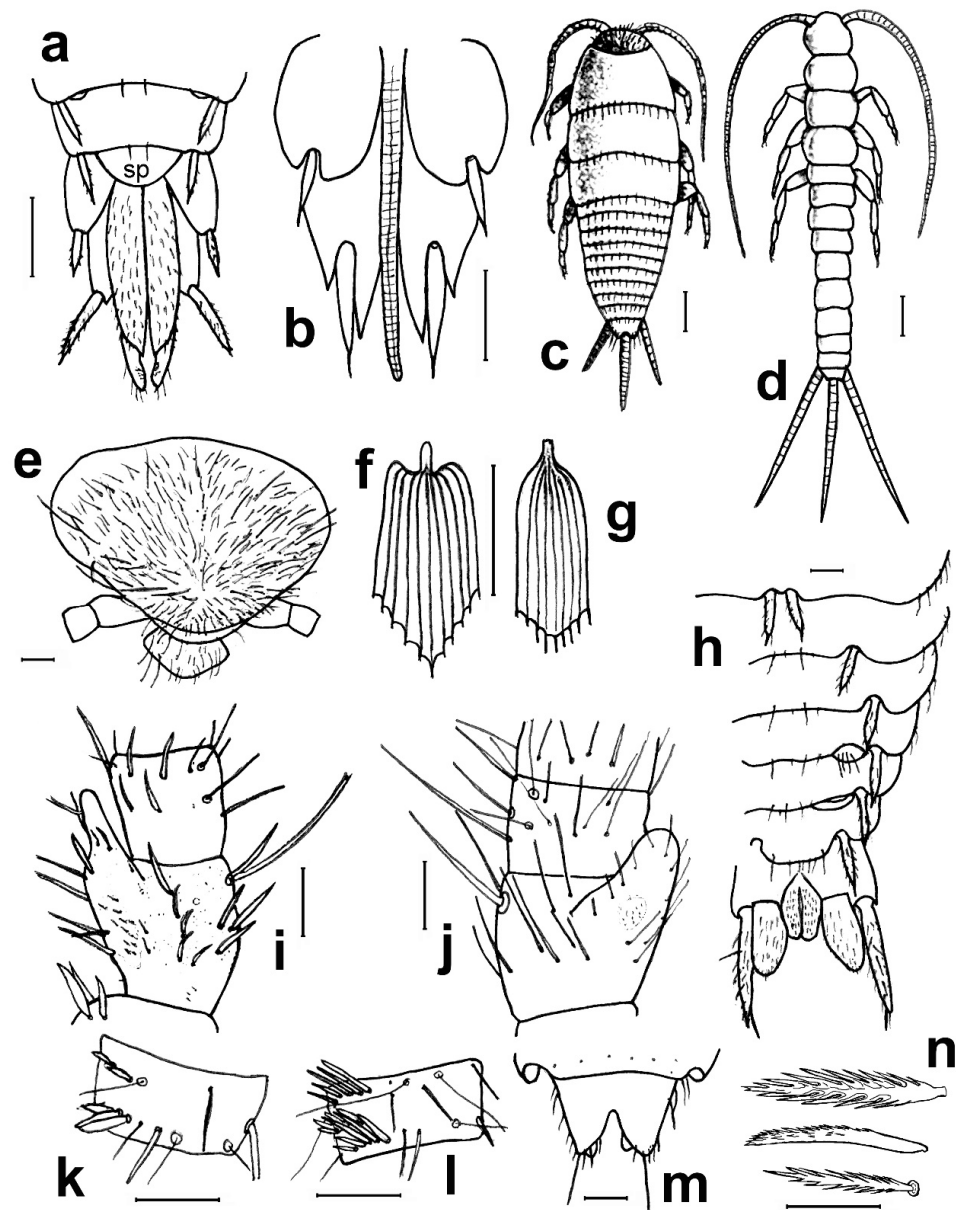


Figure 11. Some characteristics illustrating the identification key of Mediterranean myrmecophilous Zygentoma. (a): Ventral view of the last segments of a female Nicoletiidae of the subfamily Atelurinae, with a subgenital plate (sp) covering the base of the ovipositor. (b): Ventral view of the last segments of a female Lepismatidae of the subfamily Lepismatinae, without subgenital plate between the coxites VIII. (c): Habitus of a representative of the subfamily Atelurinae, dorsal view. (d): Habitus of a representative of the subfamily Coletiniinae, dorsal view. (e): Head densely setose of *Arabiatelura* sp. (f,g): Scales of Atelurinae. (h): Ventral view of the middle and left side of the abdomen of a male *Arabiatelura* sp., from urosternite III to IX, showing abdominal vesicles of urosternite VI, pseudovesicles on urosternite VII, and seven pairs of styli. (i): Pedicellus and first flagellomere of *Atelura valenciana*, showing pedicellar apophysis in dorsal view. (j): Id., of *Atelura montana*. (k): Second division of the cercus of *Atelura formicaria*. (l): Id., of *Atelura montana*. (m): Urotergite X of *Arabiatelura palaestinensis*. (n): Plumose macrochaetae of *Lepismina* spp. Scales: (a–d): 1 mm; (e,h,m): 0.1 mm; (f,g,i–l,n): 50 μ m.

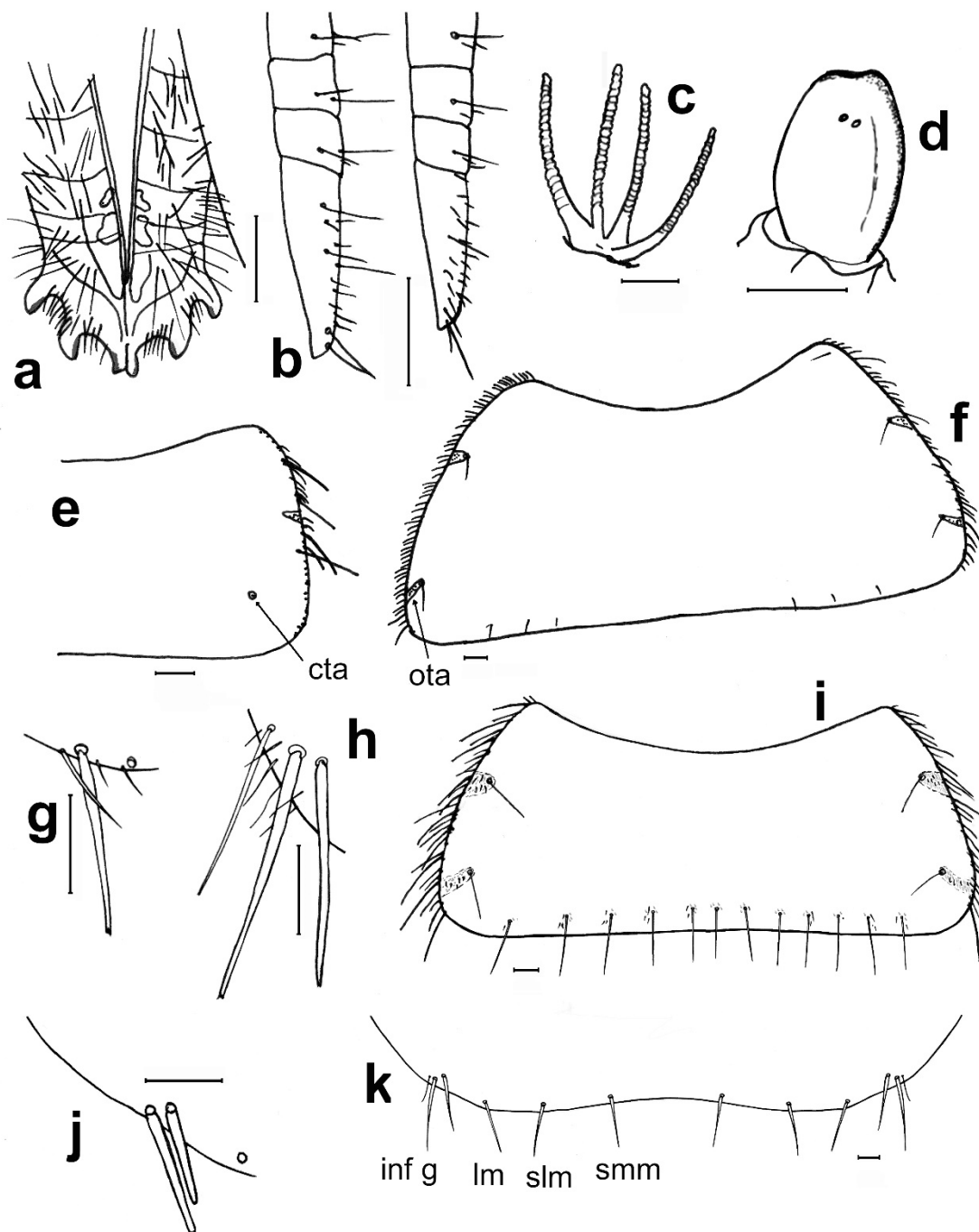


Figure 12. Some characteristics illustrating the identification key of Mediterranean myrmecophilous Zygentoma. (a): Apex of the ovipositor of *Lepismina aurisetosa*, showing apical fossorial spines. (b): Apex of gonapophyses VIII and IX of a representative of the genus *Neoasterolepisma*. (c): Asteriform sensillum of *Neoasterolepisma* sp. (d): Silvestri's basiconic sensillum of *Lepisma* sp. (e): Right side of the pronotum of *Lepisma chlorosoma*, showing closed posterior trichobothrial areas (cta). (f): Pronotum of *Neoasterolepisma* sp., showing open posterior trichobothrial areas (ota). (g): Infralateral group of the urotergite II in *L. chlorosoma*. (h): Infralateral group of macrochaetae of the urotergite II in *L. baetica*. (i): Pronotum of *Tricholepisma gyrimiforme*. (j): Infralateral group of macrochaetae of *T. indalicum*. (k): Hind margin of the urotergite II of a representative of the genus *Neoasterolepisma* with the usual chaetotaxy of this genus (and some related ones); inf g: infralateral group; lm: lateral macrochaeta; slm: sublateral macrochaeta; smm: submedian macrochaeta. Scales: 0.1 mm.

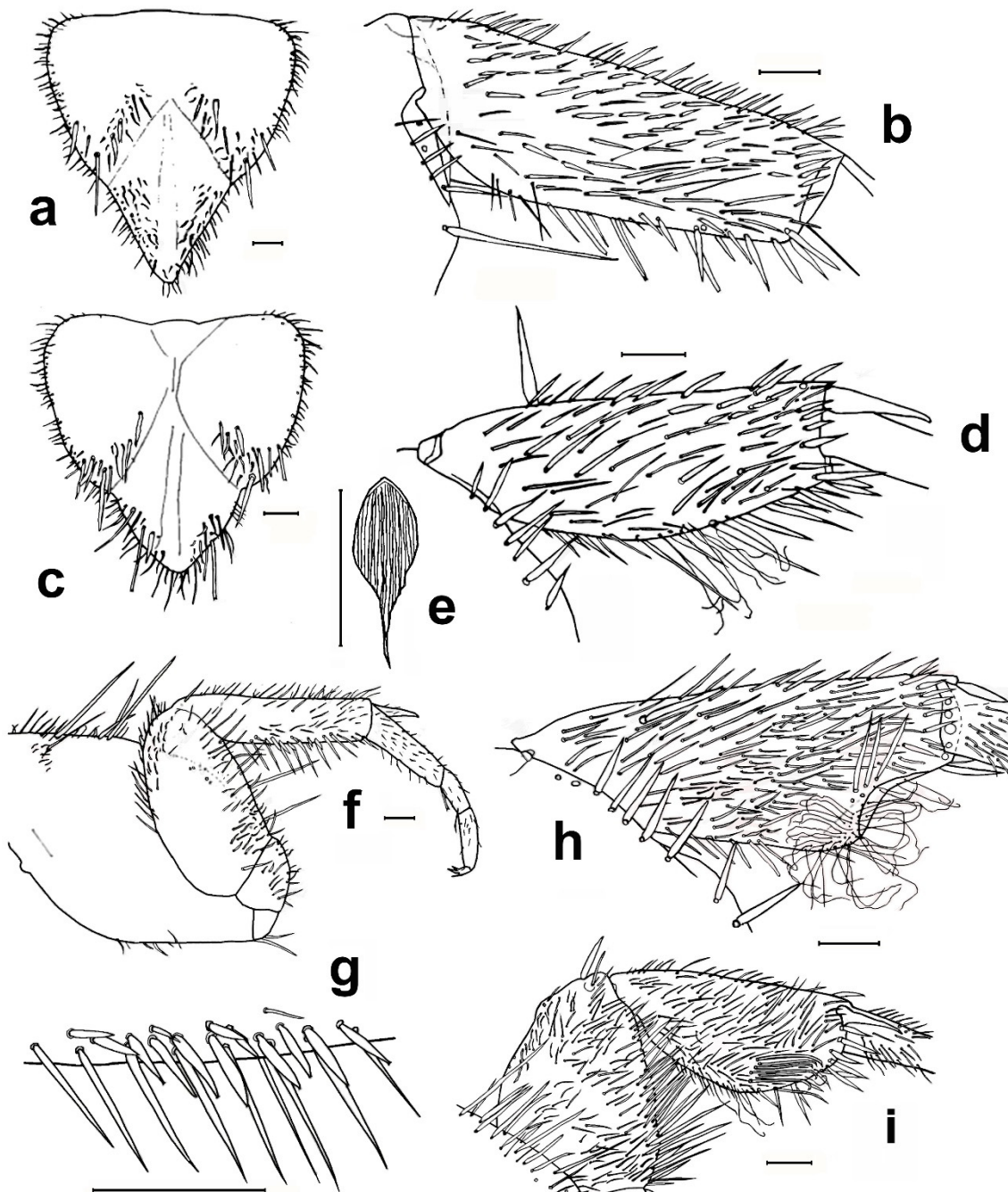


Figure 13. Some characteristics illustrating the identification key of Mediterranean myrmecophilous Zygentoma. (a): Prosternum of *Neoasterolepisma soerenseni*. (b): Hind tibia of the male of *N. soerenseni*. (c): Prosternum of *N. foreli*. (d): Hind tibia of the male of *N. foreli*. (e): Pointed scale of *N. foreli*. (f): Hind leg of the male of *N. imitans*. (g): Id., detail of the modified chaetotaxy of the ventral side of the male metatibia. (h): Metatibia of the male of *N. calvum*. (i): Metafemur and metatibiae of the male of *N. crassipes*. Scales: 0.1 mm.

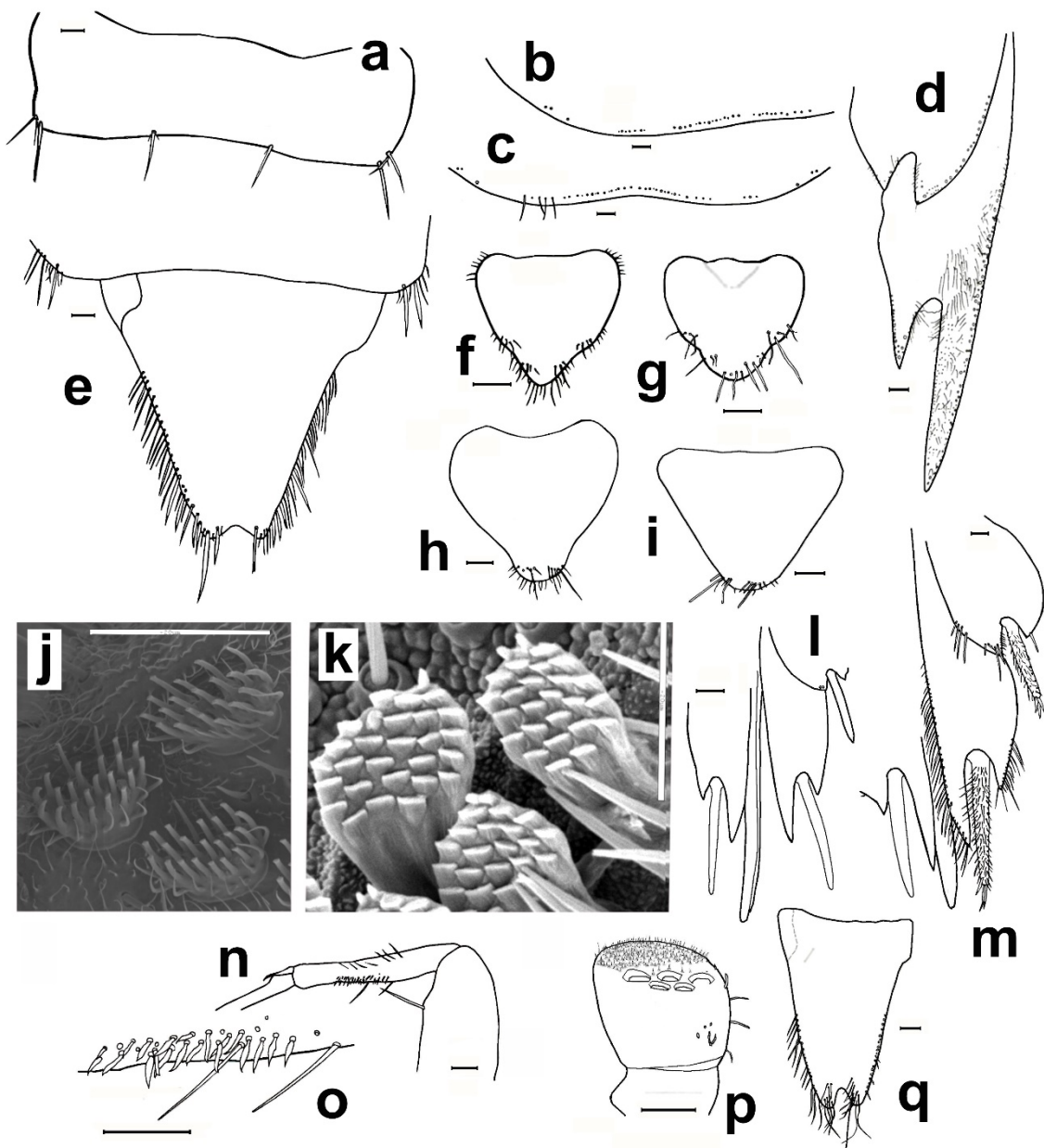


Figure 14. Some characteristics illustrating the identification key of Mediterranean myrmecophilous Zygentoma. (a): Urotergite X of *Neoasterolepisma gauthieri*. (b): Urotergite V, hind margin, of *N. evansi*. (c): Urotergite VII, hind margin, of *N. evansi*. (d): Coxites VIII and IX of *N. priesneri*. (e): Urotergites IX and X of *N. calvum*. (f): Prosternum of *N. myrmecobium*. (g): Prosternum of *N. angustothoracicum*. (h): Metasternum of *N. myrmecobium*. (i): Metasternum of *N. angustothoracicum*. (j): Disperse papillae of the labial palp of an Atelurinae (type “aufgelöst”). (k): Compact papillae of the labial palp of a Lepismatinae. (l): Right coxite VIII and coxites IX of female *N. scorpius*. (m): Idem, of female *N. curtiseta*. (n): Metatibia of the male of *N. spectabiloides*. (o): Idem, detail of the specialized chaetotaxy of the ventral side. (p): Apical article of the labial palp of *N. pallidum*. (q): Urotergite X of *N. palmonii*. Scales: 0.1 mm, except for (j,k): 20 µm.

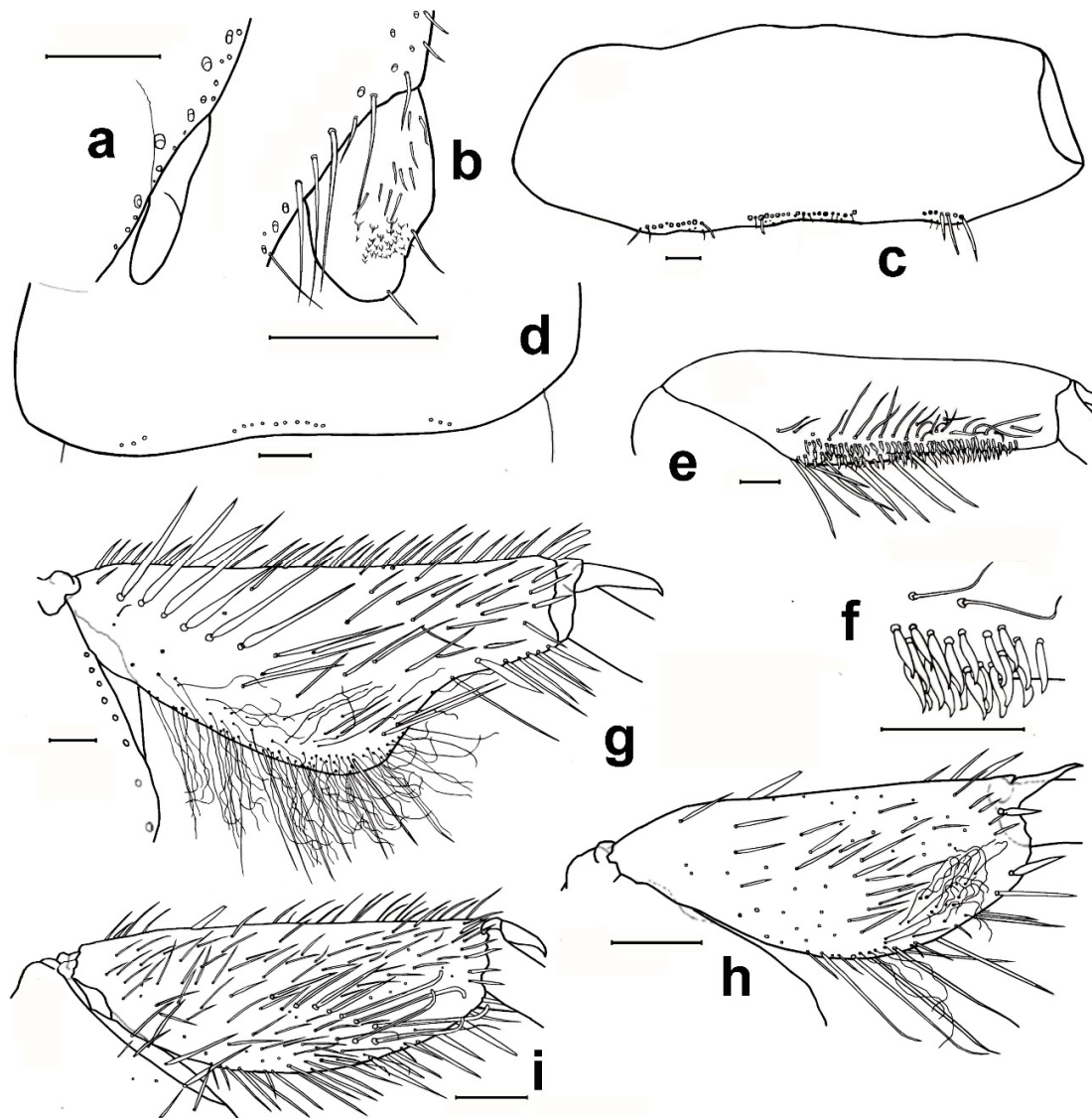


Figure 15. Some characteristics illustrating the identification key of Mediterranean myrmecophilous Zygentoma. (a): Paramere of *Neoasterolepisma palmonii*. (b): Paramere of *N. necrophilum*. (c): Urosternite IV of *N. palmonii*. (d): Urosternite VII of *N. necrophilum*. (e): Metatibia of the male of *N. spectabile*. (f): Detail of the specialized chaetotaxy of the ventral side of the male metatibia of *N. spectabile*. (g): Metatibia of an adult male of *N. wasmanni*. (h): Metatibia of an adult male of *N. hespericum*. (i): Metatibia of an adult male of *N. delator*. Scales: 0.1 mm.

3.6. State of Art of Publications

The number of publications on myrmecophilous silverfish from the Mediterranean Basin is not a prolific topic of study. From 1830 to the present, 139 works which mentioned myrmecophilous silverfish species have been published. However, there are a fairly low number of published works in periods of twenty years (Figure 16). In the last few decades, there has been a stabilization and then a slight decrease in the number of publications. For a general overview of all works, see Supplementary Materials Table S1.

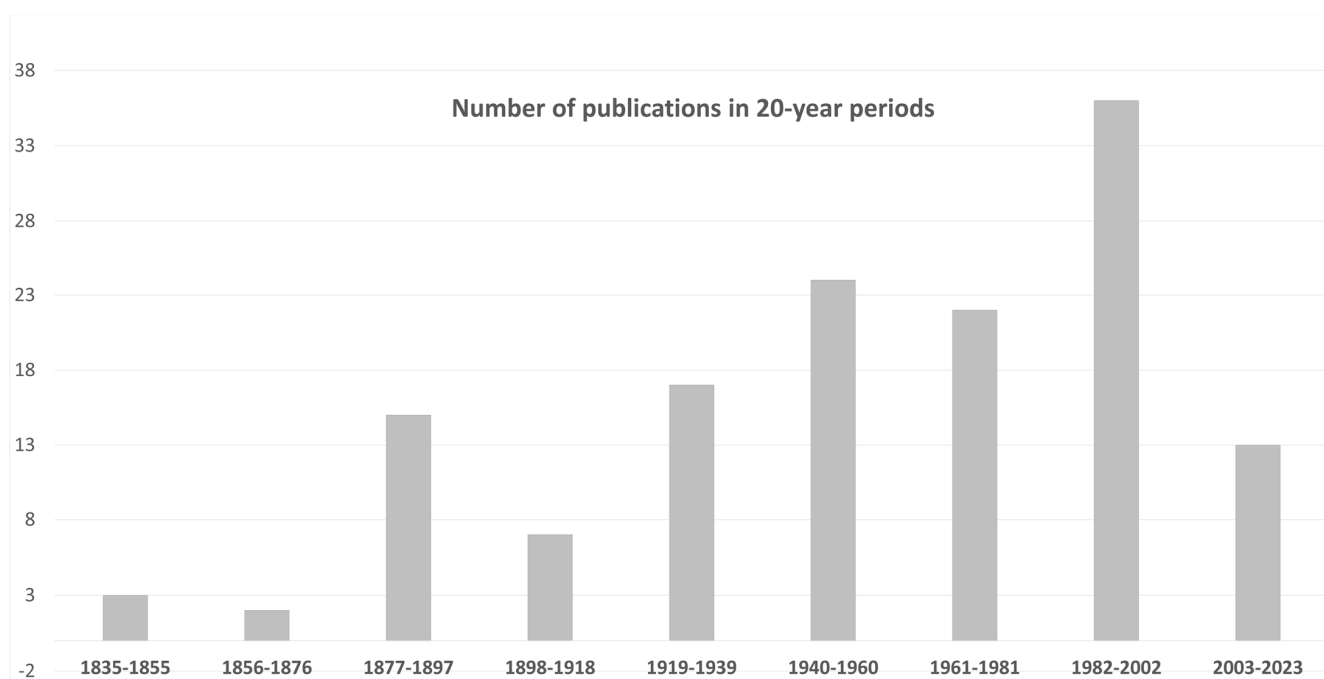


Figure 16. Number of publications of myrmecophilous silverfish of the Mediterranean Basin in 20-year periods.

4. General Discussion

Nidicolous silverfish insects, associated with ants or termites, are one of the less known groups of soil arthropods. The lack of economic interest of most free-living species from natural habitats and the scarce number of *Zygentoma* specialists around the world could be playing an important role in this bias. In addition, most of these specialists have published most of their findings in non-indexed journals due to the neglected treatment that taxonomy has received in recent decades from the scientific community. This has led to errors that could easily be fixed with a little more caution when searching for information. For example, Glasier et al. [53] used indexed journals for their global synthesis of world myrmecophiles and presented only nine species belonging to the order “Thysanura”. On one hand, it is interesting to note how even among entomologists interested in myrmecophiles, the term “Thysanura” continues to be mistakenly used. This ancient order was divided into two (*Microcoryphia* and *Zygentoma*) and therefore its use is strongly discouraged. Indeed, several entomologists keep using the term showing a lack of interest in the use of the correct taxonomy, such as the monography of ant guests [54]. On the other hand, for a *Zygentoma* specialist, only nine ant-associated silverfish species is a totally astonishing figure. After reviewing all the available literature, almost 200 myrmecophilous silverfish species exist distributed in all the continents of the world (unpublished data). In one recent paper from an indexed journal, more than 20 myrmecophilous silverfish are accounted for only in western Europe [13]. It is important to start working with an adequate silverfish taxonomic classification and to continue studying ant–host interactions considering the important role that *Zygentoma* have as hosts of ant and termite nests around the world. This work tries to contribute to a wider knowledge of the diversity of this insufficiently studied group of insects, focusing on one of the more remarkable diversity hotspots for these insects: the Mediterranean Basin. Almost 30% of all described myrmecophilous silverfish species are endemic or have been only found in the Mediterranean area, in the same way as the pattern of endemism of other taxa [2,4,6,7]. This can be interpreted by the poor knowledge of the fauna of several geographic areas, and it is also important to mention the uneven distribution of information among the different countries. Interestingly, two of the best-studied regions (southwestern Africa and south-eastern Australia) have a lower proportion of myrmecophilous silverfish, suggesting a unique evolutionary trend

in the Mediterranean Basin, especially in the subfamily Lepismatinae. Unfortunately, most of the available taxonomic studies of *Zygentoma* have become obsolete, with a decreasing number of publications over the years and coinciding with an actual shortage of *Zygentoma* specialists. There are probably many species to be described throughout the entire Mediterranean Basin and many other species to be reported. We encourage non-expert entomologists and zoologists to use this new identification key to help in identifying myrmecophilous silverfish in their geographic regions. Most identifications based on photographs are doubtful, since the reliable characteristics to identify these species require microscopic examination. Most species and genera have the same colour patterns, making the identification by photographs quite problematic. In fact, this is one of the main causes of spreading errors, based on the incorrect or non-existent information on citizen science platforms. Carrying out the identifications with a reliable taxonomic basis is important for future studies. Entomologists approaching the subject of *Zygentoma* should consider that silverfish cannot be identified at the specific level (and frequently at the generic level) using photographs and that if they dare to identify an insect based only on a photo, they should be as prudent in terms of the level of precision as experts are. Misidentifications made without a prudent judgment will have consequences if the managers of diversity repositories include them in their distribution maps, distorting the true geographic range of the species, as is the case with some Mediterranean silverfish studied in this work.

Furthermore, the study of ant-associated silverfish in the Mediterranean region faces several challenges. The shortcomings related to the lack of interest in this group of insects has led to a low sampling of most geographic areas. A complete knowledge of the diversity of these insects will require a deeper study of southern and eastern European and Asian countries and particularly the North of Africa. This could lead, not only to the description of new species, but also to the detection of species poorly recorded or presumably missing since its original description. The study of these taxa will help to obtain more accurate descriptions of some species, knowledge of their morphological variability, and obtaining a better idea of their distribution area and even their conservation status. This could help, for example, to understand the variability of morphology of the less well-known *Lepismina* species. However, there are other issues more related to understanding the relationships between species and their evolutionary history. A deep taxonomic and molecular review of *Atelura* species and of *Neoasterolepisma* and *Tricholepisma* genera as suggested in this work could be useful for understanding the biology, ecology, and evolution of closer species, some of them with different types of association. It is probably that several old genera do not have phylogenetic sense and with integrated morphological and molecular work we could shed light on this topic. Furthermore, the ecological perspective is quite important as well. The relationship between most silverfish species and ants is far from being fully understood. Intense samplings will provide additional undiscovered relationships and the most unknown species could be finally classified as specialists or generalists [13]. In fact, most ethological and ecological facts about the relationship are still unknown, and only some works provide extra information about trophic behaviour, or the way silverfish avoid ants in their nests [30,55]. The key to continue developing these studies is the correct identification of species, which this work aims to facilitate and to continue creating new sampling campaigns to try to learn more about the most unknown species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15050635/s1>, Table S1: Records and bibliography of myrmecophilous silverfish of the Mediterranean area.

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Appendix A

Table A1. Distribution of myrmecophilous silverfish of the countries of the Western Palearctic. Assured presence (●). Red circles and asterisk noted non-confirmed but probably myrmecophilous species and yellow, new records for the country. The diversity ratio is calculated only using confirmed myrmecophilous species. Note that only records with or without ants are considered for *L. saccharinum* (not the synanthropic ones) and only with ants for *Coletinia* spp., therefore their range are greater than here presented. Albania (ALB); Algeria (ALG); Bosnia and Herzegovina (BOS); Bulgaria (BUL); Croatia (CRO); Cyprus (CYP); Egypt (EGY); France (FRA); Gibraltar (UK *); Greece (GRE); Iraq (IRAQ); Israel (ISR); Italy (ITA); Jordan (JOR); Lebanon (LEB); Libya (LIB); Malta (MAL); Monaco (MON); Macedonia (MAC); Palestine (PAL); Portugal (POR); San Marino (SAN); Serbia (SER); Slovenia (SLO); Spain (SPA); Syria (SYR); Tunisia (TUN); Turkey (TUR).

Species	ALB	ALG	BOS	BUL	CRO	CYP	EGY	FRA	UK *	GRE	IRAQ	ISR	ITA	JOR	LEB	LIB	MAL	MON	MONT	MOR	MAC	PAL	POR	SAN	SER	SLO	SPA	SYR	TUN	TUR
Family Lepismatidae																														
<i>Lepismina audouinii</i>		●					●									●														
<i>Lepismina aurisetosa</i>							●																							●
<i>Lepismina persica</i>												●																		
<i>Lepismina pluriseta</i> *												●																		
<i>Lepisma chlorosoma</i>		●			●								●										●				●			
<i>Lepisma baetica</i>																														
<i>Lepisma saccharinum</i>		●						●					●								●		●				●	●	●	
<i>Neoasterolepisma angustothoracicum</i>													●																	
<i>Neoasterolepisma balcanicum</i>	●			●						●			●																	●
<i>Neoasterolepisma balearicum</i>																											●			
<i>Neoasterolepisma calvum</i>																											●			
<i>Neoasterolepisma crassipes</i>		●						●		●			●				●			●							●		●	
<i>Neoasterolepisma curtiseta</i>																				●			●				●			
<i>Neoasterolepisma delator</i>																											●			
<i>Neoasterolepisma evansi</i>												●																		
<i>Neoasterolepisma foreli</i>		●																					●				●			
<i>Neoasterolepisma gauthieri</i>		●																											●	
<i>Neoasterolepisma hespericum</i>																					●		●				●			
<i>Neoasterolepisma imitans</i>																					●									
<i>Neoasterolepisma lusitanum</i>																					●		●				●			
<i>Neoasterolepisma necrophilum</i> *																														
<i>Neoasterolepisma pallidum</i>																											●			

Table A1. Cont.

Species	ALB	ALG	BOS	BUL	CRO	CYP	EGY	FRA	UK *	GRE	IRAQ	ISR	ITA	JOR	LEB	LIB	MAL	MON	MONT	MOR	MAC	PAL	POR	SAN	SER	SLO	SPA	SYR	TUN	TUR		
Family Lepismatidae																																
<i>Neoasterolepisma palmonii</i> *																							●								●	
<i>Neoasterolepisma paucisetosum</i> *							●																									
<i>Neoasterolepisma priesneri</i>							●																									
<i>Neoasterolepisma santschii</i> *																●														●		
<i>Neoasterolepisma scorpius</i> *																				●												
<i>Neoasterolepisma soerenseni</i>																				●			●				●					
<i>Neoasterolepisma spectabile</i>																				●			●				●					
<i>Neoasterolepisma spectabiloides</i>																●																
<i>Neoasterolepisma stachi</i>		●																		●												
<i>Neoasterolepisma wasmanni</i>		●				●	●	●		●			●	●		●	●			●		●	●			●				●		
<i>Tricholepisma aureum</i>		●			●			●					●														●		●	●		
<i>Tricholepisma gyriniformis</i>		●					●			●			●							●												
<i>Tricholepisma indalicum</i>																											●					
Family Nicoletiidae																																
<i>Arabiatelura palaestinensis</i> *																																
<i>Arabiatelura spinifera</i> *							●																									
<i>Atelura formicaria</i>	●							●					●							●							●					
<i>Atelura montana</i>					●					●																						
<i>Atelura valenciana</i>																											●					
<i>Coletinia maggi</i>																											●					
<i>Coletinia mendesi</i>																								●								
<i>Grasiella leuca</i> *							●																									
<i>Proateturina pseudolepisma</i>		●						●		●			●						●		●			●			●				●	
Total myrmecophilous species	2	11	0	2	2	1	5	6	0	6	1	1	10	1	0	3	2	1	1	11	1	1	11	0	0	0	21	0	4	6		
Total species	2	11	0	2	2	1	9	6	0	6	1	3	10	1	0	4	2	1	1	12	1	2	11	0	0	0	21	0	5	7		
Diversity ratio	5.7	31.4	0.0	5.7	5.7	2.9	14.3	17.1	0.0	17.1	2.9	2.9	28.6	2.9	0.0	8.6	5.7	2.9	2.9	31.4	2.9	2.9	31.4	0.0	0.0	0.0	60.0	0.0	11.4	17.1		

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