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New insights in the taxonomy of Lepismatidae (Insecta, Zygentoma) with an updated key to genera and future challenges

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Abstract. This paper provides a revision of the morphological characters that can be used in the current taxonomy of Lepismatidae, and methodological guidelines for identification of silverfish, which requires the use of light microscope and can be helped by scanning electron microscopy. As a main objective, an updated key for the identification of all the genera of the world as they are established to date is provided and the incomplete knowledge of some of them is commented on. The insufficient knowledge of the diversity and geographic distribution of the six subfamilies of Lepismatidae is discussed, noting the most important shortcomings and problematic issues related to taxa belonging to this family, including the challenges for carrying out a comprehensive phylogeny of the group. Special attention is paid to the subfamily Ctenolepismatinae, the most diverse of Lepismatidae, erecting a new genus, *Caribesella* gen. nov., for the Caribbean species *C. impudica* comb. nov., which was previously included inside the genus *Acrotelsella*. We also consider that *Sceletolepisma* stat. nov. (i.e., sensu Irish 1987, including species with several median urosternal bristle-combs) deserves the status of a genus independent of *Ctenolepisma*, which, considered s. str. (i.e., lacking median urosternal combs), represents a heterogeneous group that requires further revision.

Keywords. *Caribesella*, geographic distribution, identification key, morphology, new genus.

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Introduction

Lepismatidae Latreille, 1802 is a family of ametabolous insects belonging to the order Zygentoma Börner, 1904 (= Thysanura s. str.) that includes six subfamilies according to Mendes (1991) and more than 340 species. They are widely known as silverfish, although sometimes this name is restricted to domestic (synanthropic) species or even only to one species, *Lepisma saccharinum* Linnaeus, 1758. But synanthropic silverfish are at most about a dozen species; the remaining representatives of the family are free-living (some of them associated with ants or termites). Mainly detritivores, these silverfish living in natural habitats are poorly known, as they do not represent important pests, lack economic or sanitary interest and have hidden habits (mainly active during night). This has led to a delay in the study of their taxonomy and systematics compared to most families of winged insects.

Lepismatidae can be distinguished from the remaining families included in the order Zygentoma (Nicoletiidae Lubbock, 1873, Maindroniidae Escherich, 1905, Lepidotrichidae Silvestri, 1912 and Protrinemuridae Mendes, 2002) by the following combination of characters: presence of scales covering their bodies, small compound eyes with about a dozen ommatidia, absence of abdominal vesicles, abdominal sternites I–VII entire in both sexes, abdominal segment VIII of females without subgenital plate.

The first important work on the taxonomy of Lepismatidae was written by Escherich (1905). This author presented a classification system for these insects, with descriptions and identification keys including most species of the order Zygentoma known at that moment, all of them considered to belong to the family Lepismatidae within the order Thysanura Leach, 1815. The insects that are considered now as Lepismatidae were considered by Escherich as a subfamily, Lepismatinae. Other subfamilies were later raised to family status (Nicoletiidae and Maindroniidae). From this fundamental work, the only revision including all the species of this family together with a key to genera was authored by Paclt (1967). Only few entomologists focused their work on Lepismatidae during the 20th century: F. Silvestri (Italy) and J.W. Stach (Poland) in the first half of the century, and J. Paclt (Czech Republic and Slovakia) and P. Wygodzinsky (Germany/Switzerland and some American countries) mainly during the second half of the century were the most important specialists. The work of L.F. Mendes (Portugal) is especially relevant in the last decades of that century and in the first years of the 21st. He proposed a phylogeny for the Lepismatidae based on morphological characters (Mendes 1991) and proposed that this family can be divided into six subfamilies: Heterolepismatinae Mendes, 1991, Lepismatinae Latreille, 1802, Acrotelsatinae Mendes, 1991, Ctenolepismatinae Mendes, 1991, Mirolepismatinae Mendes, 1991 and Silvestrellatinae Mendes, 1991. Some other authors, such as V. Kaplin, J. Irish or the authors of this work, have contributed significantly to the taxonomy of this group, but mainly focusing in the geographic areas where they live (Russia and neighbouring countries, S and SW Africa, Australia and Spain, respectively). Nevertheless, as a result of the work of these authors, some new characters have been introduced in the taxonomy of these insects, several genera have been created and the status of some others has been changed, so currently the generic key of Paclt is not very useful. Consequently, no up-to-date worldwide key exists that allows the identification of Lepismatidae at the genus level.

Moreover, the literature on taxonomic changes established since Escherich's work is very fragmentary and revision works are lacking. The Ph.D. work of J. Irish, where a revision of the characters used and potentially important in the systematics of Lepismatidae are given, is unfortunately unpublished, although he provided a key to South African genera (Irish 2018). Mendes (1986a, 1986b, 1988) wrote some papers on several interesting characters used in the current taxonomy of the family, but each of them focuses on only one character. Molero-Baltanás *et al.* (2024) discuss some of these characters, but focused only on synanthropic species.

This work aims to fill this gap in the knowledge of these insects providing:

- Recommendations on the methods for the taxonomic study of Lepismatidae (presented in the Material and methods section).
- A compilation of the characters that are currently important in the identification and taxonomy of Lepismatidae at the supraspecific level (presented at the beginning of the Results section).

- A new genus, *Caribesella* gen. nov., is established, and a subgenus is raised to the genus level to be congruent with the information on morphological characters explained in this work.
- A key to all the genera of this family that have been established until now.

We also discuss our knowledge of the geographic distribution of the six subfamilies of Lepismatidae, commenting on future challenges to the study of these insects.

Material and methods

Methods for identifying Lepismatidae

The morphological taxonomy of silverfish species requires, even at the generic level, dissection of specimens and examination under a light microscope. Since some characters are not easy to discern even with this technique, the use of scanning electron microscope is recommended for some of them, especially for phylogenetic studies and identification of very similar species.

Specimens should be collected following any method that prevents the damage of the specimens and their appendages. An entomological aspirator is advisable in most cases. It is also helpful to use a plastic container as silverfish cannot climb smooth surfaces so leaf litter can be placed into the container for slower searching. The use of pyrethrum as a bark spray is also effective. After collection, specimens should be fixed in 70–75% ethanol if they are going to be preserved and their morphology later studied in the laboratory, but 95% to pure ethanol is better used if DNA is going to be extracted from some parts of these insects. For some larger specimens or when many specimens are held in a single tube, replacing the alcohol a few weeks after initial capture will enhance their preservation.

It is better to do dissections of fresh material, since some characters, such as scale cover, can be lost in specimens preserved for a long time. Dissections are usually made with forceps with fine tips and all the pieces of the exoskeleton of one specimen should be mounted in one or several slides using Tendeiro medium (Molero-Baltanás *et al*. 2000). It is convenient to arrange the pieces on the slide to improve efficiency locating each part of the body on the slide when examining using the light microscope. Different alternative methodologies are possible (including entire specimens when they are small and with transparent teguments and body content, use of other mounting mediums, etc.) but the described method is the one we use, and our experience has shown it to be the more efficient in most cases. For some characters, such as sensilla and scales, the use of a scanning electron microscope (from now on, SEM) is appropriate if available, which requires dehydration of the specimens or their parts to be examined (with absolute alcohol and hexamethyldisilazane or using the critical point technique) and coat them with gold, platinum or other metals.

Photographs of different parts of the anatomy using cameras attached to the microscope (in our case, a Nikon DS-Fi1 digital camera attached to a Nikon Labophot light microscope) or illustrating some anatomic characters with the aid of a camera lucida are usual procedures to support the descriptions.

Material examined and literature consulted

We have examined material belonging to more than 120 species of Lepismatidae; some of these specimens come from the personal collection of the authors but most of them are deposited in the following institutions:

AMS = Australian Museum, Sydney, Australia
MFN = Museum für Naturkunde, Berlin, Germany
MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain
MUHNAC = Museu Nacional de História Natural, Entomology, Lisbon, Portugal

NMV = Museum Victoria, Melbourne, Australia
NTM = Northern Territory Museum of Arts and Sciences, Darwin, Australia
QM = Queensland Museum, Brisbane, Australia
SAMA = South Australian Museum, Adelaide, Australia
WAM = Western Australian Museum, Perth, Australia
UCO = Departamento de Zoología, University of Córdoba, Córdoba, Spain (part of the material will be transferred to the collection of MNCN)
ZMH = Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg, Germany

Several specimens of *Caribesella impudica* (Escherich, 1905) comb. nov., identified previously as *Acrotelsella impudica* (Escherich, 1905), were examined, some of them dissected and studied using light microscopy and two of them (a male and a female) using scanning electron microscopy, following the methods described above. More details about the origin of these specimens are given in Bulla & Bach (1999).

The main source for the key is the literature, since some of the genera (*Afrolepisma* Mendes, 1981, *Anallacrotelsa* Mendes, 1996, *Asiolepisma* Kaplin, 1989, *Burmalepisma* Mendes & Poinar, 2008, *Cretalepisma* Mendes & Wunderlich, 2018, *Desertinoma* Kaplin, 1992, *Gopsilepisma* Irish, 1989, *Hemilepisma* Paclt, 1967, *Hemikulina* Mendes, 2008, *Lepitrochisma* Mendes, 1988, *Leucolepisma* Wall, 1954, *Mirolepisma* Silvestri, 1938, *Monachina* Silvestri, 1908, *Mormisma* Silvestri, 1938, *Namiblepisma* Irish, 2018, *Namibmormisma* Irish, 1988, *Namunukulina* Wygodzinsky, 1957, *Nebkhalepisma* Irish, 1988, *Ornatilepisma* Irish, 1988, *Paracrotelsa* Paclt, 1967, *Primacrotelsa* Mendes, 2004, *Prolepismina* Silvestri, 1940, *Protolepisma* Mendes & Poinar, 2013, *Sabulepisma* Irish, 1988 and *Silvestrella* Escherich, 1905) have not been examined by the authors. Nevertheless, the remaining 18 genera have been checked by the examination of specimens mounted on slides.

The literature used for creating the identification key is extensive. The works where the genera are described for the first time are detailed in the Supp. file 1, which also includes those publications where the status of one or some of these genera is updated and/or more diagnostic and useful characters are provided to recognize each one.

Results

Morphological characters of more potential interest in the taxonomy and phylogeny of Lepismatidae

The plesiomorphic or apomorphic condition of the different states of each character are not discussed, since this has been indicated by Mendes (1991), by Irish in his unpublished PhD Thesis, and some of them reassessed by Smith (2016a). A more accurate revision of these traits, where some additional ones presented in this work will be introduced, should be made in the future combined with molecular data to establish a well-supported phylogeny of this family of Zygentoma. Some additional morphological characters that have not been studied so far are potentially interesting in the taxonomy and phylogeny of Lepismatidae, such as traits of the internal anatomy (structure of proventriculus, ultrastructure of spermatozoa, etc.).

A. Chaetotaxy of the head (Fig. 1)

Several patterns of distribution of large setae (macrochaetae) have been described on the frons of Lepismatidae. The most common pattern of frontal chaetotaxy consists of two lateral groups of macrochaetae that can be interrupted medially or not, but the number and arrangement of the macrochaetae, the shape of the group and its extension is variable. The chaetotaxy of clypeus and labrum is also variable from very few and scattered setae to heavily setose; the occurrence of 1+1 lateral tufts (= bushes) of macrochaetae is frequent on both sclerites, and some genera have an additional median tuft. Most of the states of these characters are appropriate to distinguish taxa at a generic or suprageneric level. The occurrence of trichobothria near the ocular area is described only in some genera (for example, in *Allacrotelsa* Silvestri, 1935) but in some others they could be present but previously unnoticed.

B. Antennal sensilla (Fig. 2)

This character was previously studied by some authors (Adel 1984; Larink 1986; Mendes 1986a; Molero-Baltanás *et al*. 2000, etc.), but different names have been given to the different types of sensilla. In our opinion, the terminology of Adel (1984) should be followed. The name "campaniform" given by Mendes (1986a) to Silvestri's sensilla is not appropriate; this type of sensilla actually corresponds to widened basiconic types that are designated by Adel as "basiconic type C" and "basiconic type F". Mendes (1991) used the absence of specialized antennal sensilla to distinguish the subfamily Heterolepismatinae, but it should be specified which types of sensilla are considered to be specialized. Mendes (1986a) considers that these types are asteriform, bidigitate, poculiform and Silvestri's sensilla (i.e., basiconic types C and F) but this author (Mendes 2011) confirmed that simple sausage-shaped sensillae do occur in Heterolepismatinae and could be considered as specialized sensilla.

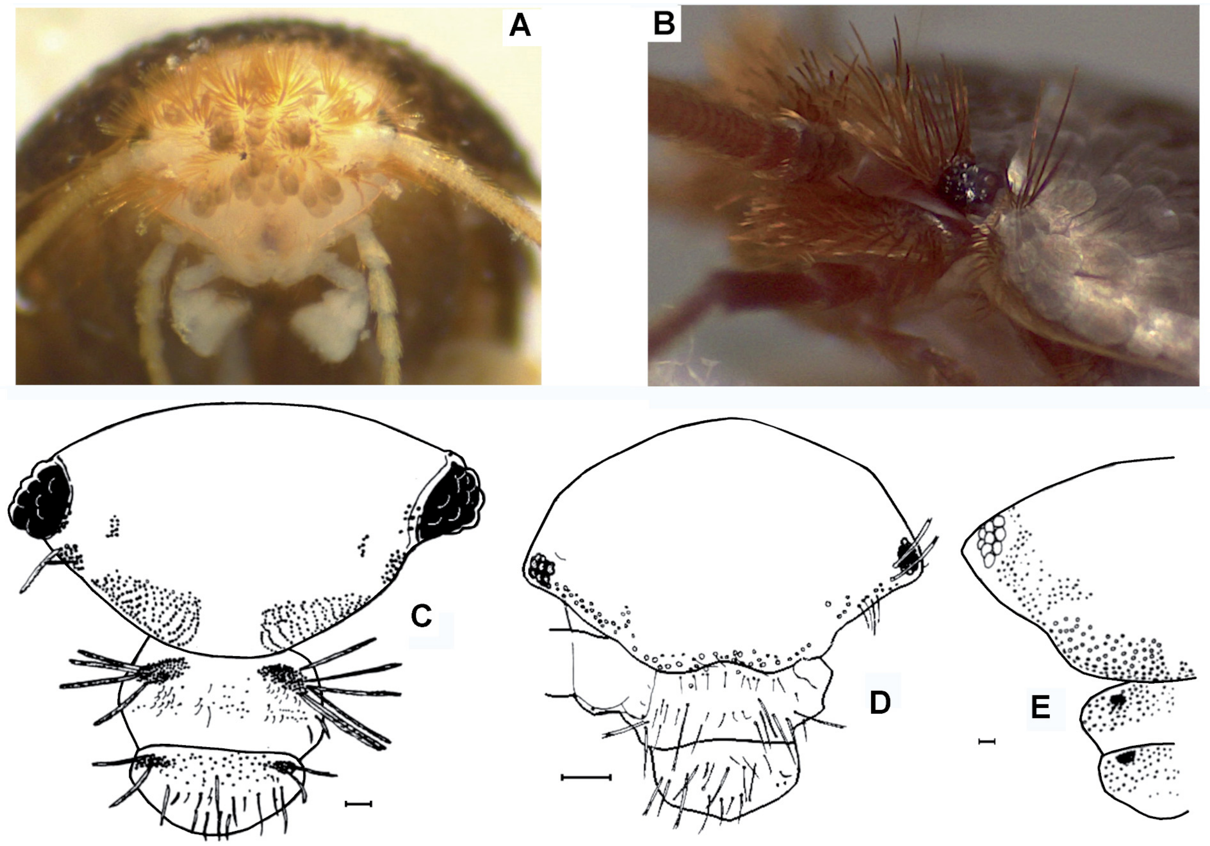

Fig. 1. Chaetotaxy of the head in Lepismatidae Latreille, 1802. **A**. Frontal view of the head of *Lepismina* sp., showing frontal tufts of macrochaetae. **B**. Lateral view of the head of *Allacrotelsa kraepelini* (Escherich, 1905), showing tufts of macrochaetae on the head and on the anterolateral corner of the pronotum. **C**. *Ctenolepisma ciliatum* (Dufour, 1831). **D**. *Lepisma baetica* Molero-Baltanás, Gaju-Ricart, Bach de Roca & Mendes, 1994. **E**. *Hyperlepisma acinacis* Irish, 1991. Images C–D adapted from Molero-Baltanás *et al*. (2010, 1994) and E from Irish (1991); in these illustrations, most macrochaetae are represented only by their insertions. Scale bars = 0.1 mm.

C. Maxillary palp

The relative length of the articles of the maxillary palp or their size with respect to the body length or to the length of the labial palp has been used to describe species, but these characters are probably not useful for generic/suprageneric distinction in Lepismatidae. Mendes (1991) used the presence or absence of pronged apical sensilla on the distal article of this palp as a relevant character (Fig. 3). These pronged sensilla are peg-like and have one to several short apical smooth projections and, according to Mendes (op. cit.), are absent in representatives of the subfamilies Acrotelsatinae and Ctenolepismatinae.

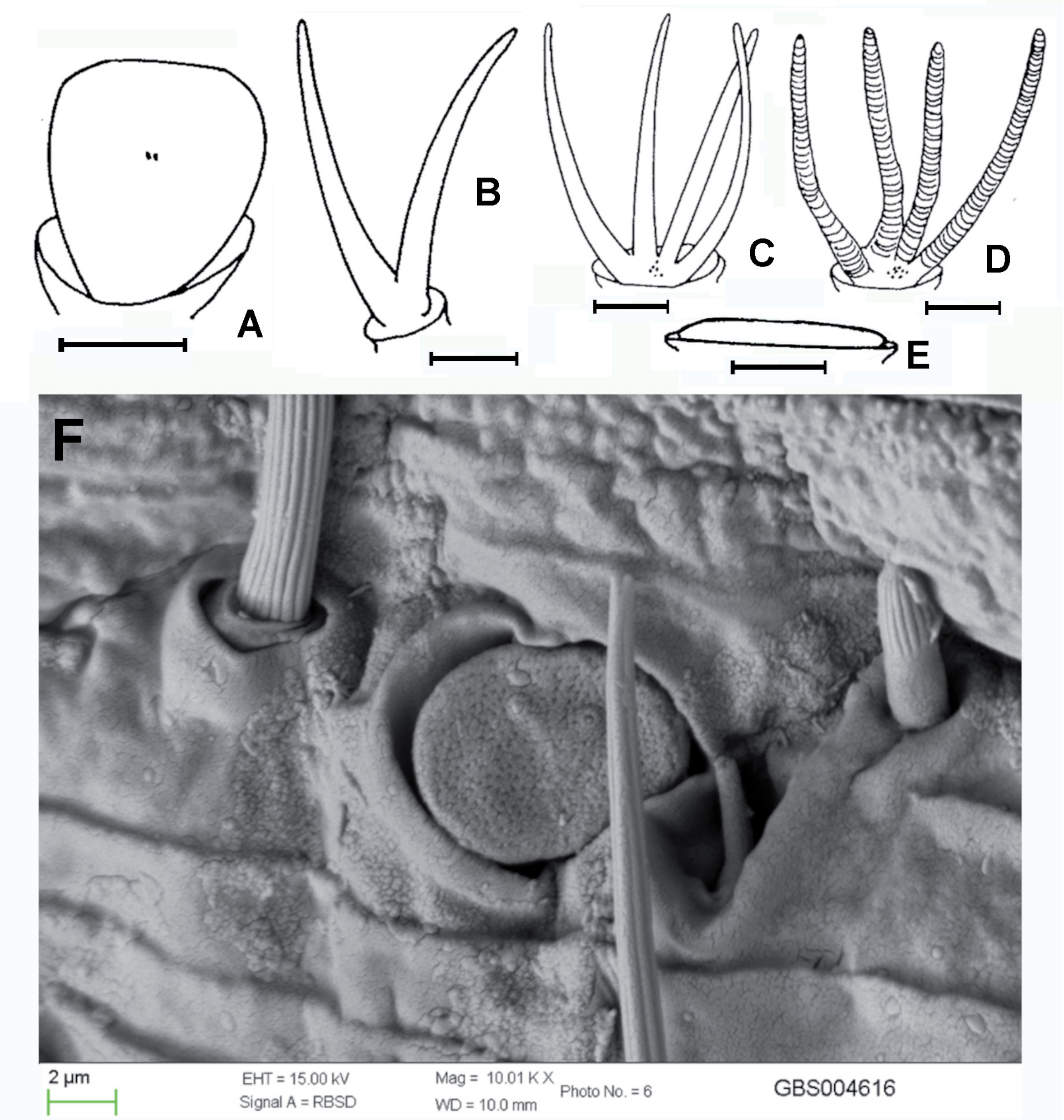

Fig. 2. Specialized sensilla of the antennae of Lepismatidae Latreille, 1802, adapted from Mendes (1986a). **A**. Silvestri’s sensillum (basiconic type F following Adel’s terminology). **B**. Bidigitate. **C**. Asteriform. **D**. Asteriform with annulated tegument. **E**. Poculiform. **F**. SEM photograph of a poculiform sensillum in *Acrotelsella transpectinata* Smith, 2016. Scale bars: A–E = 5 µm; F = 0.2 mm.

D. Sensilla of apical article of the labial palp

This character was deeply studied by Larink (1984). The most important feature is the number and arrangement of sensory papillae in this last article of the labial palp (Fig. 4). Six papillae in the 3+2+1 arrangement, found in the Lepidotrichidae Silvestri, 1912 and Nicoletiidae Escherich, 1905, has only been reported for a single species of Lepismatidae (*Heterolepisma annectens* Silvestri, 1924). In most Lepismatidae, only five papillae are present, the most frequent arrangements being 3+2 in two rows or five papillae in one row, but some modifications can be detected in different genera and species. Some *Ctenolepisma* Escherich, 1905, for example, have one row with more or less than five papillae. Some Acrotelsatinae show four papillae arranged in two rows or forming a diamond.

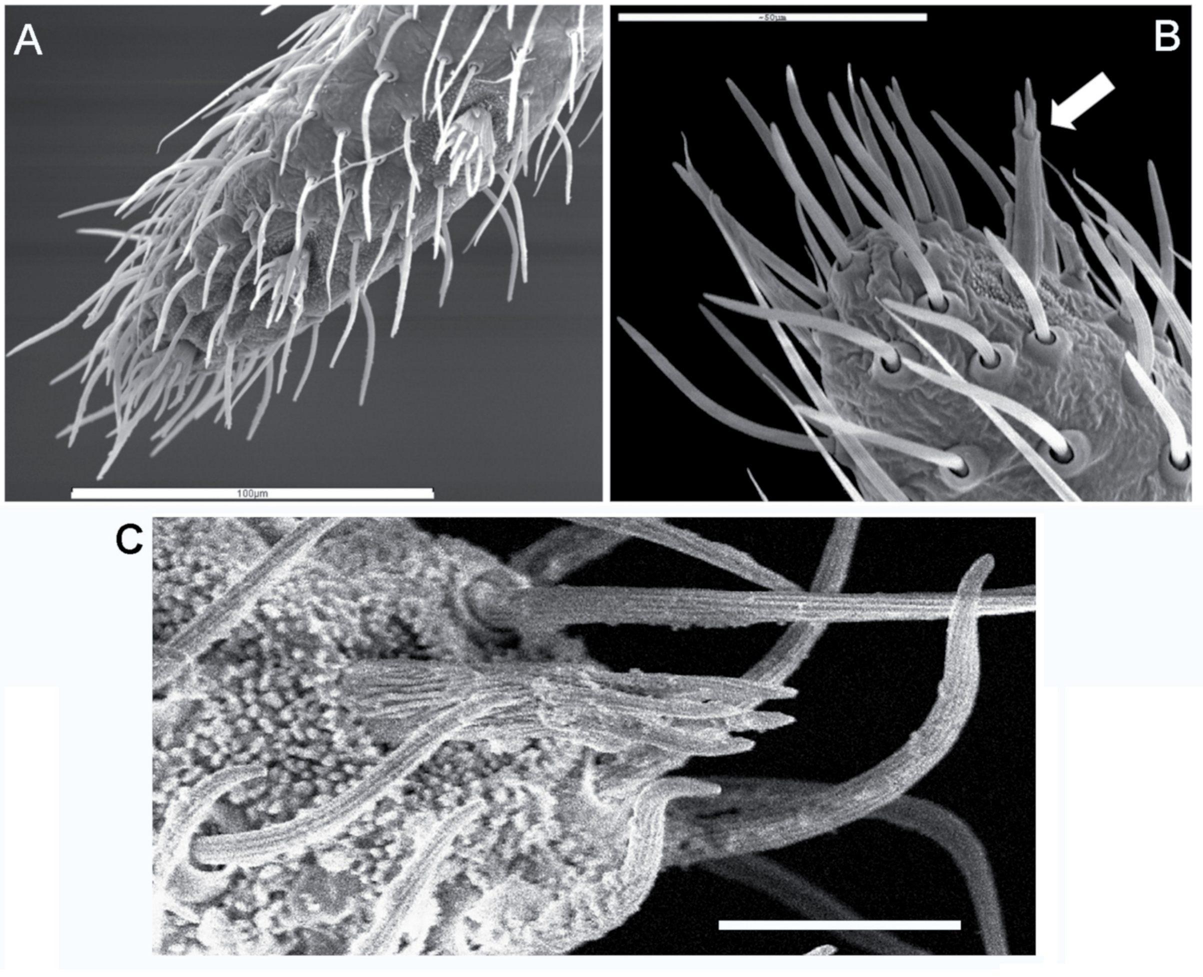

Fig. 3. Pronged sensilla of the apical article of the maxillary palp of some subfamilies of Lepismatidae Latreille, 1802, SEM photographs. **A**. Three pronged sensilla in *Heterolepisma* sp., with short and wide base and several (8–9) finger-like projections. **B**. One pronged sensilla (arrow) in *Allacrotelsa kraepelini* (Escherich, 1905), with long base and few finger-like projections. **C**. One of the three narrow multipronged sensilla of the ultimate article of the maxillary palp of *Visma* spp. They are probably homologous with the sensilla seen in *Allacrotelsa* Silvestri, 1935 and other Lepismatinae Latreille, 1802 but the other two have been lost. Scale bars: A = 0.1 mm; B = 50 µm; C = 25 µm.

E. Chaetotaxy of the anterior margin of the pronotum (Fig. 5)

The anterior margin of the pronotum can be completely devoid of setae (Fig. 5B) or provided with a uniseriate or multiseriate fringe of setae or macrochaetae, the setal collar (Fig. 5A). One intermediate state between the complete absence and the completely developed setal collar is the occurrence of some isolated and widely spaced macrochaetae or one to several tufts of macrochaetae separated by bare gaps. The anterolateral corners of the pronotum can be reduced in chaetotaxy compared to the medial part of the setal collar and can bear only one row of setae (anterolateral series) that can be different in structure to those of the medial part. Alternatively, these anterolateral corners can be multiseriate and constitute 1+1 tufts that are the only remnant of the setal collar (Fig. 5C). It seems that bare or sparsely setose napes may be more common within nidicolous genera.

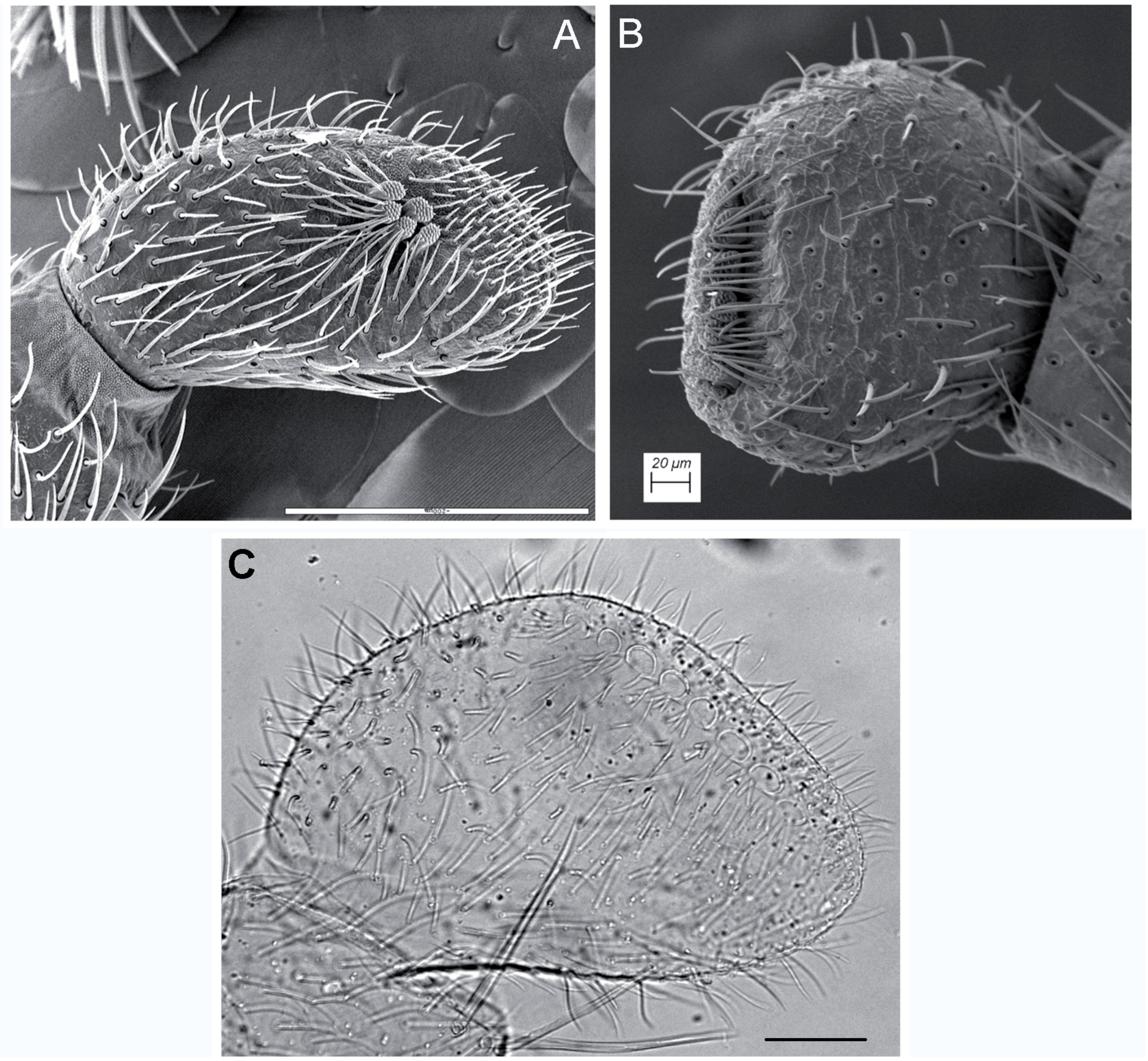

Fig. 4. Arrangement and number of labial papillae in Lepismatidae Latreille, 1802. **A**. Five labial palp papillae of *Allacrotelsa kraepelini* (Escherich, 1905), forming a circle; this arrangement can be interpreted as 3+2 (two rows). **B**. Labial palp papillae (five in one row) of *Thermobia domestica* (Packard, 1873). **C**. Micrograph of the apical article of the labial palp of *Ctenolepisma longicaudatum* Escherich, 1905 from Netherlands, showing 8 papillae on a single row (in this species, the number of papillae is variable, from 5 to 12). Scale bars: A = 0.2 mm; B = 20 µm; C = 50 µm.

F. Lateral and posterior chaetotaxy of thoracic nota (Figs 5–6)

The lateral margins of thoracic terga can have only a fringe of single macrochaetae, that can be restricted to the posterolateral angles, or can have several combs of macrochaetae. These fields of large setae, also called combs (or bristle-combs), consist of rows of macrochaetae that are more or less perpendicular to

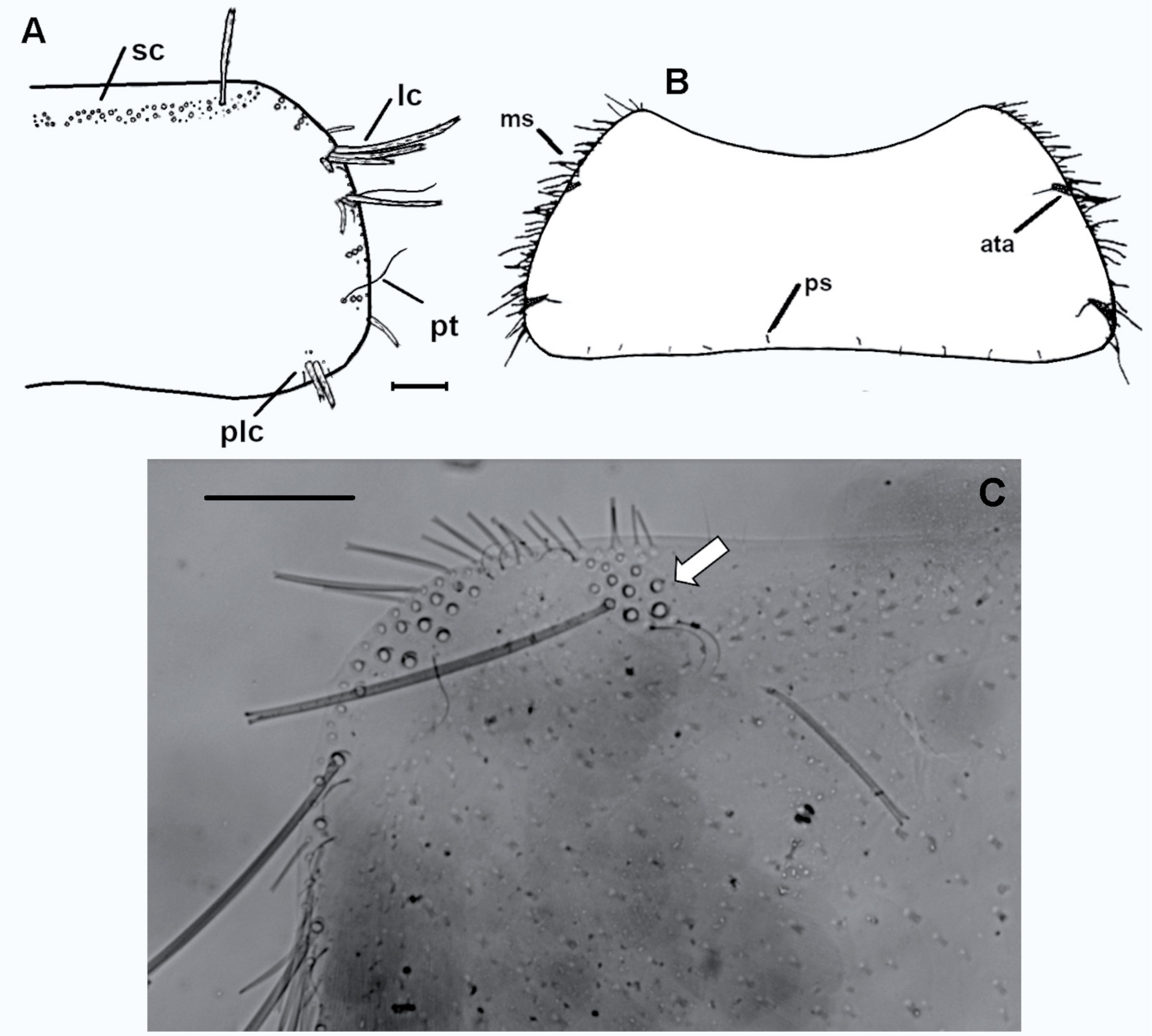

Fig. 5. Chaetotaxy of thoracic nota of Lepismatidae Latreille, 1802. **A**. Pronotum with setal collar (sc) of *Psammolepisma schultzei* (Silvestri, 1908), with lateral combs of macrochaetae (lc). Adapted from Irish (1988). Abbreviations: plc = posterolateral comb of macrochaetae, in this case inserted in a very lateral position of the posterior margin; pt = posterior trichobothrium, associated to the last lateral comb (N); the anterior trichobothrium is associated with the antepenultimate lateral comb (N–2). **B**. Pronotum with bare anterior margin of *Neoasterolepisma balcanicum* (Stach, 1922), without lateral combs of macrochaetae, only marginal setae (ms). Adapted from Molero-Baltanás *et al*. (1997). Abbreviations: ata = anterior open trichobothrial areas (the posterior ones are also open in this genus); ps = setulae associated with the posterior margin (in species of *Tricholepisma* these setae are transformed into macrochaetae: bigger and bifid apically). **C**. Micrograph of the left anterolateral corner of the pronotum of *Allacrotelsa kraepelini*, with 1+1 anterolateral groups of macrochaetae, marked with an arrow (and the remaining anterior margin bare). Scale bars = 0.2 mm.

the lateral margin. They can be composed of few (2–3) or a higher number of macrochaetae each. When this number is high, they are so wide that they can reach ¼ or ⅓ of the total width of the corresponding notum, but this state is not frequent. Some deserticolous genera from SW Africa exhibit a proliferation of the setae in these combs which results in them becoming confluent and forming into setal fields rather than independent uniseriate rows. In some cases, a comb may be reduced to a single macrochaeta but it's submarginal position makes it clear that this represents a reduced number of macrochaeta in a normally positioned comb and it is counted as a comb.

The posterior margin of thoracic nota can lack setae or can have some different types of chaetotaxy. Some species have 1+1 single or very few macrochaetae in posterolateral areas of this margin, and in some others, there are 1+1 posterolateral combs of macrochaetae that can be uniseriate or transformed into multiseriate fringes in some genera.

G. Thoracic notal trichobothrial areas (Figs 5, 7)

Trichobothria are hair-like mechanoreceptors that are present in different parts of the body and appendages of Lepismatidae. These hairs (according to some authors, "bothriotricha" is the appropriate name for the hairs) are inserted in special pits that are different from the attachment structures of other sensilla. On the nota of Lepismatidae, these insertions are surrounded by small unscaled areas that can be detected even better than the sensillum, especially when it is detached. Open trichobothrial areas are those where the unscaled area is in contact with the lateral or posterior margin of the notum (Fig. 7A), and closed areas are completely surrounded by scales, lacking connection with the margins (Fig. 7B). On each notum, there are usually 1+1 anterior and 1+1 posterior trichobothrial areas. This character was studied by Mendes (1986b), supporting its usefulness for the taxonomy of Lepismatidae at the supraspecific level and establishing several states (types) for these characters, depending on the distribution of these areas on the three thoracic segments. For example, Type 1 is the state where all areas are open, in Type 2 all anterior areas are open and all posterior ones are closed, etc. Some special states, such as the complete absence of these areas (Type 0), were also defined.

In some genera (e.g., *Anisolepisma* Paclt, 1967) the interpretation of trichobothrial areas is complicated by the presence of additional long, thin trichobothria-like setae along the margins. These are sometimes

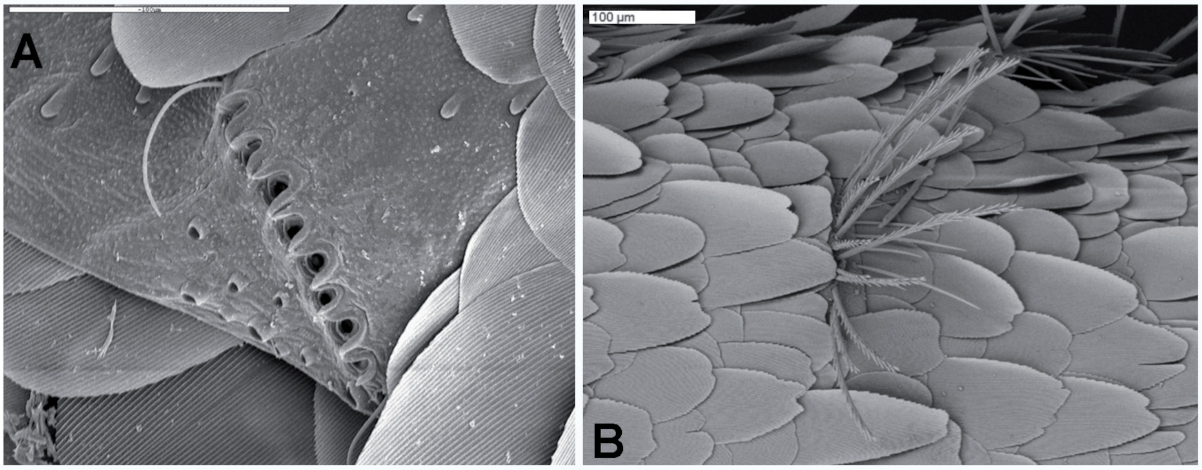

Fig. 6. Bristle-combs in Lepismatidae Latreille, 1802, SEM photographs. **A**. Ventral comb of macrochaetae of *Ctenolepisma nicoletii* (Lucas, 1846), where these are detached and only insertions are visible. **B**. Urosternal comb with macrochaetae not detached (feathered or plumose), from *Acrotelsella* sp. (probably *A. parlevar* Smith, 2016). Scale bars = 0.1 mm.

thicker at the base than typical trichobothrial hairs or the shape of the insertion is different to normal trichobothria in that the margin on one side is raised.

H. Size, shape and chaetotaxy of thoracic sternites (Fig. 8)

In most Lepismatidae, the medial part of the ventral tegument of the three thoracic segments is developed into a free plate that covers the medial base of the coxae, but some genera lack these free thoracic sternal plates and coxae cover much of the weakly developed thoracic sterna. A more detailed description of this condition, that is similar to that occurring in the remaining families of Zygentoma (Lepidotrichidae, Maindroniidae, Nicoletiidae and Protrinemuridae), is given for the genus *Anisolepisma* by Smith (2016a) and all genera that share this character have been included in the subfamily Acrotelsatinae. When free and developed, the three sternites can be similar in size, or the prosternum is more reduced than the others (for example, in the genera *Prolepismina* and *Monachina*). The shape of these sternites is also useful for distinguishing species, but variable within some genera. They are frequently heart-shaped (cordiform), more or less laterally constricted, and the posterior margin can be more or less acute or rounded (V-shaped to U-shaped, even truncate apically and with tendency to a subquadrangular shape). With few exceptions, the lateral margins of thoracic sternites bear macrochaetae that can be more or less extended onto the disc, especially in their apical area. These sternal macrochaetae are frequently arranged in combs and, in this case, the number of combs and their size/number of setae are very useful in taxonomic works to distinguish species, but variable within several genera. In some taxa, macrochaetae of these ventral plates are not ordered into combs and their arrangement is very variable, from only one marginal row to large fringes consisting of many macrochaetae.

I. Chaetotaxy of legs

The arrangement of setae and macrochaetae is very variable in Lepismatidae, but coxae are the articles that can be considered as more relevant in generic/suprageneric taxonomy (Fig. 9). They can bear only simple marginal setal fringes on their inner and outer margins, as occurs in Heterolepismatinae and Lepismatinae (Fig. 9B), but in most representatives of the other subfamilies some macrochaetae are arranged in combs (Fig. 9A, C), at least along their outer margins, in addition to the marginal fringes. In some genera belonging to Acrotelsatinae and Mirolepismatinae, coxal discs bear one large transverse

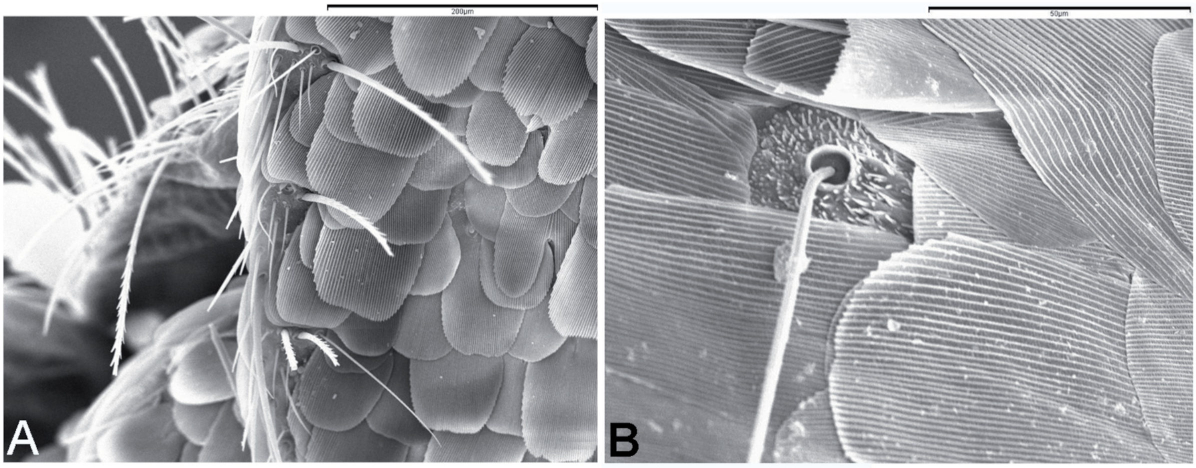

Fig. 7. Trichobothrial areas, SEM photographs. **A**. Open trichobothrial areas of the pronotum of *Sceletolepisma guadianicum* (Mendes, 1992); the anterior area is visible in the upper part of the photo, and the posterior area is placed in the lower part. **B**. Closed trichobothrial area of *Caribesella impudica* (Escherich, 1905) comb. nov. (formerly *Acrotelsella impudica*). Scale bars: A = 0.2 mm; B = 50 µm.

comb, and in some deserticolous Ctenolepismatinae these areas are provided with several wide transverse combs. Tibial chaetotaxy is also interesting; for example, in a large number of species of the genus *Neoasterolepisma* Mendes, 1988, males present modified chaetotaxy and/or shape of tibiae. In some genera, the number and arrangement of macrochaetae on the dorsal/outer and ventral/inner sides is probably constant in each species, but not described for most taxa. In *Acrotelsa* Escherich, 1905, tibial macrochaetae are arranged in transverse combs. The relative length of the three tibiae, and their size with respect to palps and body length, could also be interesting, but not always detailed in usual descriptions of these insects. Their significance at infrageneric and suprageneric levels should be assessed in the future.

J. Pretarsal claws

The pretarsus of most Lepismatidae have two symmetrical claws and a median empodium. Pulvilli are absent, except in the monospecific South African genus *Lepitrochisma*, illustrated by Mendes (1988). Some genera, most of them psammophilous, are characteristic because of a secondary loss of the empodium or even one claw, or both claws are asymmetric. We have detected that the tegument of the claws and empodium is variable, especially when appropriately examined with SEM; the claws of some species have striated surfaces and some of them are covered by microtrichia (Fig. 10). The taxonomic significance for associating these differences to generic or suprageneric levels should be assessed in the future.

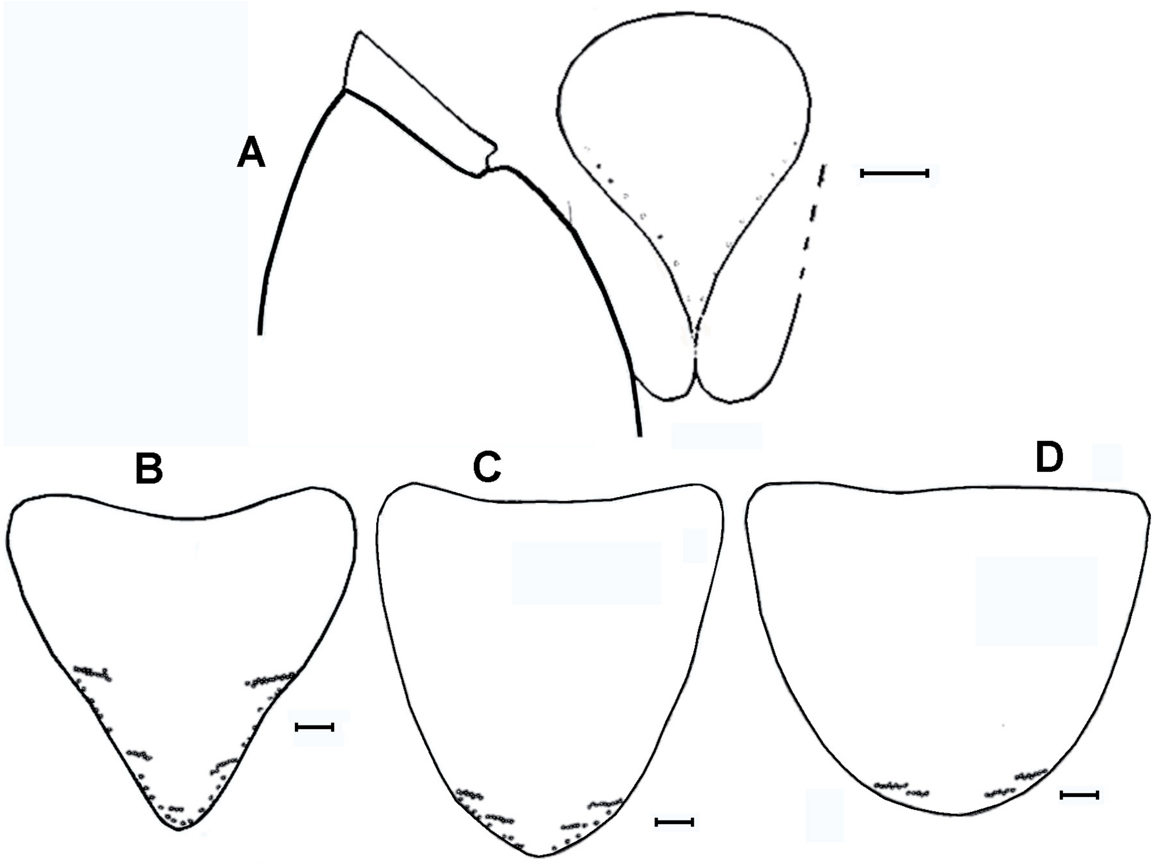

Fig. 8. Thoracic sternites in Lepismatidae Latreille, 1802. **A**. Mesosternal plate of *Anisolepisma* sp., adapted from Smith (2016a). **B–D**. Thoracic sternites (prosternum, mesosternum and metasternum, respectively) of a species of Ctenolepismatinae Mendes, 1991, *Sceletolepisma rodriguezi* (Mendes, Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1993) that cover the base of coxae. Scale bars = 0.1 mm.

K. Chaetotaxy of urotergites I–IX

The abdominal tergites of Lepismatidae have only marginal or submarginal macrochaetae on their posterior margin, with the disc covered with scales. Some macrochaetae can be inserted in an infralateral position, i.e., in the posterolateral part of the tergite where it bends ventrally to cover the pleural part, and even the lateral extremes of the ventral side. The remaining macrochaetae are inserted on different dorsal areas of this posterior margin. Two main alternatives for the arrangement of these macrochaetae occur in Lepismatidae: to form combs of macrochaetae or to be isolated along the posterior margin. In the first case, the usual number of combs is three on each side (state 3+3 combs), one in infralateral position, and two in dorsal position, that have been called lateral and submedian (or sublateral) combs. The abbreviations A, B and C have been used in some works to refer to the infralateral, lateral and submedian combs (see an example in Table 1 on the abdominal chaetotaxy of *Caribesella impudica* comb. nov.). In some urotergites, depending on the species, some of these combs are absent (for example, it is frequent that they are absent in urotergite IX and that urotergite I only bears 1+1 infralateral groups, lacking lateral and submedian combs). In some genera, such as *Thermobia* Bergroth, 1890 or *Psammolepisma*

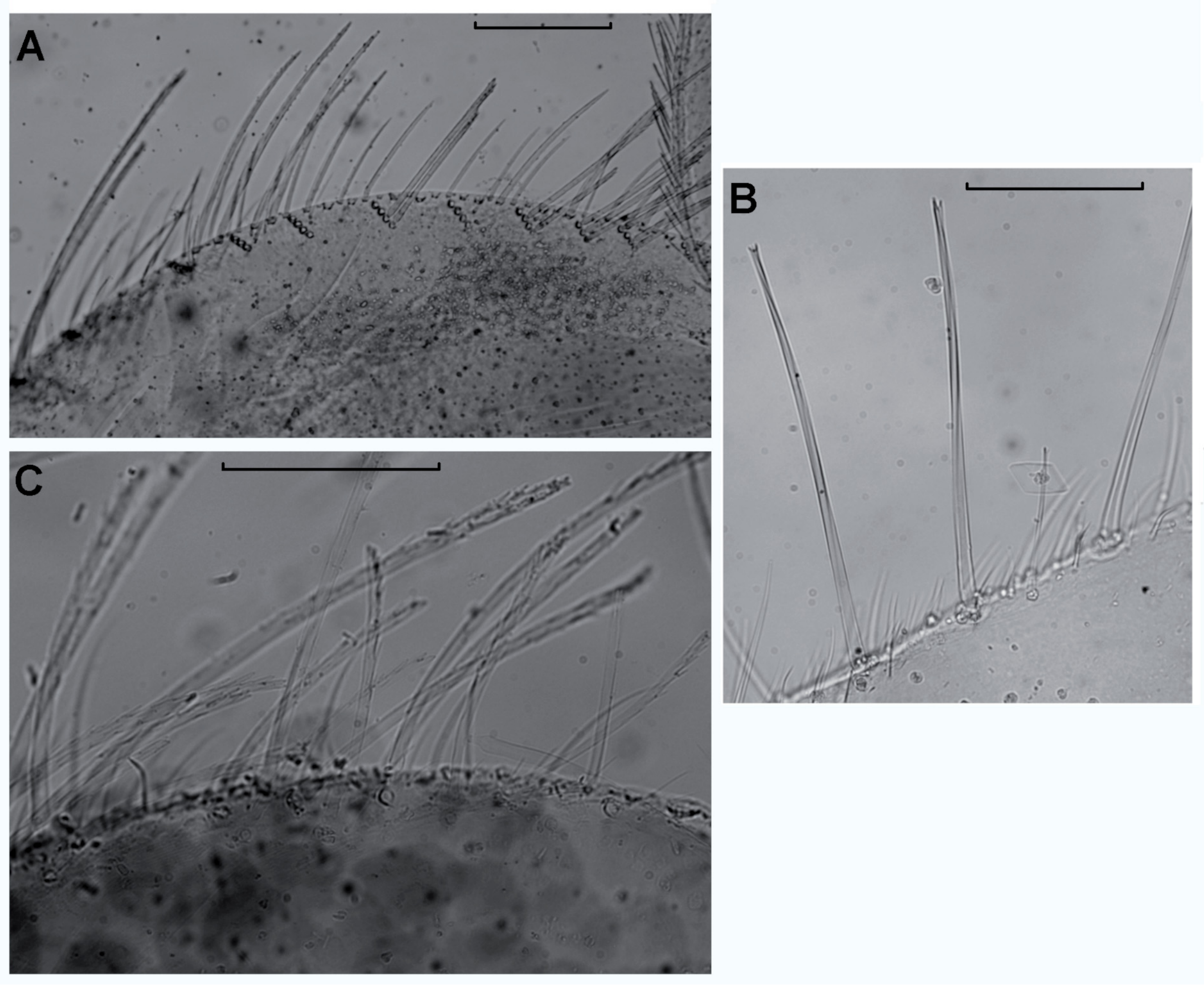

Fig. 9. Chaetotaxy of coxae in Lepismatidae Latreille, 1802, micrographs of the external margin of the coxa. **A**. *Caribesella impudica* (Escherich, 1905) comb. nov., showing discrete combs of few macrochaetae. **B**. *Neoasterolepisma curtiseta* Mendes, 1988, showing isolated macrochaetae inside a row of setulae. **C**. *Ctenolepisma nicoletii* (Lucas, 1846), with an irregular row of macrochaetae not clearly arranged in combs. Scale bars: A, C = 0.1 mm; B = 50 µm.

Irish, 1988, all urotergites lack the submedian comb (state 2+2 combs). In some genera (for example, *Mormisma* or *Sabulepisma*), the proliferation of macrochaetae can lead to the formation of groups or fringes on the posterior margin because of the coalescence of the groups of macrochaetae in the original three positions. When there are isolated macrochaetae on the posterior margin, there is one to several macrochaetae forming an infralateral group in the same position as comb "A" of genera with bristle-combs, and there are usually 3+3 additional isolated dorsal macrochaetae (called lateral, sublateral and submedian). This is the typical chaetotaxy of *Lepisma saccharinum* and most nidicolous Lepismatinae, illustrated in Mendes (1991) or in Robla *et al*. (2023). In some genera and species there are modifications in this pattern, consisting of additional isolated macrochaetae or the reduction of one or two of these setae. The urotergal chaetotaxy has been frequently used as one of the most important characters to define species and suprageneric groups within Lepismatidae, but some cases of intraspecific variability have been detected that suggest the use of more than one character is necessary to define new taxa (Molero-Baltanás 2010).

L. Shape and chaetotaxy of urotergite X (Fig. 11)

The last abdominal tergite of Lepismatidae is very variable in shape and this character has been used by most authors as an important feature to distinguish genera and groups of species. Although this shape is constant in several genera, some others show different states. In some cases (as in the genus *Ctenolepisma* Escherich, 1905 s. lat.) this could correspond to different taxa with generic or subgeneric status, but some intraspecific variability has been detected in some species; for example, it is shown in Mendes (1993) for North African *Ctenolepisma lineatum* (Fabricius, 1775), although these specimens probably correspond to two species: *C. brauni* Wygodzinsky, 1941 and *C. nicoletii* (Lucas, 1846). A similar variability in shape has been seen in some species of *Heterolepisma* (Mendes 1991). These examples lead us to consider that the shape should be used with caution as a stable character to define genera, even species. Nevertheless, it is useful in many cases since it has been proven to be constant in several genera and characteristic of most species. There is a group of genera belonging to the subfamilies Acrotelsatinae and Ctenolepismatinae (*Acrotelsa*, *Stylifera* Stach, 1932, *Acrotelsella* Silvestri, 1935, etc.) with a large, triangular, acutely pointed urotergite X. In other genera, the posterior margin is not acute but convex, straight or even concave and the general shape is described as subtrapezoidal or

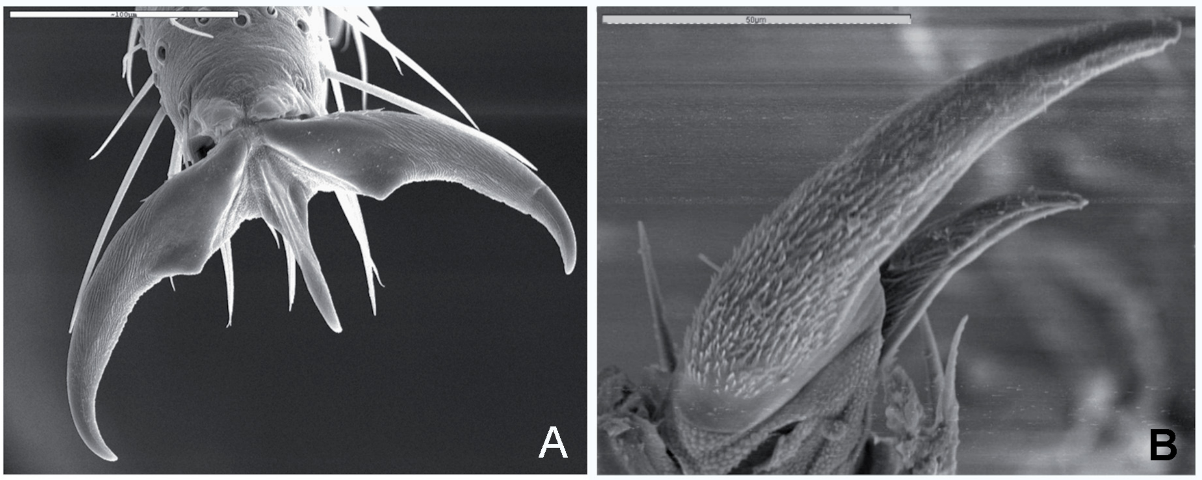

Fig. 10. Praetarsal claws in Lepismatidae Latreille, 1802, SEM photographs. **A**. Praetarsus of *Ctenolepisma nicoletii* (Lucas, 1846), showing lateral claws with smooth base and finely striated tegument. **B**. Pretarsal claw of *Caribesella impudica* (Escherich, 1905) comb. nov., with microtrichia, and the empodium with striated tegument. Scale bars: A = 100 µm; B = 50 µm.

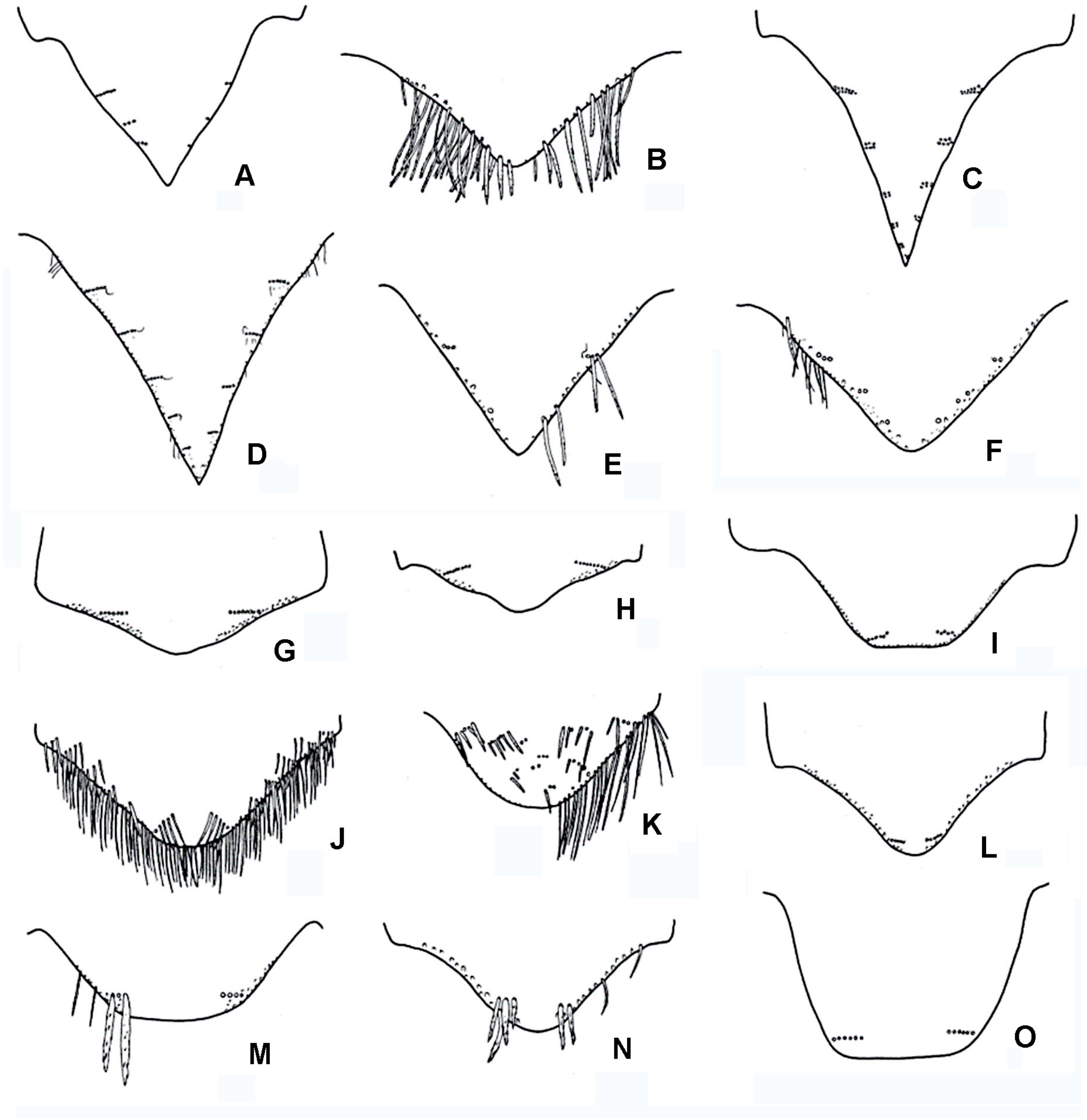

Fig. 11. Shape and chaetotaxy of the urotergite X (last abdominal tergite) of Lepismatidae Latreille, 1802, variability. **A**. *Caribesella impudica* (Escherich, 1905) comb. nov., adapted from Wygodzinsky (1959a). **B**. *Qantelsella louisae* Smith, 2015, from Smith (2015). **C**. *Stylifera gigantea* (Escherich, 1905), from Irish (1988**c**). **D**. *Acrotelsella parlevar* Smith 2016, from Smith (2016b). **E**. *Hemitelsella clarksonorum* Smith, 2016, from Smith (2016b). **F**. *Hemitelsella hortorum* Smith & Mitchell, 2021, from Smith & Mitchell (2021). **G**. *Thermobia vallaris* Irish, 1988, from Irish (1988b). **H**. *Thermobia domestica* (Packard, 1873), from Irish (1988b). **I**. *Sceletolepisma sagartianum* (Molero, Kahrarian & Gaju, 2016), from Kahrarian *et al*. (2016). **J**. *Hyperlepisma patrizii* Silvestri, 1932, from Silvestri (1932). **K**. *Nebkhalepisma australe* (Wygodzinsky, 1959), from Wygodzinsky (1959b). **L**. *Hyperlepisma arabiense* Irish, 1991, from Irish (1991). **M**. *Ornatilepisma horni* Irish, 1988, from Irish (1988a). **N**. *Swalepisma mirabile* Irish, 1988, from Irish & Mendes (1988). **O**. *Sceletolepisma occidentale* (Irish, 1987), from Irish (1987).

trapezoidal, since it has well defined posterolateral corners. Trapezoidal urotergites X are probably the most frequent in Lepismatidae and the length/width ratio at its base was proposed by Mendes (1982) as a characteristic to include in the description of species. In several genera, this last tergite of the body is short and subtriangular, lacking posterolateral corners and with the posterior margin more or less acute or rounded; this is the case, for example, of species belonging to the genus *Thermobia*. Moreover, the chaetotaxy of this tergite is also interesting, since some genera bear several combs of macrochaetae on its lateral margin (this is frequent in genera with large acute triangular and trapezoidal shapes of the urotergite X), but the most frequent state consists of bearing 1+1 lateral combs inserted close to the posterolateral margins. In some genera, mainly a group of taxa with trapezoidal or subtrapezoidal shape, this pair of combs is ill-defined and only two small groups of macrochaetae are associated with the posterior margin close to the posterolateral corners, and even in some species these macrochaetae are absent. On the contrary, in some psammophilous genera the proliferation of macrochaetae enlarges the combs of this tergite, as happens with other anterior ones, into large groups or fringes of macrochaetae.

M. Ventral chaetotaxy of the abdomen

Except for the genus *Lepismina* Gervais, 1844, where the abdomen lacks macrochaetae ventrally, all Lepismatidae present macrochaetae on the posterior margin of their abdominal sternites, usually arranged in combs, although in several taxa one or two urosternites (frequently the first or the first and second ones) lack chaetotaxy. The genus *Peliolepisma* Ritter, 1910 was defined incorrectly as lacking abdominal chaetotaxy, but it has been proven (for example, see Kulma *et al*. 2022) that it bears small combs of macrochaetae on most of their abdominal segments, dorsally and ventrally, and it should be included in the genus *Ctenolepisma*, representing a form with a reduced number of macrochaetae in its combs, probably related to *C. rothschildi* Silvestri, 1907, which shows a similar reduction of its abdominal chaetotaxy. Some genera bear 1+1 or 2+2 bristle-combs in the lateral position and in some cases combs in the median position are present. Although the plesiomorphic condition of most states of this character is under discussion (Smith 2016a), this character is very useful for distinguishing species and even genera. Irish (1987) uses the arrangement of median combs in the different urosternites to establish groups of species but, although some of these groups include phylogenetically related taxa, some of them probably include species belonging to different lineages. Moreover, intraspecific variability has been detected in this character in several species, such as *Sceletolepisma guadianicum* (Mendes, 1992) (Molero-Baltanás *et al*. 2015), so new taxa should not be defined on the basis of bearing one median comb more or less than other previously known species as a unique difference. In both sexes, the ninth sternite of Lepismatidae is divided into two lateral coxites; the inner process of these coxites can lack combs or bear one to several combs in some species, but it seems that, in most cases, this character alone is not strong enough to deserve importance at the generic level.

N. Number of abdominal styli

Styli are unsegmented appendages inserted on an indentation of the posterior margin of some abdominal sternites, usually on the ninth coxites between the inner and outer processes and in some preceding segments. Most Lepismatidae have one to three pairs of styli, but a higher number is shown by some genera (*Visma* Smith, Mitchell & Molero-Baltanás, 2021, *Stylifera*, etc.). In some psammophilous and nidicolous genera there is only one atrophied pair of styli, and as an extreme condition they are absent, although in some of these examples the indentation of the stylus is conserved. They are inserted internal to the combs of macrochaetae, but in *Stylifera* they occur between each one of the two combs of each side. Most species, and even some genera, have a constant number of pairs of styli, but this character needs to be treated carefully since juveniles have a lower number; they develop the definitive number as adults and, as in other apterygote hexapods, the adult condition is not easily established. Moreover, several taxa show sexual differences in the number of styli; in this case males bear one pair less than females. In adult states, an intraspecific variability of this character has been suggested, but discarding the postembryonic development and the sexual differences, this hypothesis has been discarded for some species, such as in *Ctenolepisma lineatum* (see Molero Baltanás *et al*. 2012), but appears valid in others such as *Visma brigalowsum* Smith, Mitchell & Molero-Baltanás, 2021 (Smith *et al*. 2021).

O. Parameres: presence and development (Fig. 12)

The presence or absence of parameres very probably represents a character that deserves taxonomic relevance at the superfamily level. Parameres (or paramera) are absent in Ctenolepismatinae, Mirolepismatinae and Silvestrellatinae. Other characters of the parameres can be useful for distinguishing genera and species; for example, *Allacrotelsa* has pseudoarticulated parameres. In most Lepismatinae parameres have a glandular area on their inner surface.

P. Ovipositor: type and other morphological characters (Fig. 13)

Two main types of ovipositors have been distinguished in Lepismatidae. The primary type is thin, with its tip rounded or acute but not sclerotized (Fig. 13A). The secondary type has fossorial sclerotized spines and sometimes the entire tegument of the apical part of the gonapophyses is sclerotized (Fig. 13B–C). The secondary type is frequent in representatives of Acrotelsatinae and Mirolepismatinae but also occurs sporadically in some genera of Ctenolepismatinae. The different morphologies of the secondary types do not seem to be homologous in all species/genera, but it is useful to distinguish the taxa presenting these apomorphic structures. Other characters of the chaetotaxy, shape and length can be useful at specific and generic levels. For example, genera belonging to the subfamily Silvestrellatinae have a cluster of minute spinelets on the apex of posterior gonapophyses and their apophyses are short and conical. Other genera with this shape are found in psammophilous genera of the subfamily Ctenolepismatinae. Lepismatinae have thin ovipositors that do not surpass the apex of the styli. The number of divisions of the gonapophyses and their length relative to the ninth coxites or to the apex of the ninth styli also deserve taxonomic relevance, at least at specific level, but the intraspecific variability of these character needs to be assessed for each species.

Q. Relative length of terminal filaments and antennae

These characters are usually included in descriptions of species. In some genera and groups of species, antennae or caudal appendages (or terminal filaments) are shorter than half the body length and in some others, they are longer than the body length. Although these characteristics are useful in the taxonomy of Lepismatidae, there is intraspecific variability and the maximum length is frequently not known for a large number of species, because the studied specimens presented broken appendages when collected. The chaetotaxy and distribution pattern of caudal filaments is not sufficiently studied, except in some species (Kränzler & Larink, 1980), but it is probably more interesting for the taxonomy of these insects than its current treatment.

R. Body scales: shape and structure (Fig. 14)

Until recently, little attention has been paid to this character because the scale cover on the body of Lepismatidae has been considered to be generally uniform. For some species, some special types of dorsal scales have been described; for example, some acutely pointed scales in *Neoasterolepisma foreli* (Moniez, 1894) and *N. soerenseni* (Silvestri, 1908), some heterogeneous scales on the nota of a few species of *Ctenolepisma*, where large scales with widely spaced ribs contrast with other smaller and with more dense ribs (for example, in *C. rothschildi*). But the diversity of shapes of scales and the spacing of their ribs are more variable in a higher number of taxa, as revealed for some genera such as *Visma* (Smith *et al*. 2021). This variability requires the use of SEM for an appropriate assessment, and further studies will reveal whether it is only useful for distinguishing species or if some states might correspond to lineages with generic or suprageneric relevance.

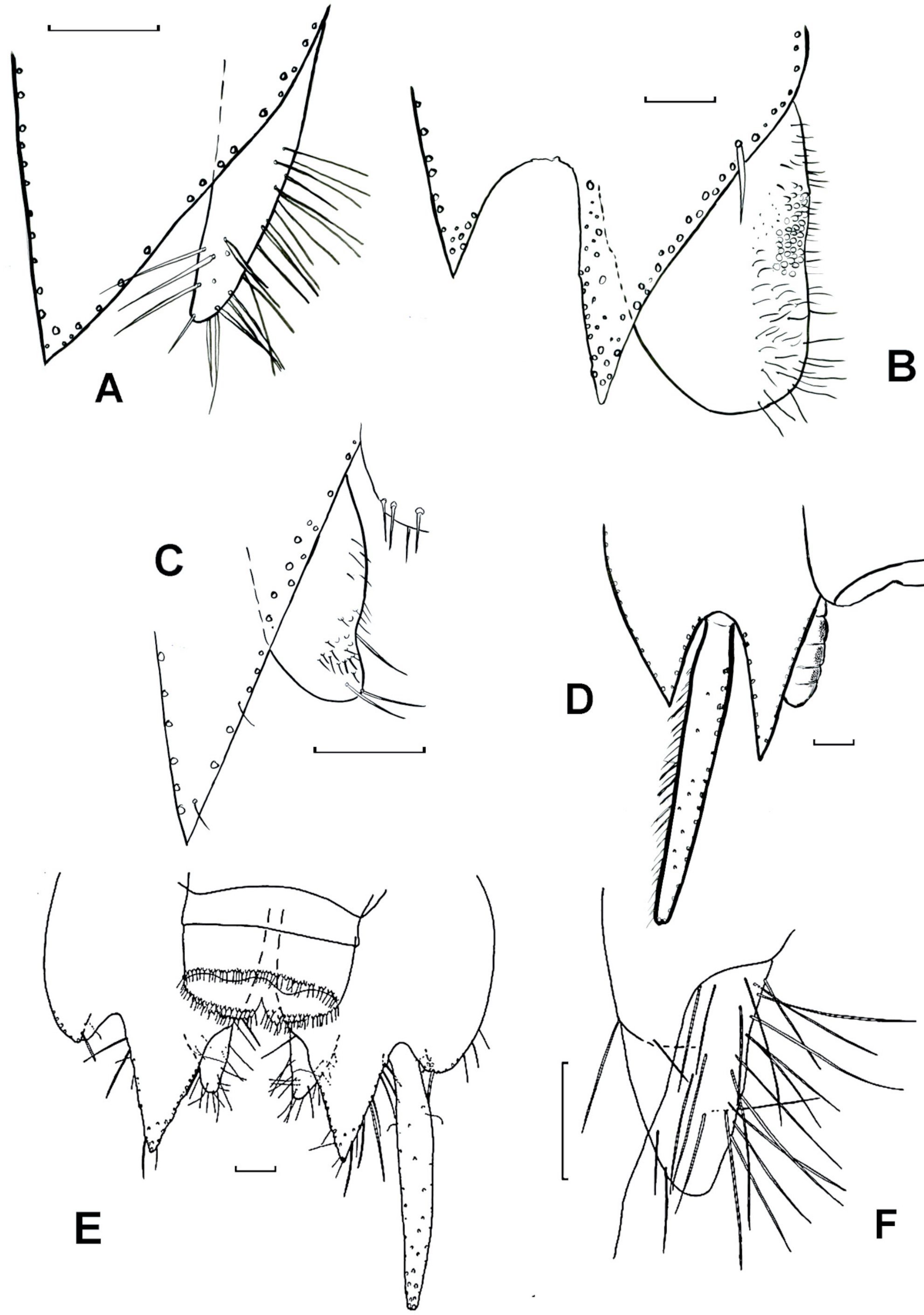

Fig. 12. Paramera of Lepismatidae Latreille, 1802. **A**. Tubuliform paramere of *Acrotelsa collaris* (Fabricius, 1793). **B**. Big swollen paramere of *Lepisma saccharinum* Linnaeus, 1758, larger than the inner process of coxite IX and with glandular area. **C**. Medium-sized to small paramere of *Neoasterolepisma hespericum* Molero-Baltanás, Bach de Roca & Gaju-Ricart, 1997, with a small glandular area. **D**. Pseudoarticulated paramere with glandular area of *Allacrotelsa kraepelini* (Escherich, 1905). **E**. Pseudoarticulated paramere of *Visma brigalowsum* Smith, Mitchell & Molero-Baltanás 2021. **F**. A detail of a similar pseudoarticulated paramere, of *Visma bingara* Smith, Mitchell & Molero-Baltanás 2021. Scale bars = 0.1 mm.

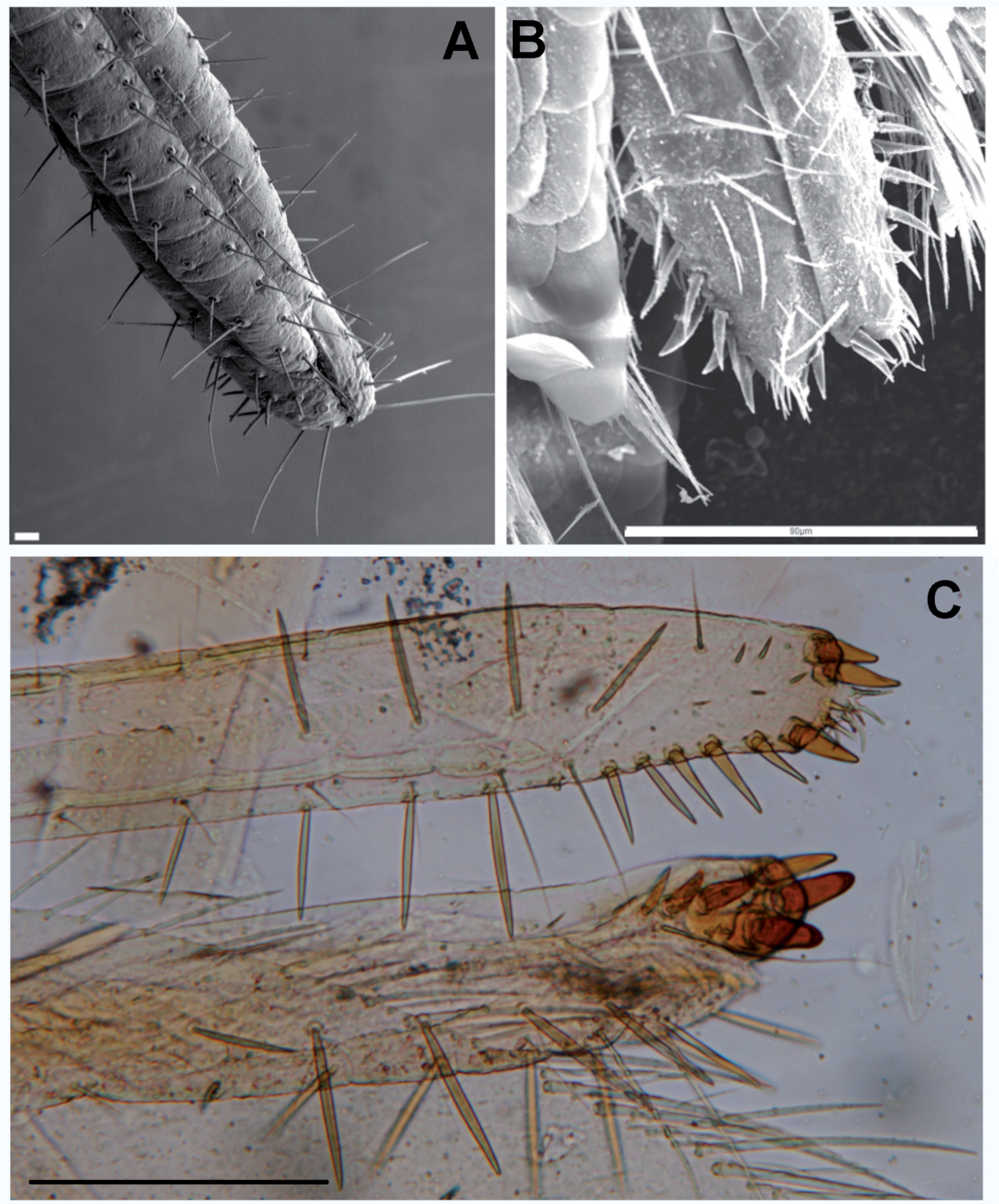

Fig. 13. Ovipositor types in Lepismatidae Latreille, 1802. **A**. Primary ovipositor of *Ctenolepisma rothschildi* Silvestri, 1907, SEM photograph. **B–C**. Secondary ovipositor of *Caribesella impudica* (Escherich, 1905) comb. nov., SEM photograph (B) and micrograph (C). Scale bars: A = 10 µm; B = 90 µm; C = 0.1 mm.

S. Scales on appendages: shape and distribution (Fig. 15)

The coverage of scales of appendages has been insufficiently studied in Lepismatidae, assuming that appendages lack scales or that some articles, such as coxae, bear scales similar to those of the body. But recent studies mainly carried out by the authors of this work have revealed that there is a high variability in the scale cover of appendages, that involves diverse shapes of scales and diverse distribution patterns in the different appendages and articles. Most of this information is still unpublished, but information on the scale cover of legs of some species of the genera *Heterolepisma* and *Visma* has been included in their descriptions and identification keys (Smith *et al*. 2021) and different shapes and distributions of scales have been shown for some species of *Ctenolepisma* (Molero-Baltanás *et al*. 2010, 2012, etc.). It seems that some patterns of distribution are constant in some genera and groups of genera. For example, all Lepismatinae examined lack scales on femora and tibiae, but all *Ctenolepisma* examined have scales on femora, at least on some parts of its inner side but usually covering all this side and the apex of the outer side. Moreover, all *Ctenolepisma* s. str. with a trapezoidal tenth urotergite examined and most species included in the subgenus *Sceletolepisma* Wygodzinsky, 1955 sensu Irish 1987 (in this work proposed as an independent genus) that share the same shape of the last urotergite, lack scales on tibiae, but all *Ctenolepisma* s. str. with short subtriangular tenth urotergite have scales on this article. All of these genera lack scales on maxillary and labial palps, but some Acrotelsatinae have scales at least on the basal articles of both appendages or, alternatively, on one of them. Most genera lack scales on pedicels, but some of them (as *Acrotelsa*) have scales on this antennal division. Some genera lack scales on cerci or on terminal filaments, and some others have scales on these appendages, showing different shapes in different taxa, etc. For example, lanceolate scales have been observed in *Ctenolepisma lineatum* and other species with a short subtriangular tenth urotergite (Fig. 15E), but these scales have not been detected in *Sceletolepisma* or in *Ctenolepisma* s. str. with a trapezoidal tenth urotergite. Even the flagellum of the antenna is covered by scales in one genus (*Stylifera*), which represents a new character for Lepismatidae presented in this work and included in the identification key (Fig. 15A–B). Unfortunately, there are a lot of genera where these characters have not yet been examined, so they cannot be included in most parts of an identification key like the one presented in this work. For several genera, fresh material is needed because this cover of scales can easily be lost in specimens preserved in liquid mediums for a

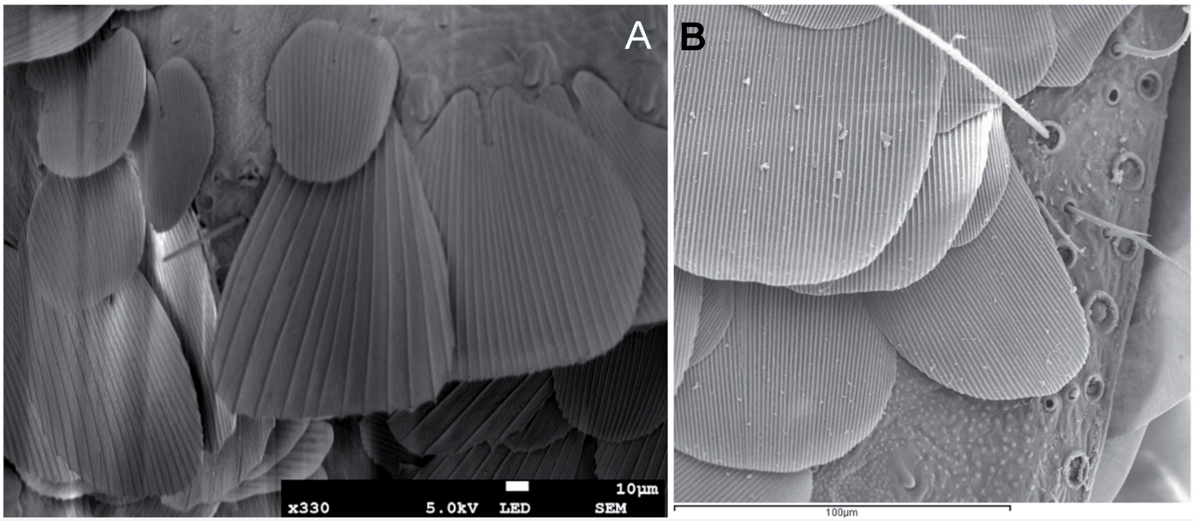

Fig. 14. Body scales of Lepismatidae Latreille, 1802, variability. **A**. Dorsal scales of *Ctenolepisma rothschildi* Silvestri, 1907, showing heterogeneity of sizes and spacing of ribs. **B**. Dorsal scales of *Heterolepisma sclerophyllum* Smith, 2014, showing more homogeneous scales with dense ribs. Scale bars indicated in the photographs: A = 10 µm; B = 100 µm.

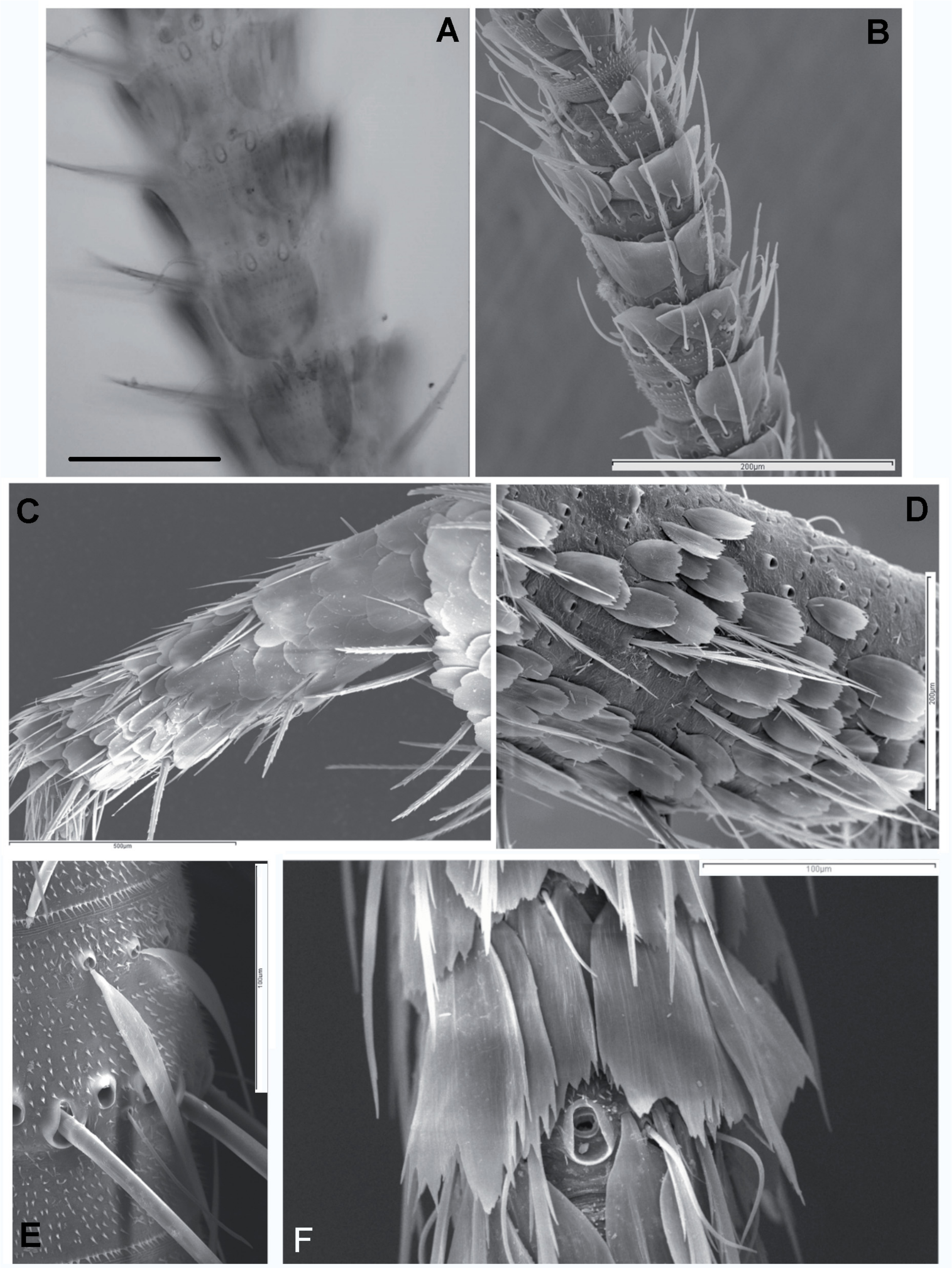

Fig. 15. Scales on appendages of Lepismatidae Latreille, 1802, variability in shape and distribution pattern. **A–B**. Fan-shaped scales on antennae of *Stylifera gigantea* (Escherich, 1905), with light microscope (A) and with SEM (B). **C**. Tibial scales of *Acrotelsella* sp. from Australia, similar to those of the femur. **D**. Tibial scales of *Stylifera gigantea* from Venezuela. **E–F**. Scales on cerci of *Ctenolepisma lineatum* (Fabricius, 1775) (E) and *Stylifera gigantea* (F). Scale bars: A, E–F = 0.1 mm; B, D = 0.2 mm; C = 0.5 mm.

long period of time, and an appropriate description of their shapes and distribution frequently requires examination by SEM. When these difficulties are overcome, it is very likely that it will even be possible to elaborate a key to the genera of Lepismatidae based mainly on these scale characteristics, and that phylogenetic affinities between groups with similar patterns can be inferred which could be consistent with the results of future molecular studies.

T. Type of macrochaetae (Figs 9, 16)

This character has frequently been used in the suprageneric classification of Lepismatidae, considering initially two types of macrochaetae: smooth with bifid apex (Figs 9B, 16A–B) and feathered or plumose (Figs 9A, C, 16C–D, F). Actually, smooth macrochaetae are not completely smooth, because with high magnification it can be observed that the tegument is striated. This character was studied in depth by Mendes (1988), who considered that there are at least two different types of feathered macrochaetae, one of them (named as Type 2) is exclusive to Mirolepismatinae. Actually, there are more types of feathered macrochaetae, with different arrangements and size of pectinations (compare Fig. 16D and 16F), and some genera show smooth macrochaetae with an acute or blunt tip, not bifurcate, that are probably apomorphic conditions of desert-living forms (Fig. 16E).

U. Body shape and colour pattern (Fig. 17)

These characters are included here together because they are the main features that are shown in photographs of Lepismatidae. The usual body shape of Lepismatidae is fusiform (i.e., spindle-shaped, elongated and tapering at both ends) and slightly flattened dorsoventrally (as in Fig. 17B). But there is some variation in this shape depending on species: some have a subcylindrical shape because the thorax is not clearly wider than the base of the abdomen and the head is similar in width (Fig. 17A) and some ant-associated species have a limuloid shape, with a wide thorax compared to the abdomen base (Fig. 17C). Smith (2013) used some metrics to provide for the description of species. The most important are body length excluding antennae and terminal filaments (head+body length), and the maximum width of the thorax. But these characters can show intraspecific variability, including variation during individual development, that should be assessed (young specimens are usually more subcylindrical than adults, which show a wider thorax). So, these metrics should be considered with caution when identifying species. Species belonging to genera associated with ants have a thorax that is clearly wider than the head and abdomen base because of the strong development of the lateral sides of the nota, but in species of the same genera that are not associated to ant colonies, the thorax is usually narrower. In some species, the abdomen is longer than the thorax and in others it is small and narrow, tapering towards the posterior end, but in living silverfish the size of the abdomen can be variable depending on the physiological condition of the insect, and in specimens preserved in alcohol the abdomen can be distended by extension of the intersegmental membranes.

Regarding colour pattern, each species usually shows a characteristic colour pattern of dorsal scales. However, this does not mean that Lepismatidae can be identified at the specific level exclusively by this characteristic, as some participants in citizen science platforms are doing (they are amateur or professional entomologists, but not experts in Zygentoma). Most colour patterns are not exclusive to only one species, and in a single species there is a wide range of variation in colour; moreover, the colour of scales can be lighter or darker depending on the moulting state. For example, *Ctenolepisma lineatum* has received the common name of four-lined silverfish, referring to a pattern of scales that are arranged in longitudinal rows alternately dark and lighter, but this does not mean that this is the only species with this pattern. There are several species of the genus *Ctenolepisma* and some other related silverfish showing these rows of dorsal scales. Moreover, lighter scales become darker in some specimens of *C. lineatum*, so the general aspect of the insect is almost uniformly dark greyish, blackish or brown, and the identification must be complemented with the observation of several characters that can only be

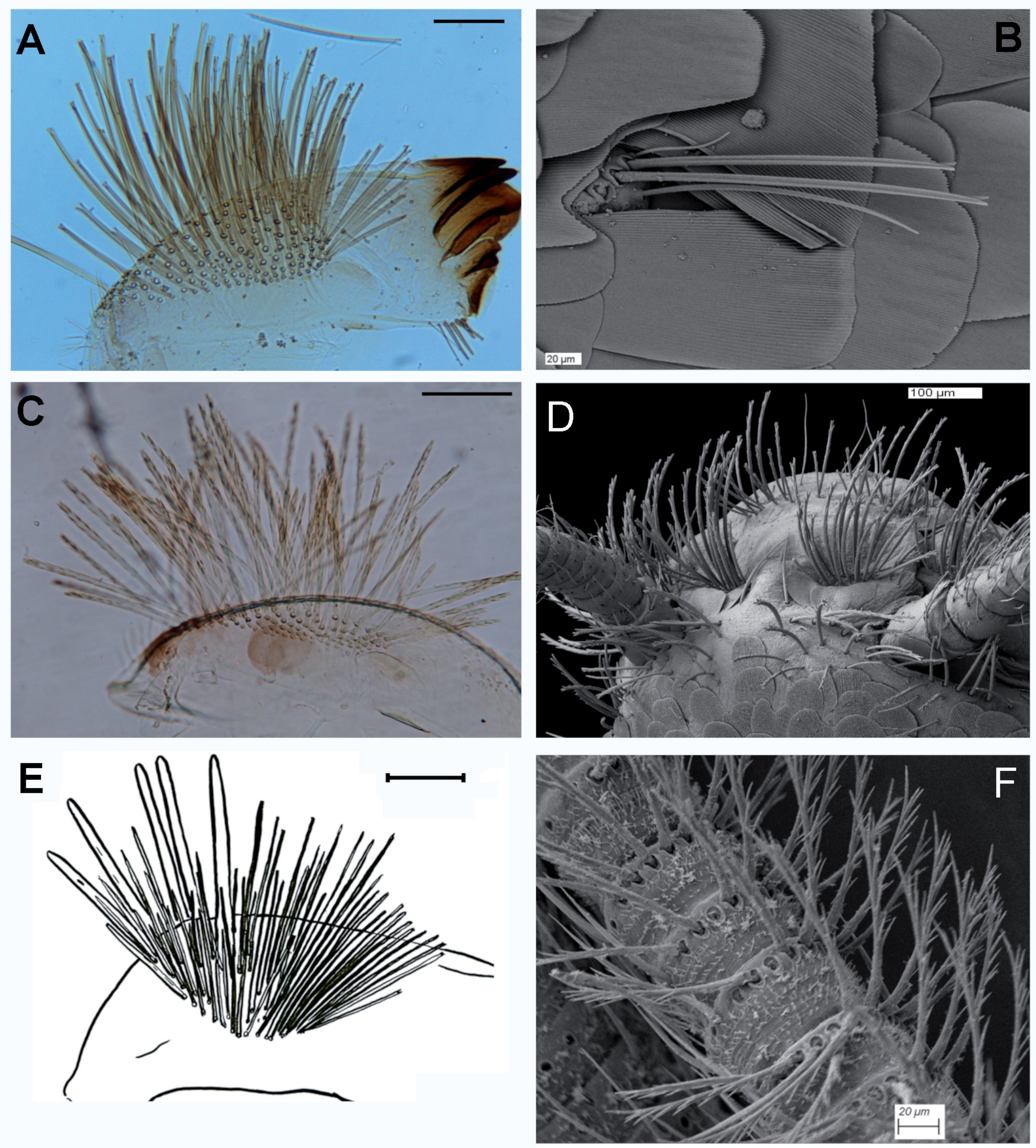

Fig. 16. Types of macrochaetae in Lepismatidae Latreille, 1802. **A**. Micrograph of smooth bifid macrochaetae on the mandible of *Allacrotelsa kraepelini* (Escherich, 1905). **B**. Comb of smooth and apically bifid macrochaetae of *Anisolepisma aquilonaridum* Smith, 2016, SEM photograph. **C**. Micrograph of feathered macrochaetae on the mandible of *Ctenolepisma iranicum* Molero, Kahrarian & Gaju, 2016. **D**. Feathered macrochaetae on the frontal area of the head of *Hemitelsella transpectinata* (Smith, 2015). **E**. Design of the smooth macrochetae with a round tip on the mandible of *Mormisma peyerimhoffi* (Silvestri, 1938), adapted from Silvestri (1938). **F**. Feathered/plumose macrochaeta of the cerci of *Swalepisma mirabile* Irish, 1988, SEM photograph. Scale bars: A, C–E = 0.1 mm; B, F = 20 µm.

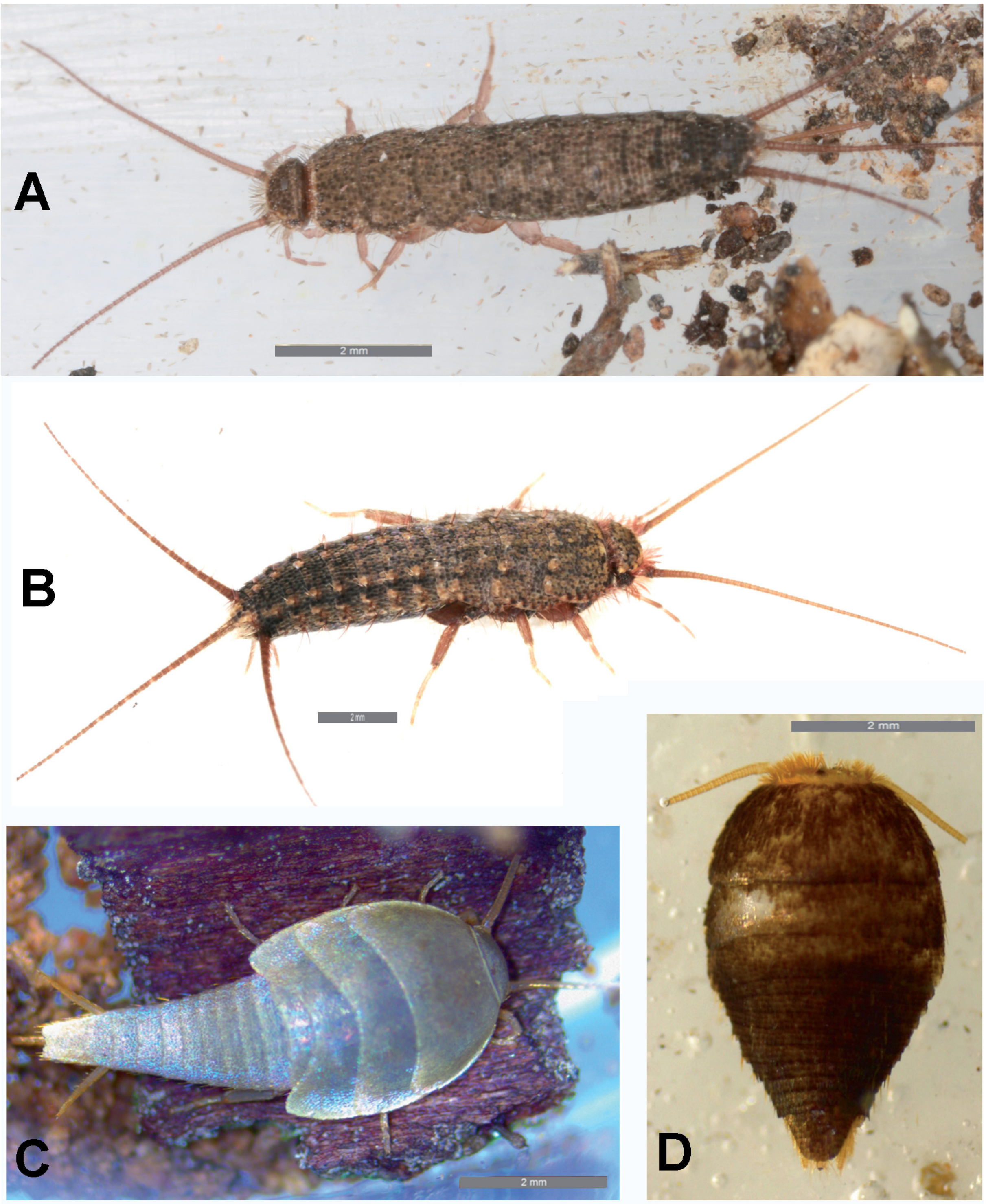

Fig. 17. Some examples of variability in the body shape and scale pattern of Lepismatidae. **A**. *Sceletolepisma guadianicum* (Mendes, 1992), with body shape subcylindrical and greyish-brown uniform dorsal scales. **B**. *Ctenolepisma nicoletii* (Lucas, 1846), with the thorax slightly wider than the abdomen and dorsal scales forming longitudinal stripes. **C**. *Neoasterolepisma curtiseta* Mendes, 1988, with a wide thorax, detaching from abdomen base, and yellowish scales. **D**. *Lepismina* sp., with short body, wide thorax but not markedly detaching from abdomen base, and hypognathous head, not visible dorsally. Scale bars = 2 mm.

appreciated under the microscope. Even some diagnostic characters that could be seen in a photograph are visible only on the ventral side, when most photographs show the insect in dorsal view. Moreover, the original description of several species did not provide the colour pattern of the scales of the insects, because they were based on specimens preserved in alcohol where the colour (even the scales) is lost. So, most of the identifications of Lepismatidae (and all basal hexapods, in general) provided in those platforms (for example, i-Naturalist), are incorrect or doubtful, which leads to a biogeographic problem if managers of biodiversity platforms allow inclusion of these records in their distributions maps, distorting the knowledge of the actual geographic range of most species (curiously, these platforms do not include the records of scientific papers given by experts). Non-expert people should be more prudent than specialists are when daring to identify a silverfish, and probably subfamily-level or genus-level identifications are advisable for these platforms.

Taxonomic actions

Class Insecta Linnaeus, 1758
Order Zygentoma Börner, 1904
Family Lepismatidae Latreille, 1802
Subfamily Ctenolepismatinae Mendes, 1991

Genus ***Caribesella*** gen. nov.

urn:lsid:zoobank.org:act:BF259603-3537-47A4-9033-DF6D14FCB007
Figs 7B, 9A, 10B, 13B–C, 18–19

Type species

Acrotelsa impudica Escherich, 1905: 112.

Diagnostic description

Body fusiform, with abundant feathered macrochaetae, as typical in subfamily Ctenolepismatinae. Chaetotaxy of head as shown in Wygodzinsky (1959a: fig. 35), with two subtriangular setal areas on the frontal margin anteromedially interrupted by a wide gap; in each subtriangular area macrochaetae are arranged in longitudinal rows that are longer near the median gap. On each side, there is also a periocular group, an antennal basal setal group that is not clearly separated from the subtriangular frontal group and a smaller group longitudinally elongated at each side. Clypeus with 1+1 tufts of macrochaetae, labrum with disperse setae but lacking tufts (Fig. 18). Scales orbicular (i.e., with their bases extended to surround more or less the posterior part of the socket area), rounded or elliptical, but variable in shape, with numerous thin rays that do not surpass or slightly surpass their apical margins, covering all the body dorsally and ventrally. The scales illustrated by Wygodzinsky (1959a) have not been found (in our opinion, they could be an artifact coming from another insect). Scales covering the scapus, legs (except on tarsal articles) and abdominal styli but absent from the pedicel and the flagellum of the antennae, maxillary and labial palps, and terminal filaments. The scales of appendages are different in size and shape to those covering the body; they are smaller, not orbicular in their basal area, rounded or subquadrangular and with the distal margin more or less denticulate.

Flagellum of the antenna with trichobothria, trichoid sensilla, basiconic sensilla of several types, as well as coeloconic and chaetic sensilla that are feathered in the basal part of the antenna.

Labial palp with five papillae on its ultimate article, arranged in a single row. The apical articles of maxillary and labial palps have some basiconic sensilla.

Pronotum with setal collar. Lateral margins of nota with several combs of macrochaetae; posterior margin with 1+1 combs. Trichobothrial areas of nota open, with the exception of posterior areas of the

Fig. 18. *Caribesella* gen. nov., diagnostic characters of the head not previously illustrated. Micrograph showing part of the head chaetotaxy: the clypeal tuft of one side (white arrow) and the labrum with no tufts (blue arrow); the frontal tuft of the same side is visible (yellow arrow). Scale bar = 0.1 mm.

pronotum, which are closed (Fig. 19G). Thoracic sterna well developed, covering coxae, each one with 1 or 2 pairs of combs of macrochaetae.

Outer coxal margins with several submarginal combs of macrochaetae. Praetarsi with microtrichia covering the surface of empodium and lateral claws (those of the empodium fused to form parallel ribs).

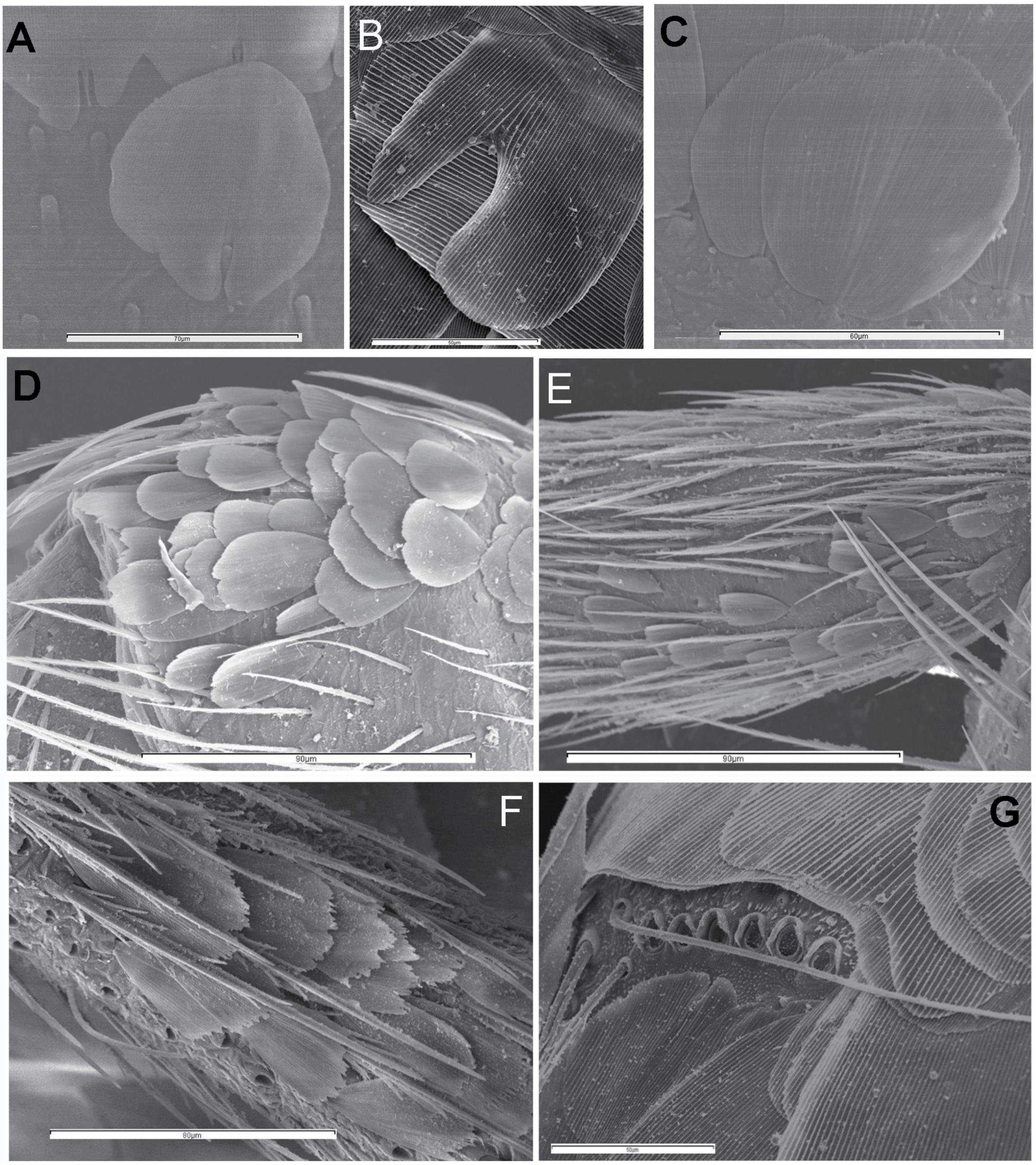

Fig. 19. *Caribesella* gen. nov., diagnostic characters not previously illustrated, SEM photographs. **A**. Orbicular scales of dorsal side of the abdomen. **B**. An indented scale of the dorsal side of the thorax. **C**. Coxal scales. **D**. Scales on the apex of the femur. **E**. Scales and setae on the basal part of the tibia. **F**. Scales on stylus IX. **G**. Open anterior trichobothrial area of the pronotum. Scale bars: A = 70 µm; B, G = 50 µm; C = 60 µm; D–E = 90 µm; F = 80 µm.

Urotergite I with 1+1 combs of macrochaetae, urotergites II–VII with 3+3 combs, urotergite VIII with 2+2 combs and urotergite IX bare. Urosternites I and II bare, III–VIII with 1+1 lateral combs. Urotergite X triangular, acute or almost acute at its hind apex, with several pairs of combs inserted along their lateral margins, usually 3+3.

Two pairs of styli on abdominal sternites VIII and IX. Inner process of the coxite IX of the females triangular, with acute apex. Parameres lacking. Ovipositor short, of secondary type, with several spiniform setae on the apical divisions, and at the apex of gonapophyses with short, heavily sclerotized spines, more or less hook-shaped (fossorial).

Etymology

The name of the new genus refers to the Caribbean Sea, with the same ending as the related genus *Acrotelsella*. The word Caribbean means 'relating to the Caribs' and comes from the name that Taino Indians living in the Lesser Antilles at the end of the 15th century gave to another group of Indian people of this area. The name was transferred to the Spanish word for Caribbean: 'Caribe', meaning 'strong, brave', as opposed to the Taino tribe, meaning 'gentle'.

Remarks

Escherich (1905) described the species *Acrotelsa impudica* on the basis of specimens collected in Santa Marta (Colombia). This species was later redescribed by Wygodzinsky (1959a) as *Stylifera impudica*, who reported it from several areas of Central and South America, including continental South America and several Caribbean islands. When the genus *Stylifera* was divided into two genera, this species was included in the genus *Acrotelsella*, characterized by a lower number of abdominal styli than *Stylifera*. This division was used by Mendes (1986c) and accepted by Irish (1988d). *Acrotelsella impudica* was the only American species of the genus *Acrotelsella*, while the remaining species were recorded in Australia, Africa and South Asia. Australian species include the type-species of this genus, *Acrotelsella producta* (Escherich, 1905). A comparison of the American species with several collected in Australia and some from Africa and Asia reveals that the South American taxon is sufficiently different to consider it as belonging to an independent genus. The arrangement of trichobothrial areas of the pronotum, that which all open in Australian species, the absence of tufts on the labrum and the absence of scales on the maxillary palps and terminal filaments, which are always present in Australian species, the microtrichiae of praetarsal claws (a character shared with the American genus *Stylifera*), the special type of spines of the ovipositor and the different shape of the inner process of the coxite IX (longer and with rounded apex in most Australian and Asian species) are, among others, distinctive characters to support this new genus.

Caribesella impudica (Escherich, 1905) comb. nov.
Figs 7B, 9A, 10B, 11A, 13A

Acrotelsa impudica Escherich, 1905: 112 [holotype female, Santa Marta, Colombia (ZMA)].

Stylifera impudica – Wygodzinsky 1959a: 39 [supplementary description based on specimens from Venezuela (Paraguaná), Aruba, Curaçao, Little Curaçao (as Klein Curaçao), Bonaire, Margarita, Los Frailes, Los Testigos, Trinidad (ZMA)].
Stylifera (Acrotelsella) impudica – Paclt 1966: 156 [supplementary description based on intercepted quarantine material from Venezuela or Colombia and from a boat on the Pacific (ZMH)].
Acrotelsella impudica – Mendes 1986c: 334 [treated *Acrotelsella* as a genus independent of *Stylifera*, first published use of combination].

Material examined

VENEZUELA • 10 ♂♂, 5 ♀♀ (3 ♂♂ and 3 ♀♀ mounted on slides, 1 ♂ and 1 ♀ mounted for SEM study, remaining specimens preserved in 70% alcohol); Monagas State, Uverito Forest; 8°39′ N, 62°37′ W; 15 Aug. 1996; C. Bach leg.; pitfall traps in a plantation of *Pinus caribea* formerly occupied by a savanna; UCO Z2561, Z2565.

Remarks

Most of the descriptive details of this species were provided by Wygodzinsky (1959a) as *Stylifera impudica*, except for some of the new characters described here for the diagnosis of the new genus which include the clypeal tufts, trichobothrial areas, coxal combs of macrochaetae, pattern and distribution of scales on appendages, and pretarsal microtrichia. Dorsal scales are illustrated in Fig. 19A–B and scales of different appendages in Fig. 19C–F. The scales of the coxae are rounded, but not orbicular (i.e., with the basal part not surrounding the insertion), with a finely denticulate apical margin. Femoral scales are similar in shape to coxal scales, but slightly smaller and apically narrower. Tibial scales are narrower and smaller than those of the femora. Scales covering styli are even smaller, with their apical margin more denticulate. Coxal combs have 3–6 macrochaetae, some of them as long as half the width of the coxa. Details of abdominal chaetotaxy are presented in Table 1, although most of them do not represent an increase of the variability given by Wygodzinsky.

Genus ***Sceletolepisma*** Wygodzinsky, 1955 sensu Irish, 1987, stat. nov.

Ctenolepisma (*Sceletolepisma*) Wygodzinsky, 1955: 154. Type species: *Ctenolepisma* (*Sceletolepisma*) *arenicola* Wygodzinsky, 1955 by original designation [created as monotypic subgenus of *Ctenolepisma* Escherich for *C.* (*S.*) *arenicola* Wygodzinsky, 1955 on the basis of the 2+2 combs on urotergite I].

Ctenolepisma (*Sceletolepisma*) – Irish 1987: 149 [redefined subgenus to include all species with at least one pair of medial urosternal combs irrespective of the arrangement of urotergal combs].

Diagnosis

Silverfish with fusiform or subcylindrical shape, bearing feathered macrochaetae and lacking pronged sensilla on apical article of maxillary palp. Frontal area with a bare gap between two big lateral tufts of macrochaetae; clypeus and labrum usually with 1+1 tufts. Apical article of labial palp with (2)3–5 papillae arranged in one row. Pronotum with setal collar; all thoracic nota with several lateral combs and usually with 1+1 posterolateral combs. Anterior trichobothrial areas of pronotum and mesonotum associated with antepenultimate lateral combs (N−2); sometimes those of pronotum in anterior to antepenultimate (N−3) lateral combs. Thoracic sternites variable in shape, usually cordiform with convex hind margin, prosternum usually smaller than meso- and metasternum. Coxae and femora covered with rounded orbicular scales similar to those of body; tibiae and tarsi without scales, only covered by setae; remaining appendages without scales. Several urotergites (usually II–V, II–VI, II–VII or II–VIII) with 3+3 combs of macrochaetae. Urotergite I with 1+1 or 2+2 combs. Tenth urotergite trapezoidal, with straight hind margin, sometimes slightly concave or convex. Several urosternites (at least four) with one median comb, usually present on abdominal sternites I–VI, I–VII, II–VI or II–VII); 1+1 lateral combs on some urosternites (usually on II–VIII or III–VIII). Coxites IX with or without a transverse comb. One to three pairs of abdominal styli. Males without paramera. Ovipositor of primary type or apically sclerotized.

Remarks

This taxon was erected to include only one species, *Ctenolepisma arenicola* Wygodzinsky, 1955, which has 2+2 combs on urotergite I; this character was exclusive to this species at that moment within

Table 1. Abdominal chaetotaxy of *Caribesella impudica* (Escherich, 1905) comb. nov., from Uverito (Venezuela). The number of macrochaetae per comb is indicated in each position (minimum and maximum number observed). The variability indicated by Wygodzinsky (1959a) for specimens from different localities fits inside the range of variation shown in the table.

Abdominal segment	Urotergal comb A (infralateral)	Urotergal comb B (lateral)	Urotergal comb C (sublateral)	Urosternal lateral comb (L)	Urosternal median comb (M)
I	7–9	–	–	–	–
II	6–10	4–7	4–7	–	–
III	6–9	4–7	4–7	9–11	–
IV	7–9	5–8	5–7	10–12	–
V	9–11	5–8	5–7	9–12	–
VI	9–13	5–8	5–8	10–14	–
VII	8–12	6–11	6–9	10–14	–
VIII	9–10	6–8	–	10–13	–
IX	–	–	–	–	–
X	6–8 5–8 3–6	–	–	–	–

Ctenolepisma, but several additional species sharing this character were discovered afterwards. Irish (1987) redefined *Sceletolepisma* using a different criterion for distinguishing this subgenus from the remaining species of *Ctenolepisma*, a group that includes the type species of the genus *Ctenolepisma*, *C. lineatum*. The new criterion was the possession of at least one median comb of macrochaetae on some urosternites, a character also present in *C. arenicola*. The subgenus *Ctenolepisma* s. str. includes, according to Irish, all species without median bristle-combs, only having 1+1 lateral combs of macrochaetae on most urosternites (usually III–VIII), but he suggested that this group could be heterogeneous. At the moment, the group with median urosternal bristle combs includes about 80 species. We consider that *Sceletolepisma*, in the sense established by Irish (1987), should be considered as an independent genus because all species examined share several characters apart from the presence of the median combs of macrochaetae; these characters are constant in *Sceletolepisma*, while in *Ctenolepisma* s. str. they are variable. Although the presence or absence of median combs is diagnostic in most cases, some exceptions have occasionally been observed in some *Ctenolepisma* s. str.

The additional characters that need to be considered include the following:

a) The scales of the appendages of all species of *Sceletolepisma* have a similar shape and distribution, where all appendages are covered with setae (not scales) with the exception of the scapus of the antennae and coxae of legs, which are covered with rounded scales similar to those covering the body. This distribution is, however, not exclusive to *Sceletolepisma* since it can also be found in *Ctenolepisma* (*C.*) *ciliatum* (Dufour, 1831) and related Palaearctic species of *Ctenolepisma* s. str. with a trapezoidal tenth urotergite (Molero-Baltanás *et al*. 2010), but different to other species of the genus, such as *C.* (*C.*) *lineatum*. In this species, for example, scales are also present on the femora as described in Molero Baltanás *et al*. (2012).

b) The arrangement of their trichobothrial areas is similar (contiguous on the metanotum, i.e., associated with the two last lateral combs; separated by one lateral comb on the mesonotum, i.e., associated with the last (N) and antepenultimate lateral comb (N−2) and separated by one or two lateral combs on the pronotum (associated with N and N−2 or N−3 combs)). This arrangement is also not exclusive to *Sceletolepisma*, but present in several genera of Ctenolepismatinae and in some species of *Ctenolepisma* s. str., but in this latter genus several types of arrangement of trichobothrial areas have been detected, suggesting that it represents a more heterogeneous group than *Sceletolepisma*.

c) Within *Ctenolepisma* s. lat., species having transverse bristle-combs on the inner process of the coxite IX belong only to *Sceletolepisma*, suggesting that only the lineage with median urosternal combs has developed this character (perhaps more than once). Probably the same happens with the occurrence of 2+2 pairs of combs on urotergite I and other apomorphies that are shared only by several species from South Africa, such as *S. arenicola*.

According to Irish (1987), the species *Ctenolepisma unipectinatum* Mendes, 1982 and *Ctenolepisma howa* Escherich, 1910 could be included inside *Sceletolepisma*, as bearing one and two median urosternal combs respectively. Nevertheless, types of both species have been re-examined (loaned by MUHNAC and MFN), concluding that the first one should be excluded from *Sceletolepisma* and the second has several additional median combs and not only two, fitting into the present diagnosis of the genus. A slide mounted paratype of *Ctenolepisma unipectinatum*, loaned by Luis F. Mendes, described as bearing only one small median comb on urosternite II, was checked and the occurrence of scales on the tibiae and narrow truncate or emarginate scales on the femora has been confirmed, so it should be excluded from *Sceletolepisma*. It is probably related to African species of *Ctenolepisma* s. str. showing similar scales on the legs. We have also examined a specimen collected in the Atlas Mountains in Morocco, related to *C. brauni* or *C. lineatum* (probably belonging to an undescribed species), that also has one small median comb on one abdominal sternite, so the occurrence of urosternal combs, at least if they are small and occurring on only one urosternite, is not a diagnostic character to separate *Sceletolepisma* from *Ctenolepisma*, but a combination of characteristics is necessary.

Although *Ctenolepisma arenicola* Wygodzinsky, 1955 is the type species of the genus, since it was the first to be included in the genus *Sceletolepisma*, it is not the first species to be described that can be assigned to this genus as defined here (sensu Irish, 1987), which would be *Lepisma villosum* Fabricius, 1775.

Kaplin (1993), considering urotergal chaetotaxy as the key character for subdividing *Ctenolepisma*, raised the subgenus *Sceletolepisma* to the generic level but maintaining the criterion of Wygodzinsky (op. cit.); he also created three new subgenera within *Ctenolepisma* (*Allolepisma*, *Escherichisma* and *Silvestrellisma*). Irish (1994) rejected Kaplin's arrangement as probably not reflecting phylogenetic history, retaining his earlier definitions when describing new species from southern Africa. Here the criterion of Irish is followed. Although a more extensive revision is required, Kaplin's criteria make neither phylogenetic nor biogeographic sense. The character separating *Sceletolepisma* sensu Wygodzinsky from the remaining *Ctenolepisma* taxa, i.e., those bearing 2+2 combs on urotergite I instead of 1+1 combs, appears in several South African species that are closely related with those that do not have this character. However, species of *Ctenolepisma* s. lat. bearing median urosternal combs can be considered as a more uniform group sharing the characters indicated in the present diagnosis, and species lacking several median combs on abdominal sternites (in the present arrangement, the only representatives of the genus *Ctenolepisma*) form a more heterogeneous group which requires a thorough revision, but not using the urotergal chaetotaxy as the unique character for splitting into subgroups.

Distribution

Representatives of *Sceletolepisma* are absent from America, while species belonging to *Ctenolepisma* s. str. are widespread on both sides of the Atlantic Ocean. This suggests that *Sceletolepisma* first appeared after the opening of this ocean, but we cannot discard a previous origin and a later extinction event in South America after its separation from Africa.

Key to genera of Lepismatidae

The number of genera previously known and considered as valid in the family Lepismatidae is 43. As a 44th genus is erected in this work, and a genus is split into two, the definitive number increases to 45 extant genera. The following key also includes additional fossil genera, but not *Apteryskenoma* Paclt, 1953 and *Panlepisma* Silvestri, 1940; these genera remain unplaced, although their potential position in the key is commented on below the key, together with some additional comments.

1. Thoracic sternites reduced, not free and largely covered by coxae, usually with an acute posterior angle (Fig. 8A). Males with paramera (1), thin and tubuliform, without a subapical glandular area (Fig. 12A) .... subfam. Acrotelsatinae 2
– Thoracic sternites developed, covering coxae, frequently with a more or less rounded hind margin (for example, as in Fig. 8B-D). With or without paramera. If the prosternum is reduced, antennae have specialized bidigitate sensilla (Fig. 2B) and males lack paramera 7

2. Head hypognathous, body short and thorax width usually greater than abdominal length (Fig. 17D). Ventral abdominal segments bare, without chaetotaxy. SE Palaearctic ......***Lepismina*** Gervais, 1844
– Head not hypognathous, body usually elongate and thorax shorter than length of the abdomen. Most ventral abdominal segments with some combs of macrochaetae (usually 2+2 combs on urosternites III–VIII and sometimes one median comb on urosternites I–VII or I–VIII) 3

3. Urotergite X triangular, with acute posterior margin, with several lateral combs (similar to Fig. 11D) 4
– Urotergite X trapezoidal or rounded, with posterior margin more or less straight or rounded but not clearly acute, with 1+1 lateral combs 5

4. Hind margins of thoracic tergites with 1+1 combs of macrochaetae. Ovipositor thin, with fine setae apically (primary type). New Guinea ....***Paracrotelsa*** Paclt, 1967
– Hind margins of thoracic tergites without 1+1 combs of macrochaetae. Ovipositor with some subapical sclerotized spines (secondary type). Pantropical, synanthropic ....
....***Acrotelsa*** Escherich, 1905

5. Last segment of labial palp with five papillae arranged in two rows (2+3). Some macrochaetae slightly feathered. Setal collar of pronotum covering 50–60% of anterior margin. E Palaearctic (2) **..**
.... ***Desertinoma*** Kaplin, 1992
– Last segment of labial palp with four papillae arranged in two rows or forming a diamond. All macrochaetae smooth. Without a setal collar on the pronotum, only with 1+1 setal tufts 6

6. Hind margin of urotergite X concave. Without median combs on all urosternites. Yemen ....
....***Primacrotelsa*** Mendes, 2004
– Hind margin of urotergite X rounded, convex. Median combs present on one or more urosternites. Australia ....***Anisolepisma*** Paclt, 1967

7. Macrochaetae smooth, usually bifid apically (Figs 9B, 16A, 16E). Males with paramera 8
– Macrochaetae frequently feathered (Figs 9C, 16C–D, F); if smooth, some may have rounded tip (“false-smooth” macrochaetae, as the bigger ones in Fig. 16E) and urotergal setation is very dense,

consisting mainly of wide setal fringes and if grouped, spaces between groups are narrower than groups and these species are found only in Namib Desert dunes. Males lacking paramera 21

8. Anterior margin of pronotum with setal collar (as in Fig. 5A). Antennae usually with a poor diversity of sensilla (basiconic, trichobothria, chaetic and trichoid sensilla). Femora and tibiae with or without scales; if present, these scales are different to those covering coxae and body ....subfam. Heterolepismatinae 9
– Anterior margin of pronotum without setal collar (as in Fig. 5B), at most one group of anterolateral macrochaetae inserted on each corner (Fig. 5C). Antennae usually with a higher diversity of sensilla; some basiconic transformed into more specialized types such basiconic F sensu Adel (Silvestri's type, Fig. 2A) or asteriform sensilla (Fig. 2C–D). Femora and tibiae always without scales, only covered with setae (3) .... subfam. Lepismatinae 11

9. Femoral and tibial scales wide, rounded, triangular or sub-rectangular. With three or more pairs of styli. Thoracic sternites wide, trapezoidal, with a broad truncated posterior margin. Hind margin of urotergite X rounded. Australia .... ***Visma*** Smith, Mitchell & Molero- Baltanás, 2021
– Femoral and tibial scales absent; if present, they are lanceolate. No more than three pairs of styli, frequently one or two pairs. Thoracic sternites parabolic or heart-shaped, with a convex posterior margin; if truncate, straight part not wide. Hind margin of urotergite X variable 10

10. Labrum with thin setae. Urotergite X usually trapezoidal or parabolic, relatively long. One to three pairs of styli. Urosternal combs short of less than four macrochaetae. Widely distributed in S and C America, E Africa, S Asia and Australia ....***Heterolepisma*** Escherich, 1905
– Labrum with macrochaetae and thin setae. Urotergite X very short and slightly convex. Only one pair of styli. Urosternal combs long, especially medially. Japan, coral cays of E Australia ....***Maritisma*** Smith & Mitchell, 2019

11. Abdominal sternites lacking median combs of macrochaetae 12
– At least some abdominal sternites with a median comb of macrochaetae 14

12. Pronotum with 1+1 tufts of macrochaetae on its anterolateral corners. Last abdominal tergite (segment X) triangular, acutely pointed posteriorly. Two pairs of abdominal styli. North America .. ..***Anallacrotelsa*** Mendes, 1996
– Pronotum without tufts on its anterolateral corners. Last abdominal segment not triangular, with subtrapezoidal shape. One or 3 pairs of abdominal styli. Burmese amber 13

13. Three pairs of abdominal styli. Thorax much wider and clearly detached from abdomen base, which tapers visibly to posterior end ....***Cretalepisma* (†)** Mendes & Wunderlich, 2013
– One pair of abdominal styli. Body shape almost parallel-sided ....***Burmalepisma* (†)** Mendes & Poinar, 2008

14. Abdominal tergites with combs of macrochaetae, most of them with 3+3 combs. Paramera pseudo-articulated. Urotergite X acutely pointed or subtrapezoidal with convex hind margin. Holarctic extant species and Baltic amber .... ***Allacrotelsa*** Silvestri, 1935
– Dorsal chaetotaxy of abdomen transformed: combs reduced to one or two isolated setae; typical arrangement on a tergite: 1+1 infralateral groups (usually consisting of 1–3 macrochaetae), 1+1 lateral isolated macrochaetae, 1+1 sublateral and 1+1 submedian (in some species or in some tergites one or two of these isolated setae can be absent or there are supernumerary isolated setae, but not forming combs). Urotergite trapezoidal, usually with a straight, slightly concave or convex hind margin 15

15. Without asteriform sensilla on antennae and maxillary palps; instead with specialized sensilla of a globular shape (basiconic type F of Adel or Silvestri's sensilla, wrongly referred to in some papers as campaniform). Paramera well developed, sacciform, in extant forms they attain or even surpass apex of inner process of ninth coxite (Fig. 12B)(4) 16
– With asteriform sensilla on antennae and usually also on maxillary palps. Paramera small or medium-sized, clearly not attaining apex of inner process of ninth coxite (Fig. 12C) 17

16. Posterior trichobothrial areas of pronotum closed, encircled by scales and not in contact with edges of notum. Abdominal tergites II–VIII with 3+3 isolated macrochaetae (infralateral, lateral and sublateral). Dominican amber ....***Protolepisma* (†)** Mendes & Poinar, 2013
– Posterior trichobothrial areas of the pronotum open, contacting with lateral edge of notum. Abdominal tergites II–VIII or III–VIII usually with 4+4 isolated macrochaetae (infralateral, lateral, sublateral and submedian); infralateral macrochaetae usually not isolated but forming a group with another macrochaeta and/or with a thin seta. West Palaearctic and Australia, one species synanthropic, cosmopolitan by human dispersal ....***Lepisma*** Linnaeus, 1758

17. All trichobothrial areas of nota closed, encircled by scales that avoid contact with the edges of respective nota. Clypeus not reduced. Paramera very reduced. S Africa, India, Malaysia, Australia .... ***Xenolepisma*** Mendes, 1981
– At least anterior trichobothrial areas of nota open, contacting with edges of nota. Clypeus strongly reduced. Paramera small or medium-sized 18

18. Praetarsus with two well developed pulvilli additional to lateral claws and empodium. With 5+5 to 7+7 isolated macrochaetae on urotergites II–VIII additional to infralateral group. E Africa ....***Lepitrochisma*** Mendes, 1988
– Praetarsus without pulvilli. Usually with 3+3 isolated macrochaetae additional to infralateral group, but variable 19

19. Posterior trichobothrial areas of pronotum closed, encircled by scales that avoid contact with edges of notum. Hind tibiae of males not modified. Afrotropical, India ....***Afrolepisma*** Mendes, 1981
– Posterior trichobothrial areas of pronotum open, contacting edge of notum (Fig. 5B). Hind tibiae of males modified in chaetotaxy and/or shape or not 20

20. With a row of small macrochaetae on hind margin of nota (5) ....***Tricholepisma*** Paclt, 1967
– Hind margin of nota without bifid macrochaetae, sometimes with very small, thin and acute setulae (Fig. 5B) .... ***Neoasterolepisma*** Mendes, 1988

21. Anterior margin of pronotum devoid of setal collar, at most with a row of a few isolated setae. Papillae of apical article of labial palp arranged in two rows (2+3) .....subfam. Silvestrellatinae 24
– Anterior margin of pronotum with a setal collar. Papillae of apical article of labial palp arranged in a single row (number variable) 22

22. Antennae with bidigitate specialized sensilla (Fig. 2B). Apex of distal article of maxillary palp with a cylindrical sensillum. Prosternum strongly reduced. Mainly in North America .... subfam. Mirolepismatinae 23
– Antennae with different types of sensilla, more or less diverse, but lacking bidigitate type. Apex of distal article of maxillary palp without a cylindrical sensillum. Prosternum often slightly smaller than meso- and metasternum, but rarely with a strong reduction (except in *Monachina* and some psammophilous species) ....subfam. Ctenolepismatinae 27

23. Chaetotaxy of abdominal tergites consisting of 1+1 infralateral groups of macrochaetae (combs), 1+1 isolated lateral macrochaetae and 1+1 isolated submedian macrochaetae .... ***Prolepismina*** Silvestri, 1940
– Chaetotaxy of abdominal tergites consisting of 1+1 infralateral groups of macrochaetae (combs), 1+1 combs of macrochaetae in lateral position and 1+1 combs of macrochaetae in submedian position (6) .... ***Mirolepisma*** Silvestri, 1938

24. Hind margin of abdominal sternites only with 1+1 isolated or 1+1 pairs of lateral macrochaetae; macrochaetae in median position absent or only present on one abdominal sternite (I or II) 25
– Hind margin of abdominal sternites (at least II–VI) with one or more macrochaetae in median position, in addition to lateral macrochaetae; these can be isolated or forming small combs 26

25. Pronotum with a row of at least 3+3 isolated setae in its anterior margin and at least 2+2 isolated setae inserted on disc, not very close to hind margin. Some urotergites with 1+1 isolated macrochaetae or 1+1 pairs in lateral and submedian positions, not very close to the hind margin. S Africa .... ***Silvestrella*** Escherich, 1905
– Anterior margin of pronotum bare, posterior margin with 1+1 isolated setae or 1+1 pairs, inserted very close to hind margin. Most urotergites with 1+1 isolated macrochaetae in lateral and submedian positions inserted very close to hind margin. Afrotropical and occurring in other regions (S America, Sri Lanka, Cape Verde), probably as a result of human dispersal .... ***Namunukulina*** Wygodzinsky, 1957

26. Abdominal tergites with 1–2+1–2 infralateral macrochaetae only, lacking macrochaetae in lateral and submedian positions. Hind margin of pronotum bare. SW Africa ....***Hemilepisma*** Paclt, 1967
– Abdominal tergites with macrochaetae in lateral and submedian positions, in addition to 1+1 infralateral groups of macrochaetae. Hind margin of pronotum with 1+1 isolated lateral macrochaetae. Arabian Peninsula .... ***Hemikulina*** Mendes, 2008

27. Abdominal dorsal setation of segments I–VIII or II–VIII forming discrete combs on hind margin; at least with 1+1 small infralateral combs and 1+1 isolated macrochaetae, but more frequently consisting of 2+2 or 3+3 bristle-combs on abdominal tergites II–VIII, separated from each other by distances similar to or higher than width of a comb 31
– Abdominal dorsal setation consisting of a continuous fringe of macrochaetae, not forming discrete combs; if there are separated groups of macrochaetae, distance between them less than width of a group. Genera exclusive to Namib or Palaearctic deserts 28

28. Macrochaetae smooth, some with rounded tip (Fig. 16E) 29
– Macrochaetae feathered. Namib desert ....***Sabulepisma*** Irish, 1988

29. One pair of abdominal styli. Without a median group of macrochaetae on abdominal sternite VII. Labrum with three tufts of macrochaetae. Palaearctic deserts ....***Mormisma*** Silvestri, 1938
– Without abdominal styli. With a median group of macrochaetae on abdominal sternite VII. Labrum with two tufts of macrochaetae. Namib desert 30

30. Antennae clearly shorter than body length. Setal fringes of anterior urotergites with some gaps at each side, forming 3+3 groups of macrochaetae; setal fringes of the last urotergites continuous. Coxal disc with wide transverse bristle-combs .... ***Namibmormisma*** Irish, 1988
– Antennae as long as body length or even longer. Setal fringes of anterior urotergites without gaps, continuous, with only one median gap in middle, so only 1+1 wide groups of macrochaetae can be distinguished .... ***Namiblepisma*** Irish, 2018

31. Abdominal segments I–VIII only with 1+1 infralateral small combs of macrochaetae and 1+1 isolated lateral macrochaetae. There are no urotergites with 2+2 or 3+3 bristle-combs. Afrotropical, including Cape Verde Islands .... ***Monachina*** Silvestri, 1908
– Abdominal segments I–VIII with a higher number of combs of macrochaetae. Some urotergites with 2+2 or 3+3 bristle-combs in infralateral, lateral and submedian positions 32

32. Last abdominal tergite triangular or subtriangular, posteriorly acute or somewhat rounded; its lateral margins frequently with more than 1+1 bristle-combs, but sometimes with only 1+1 combs or without defined combs, only with marginal setae. When 1+1 combs are present, they rarely have more than three macrochaetae and are not located close to posterior margin (Fig. 11A–F) 33
– Last abdominal tergite with a different shape (trapezoidal, subtriangular) but not posteriorly acute, convex, straight or slightly convex, usually with quite prominent 1+1 combs near posterior margin (Fig. 11G–O) 37

33. Abdominal styli on segments III–IX (seven pairs). Lateral combs of urosternites divided by insertion of styli, resulting in 2+2 lateral combs. Antennae with fan-shaped scales (Fig. 15A–B). Terminal filaments covered by scales (Fig. 15F). South America, Caribbean coasts, Galapagos islands, SW Africa (introduced?) .... ***Stylifera*** Stach, 1932
– Abdominal styli on segments VIII–IX or VII–IX (2 or 3 pairs). 1+1 lateral combs on urosternites (rarely 1+1 +1). Antennae without fan-shaped scales. Terminal filaments with or without scales 34

34. Posterior trichobothrial areas of nota closed (Fig. 7B). Terminal filaments without scales. Caribbean area .... ***Caribesella*** gen. nov.
– All trichobothrial areas open. Terminal filaments with or without scales 35

35. Urotergites II–VII with 3+3 combs 36
– Urotergites II–VII with 2+2 combs (Australia) .... ***Qantelsella*** Smith, 2015

36. Usually two pairs of styli, rarely three or one pair; coxites IX of female usually elongate (three or more times as long as wide at base); coxites IX lacking long transverse combs, although some short combs may occur along inner margins (11) .... ***Acrotelsella*** Silvestri, 1935
– One pair of abdominal styli only; coxites IX of female short (less than two times as long as wide at base, with long transverse combs (Australia) .... ***Hemitelsella*** Smith, 2016

37. At least some abdominal tergites with 3+3 bristle-combs 38
– All urotergites with at most 2+2 bristle-combs 44

38. Abdominal tergite I usually with 1+1 bristle-combs, sometimes with 2+2 39
– Abdominal tergite I with 3+3 bristle-combs 42

39. Median bristle-comb of abdominal sternites divided into two combs. Praetarsus without empodium. Namib desert .... ***Swalepisma*** Irish, 1988
– Median bristle-comb of abdominal sternites single or absent. Praetarsus with empodium 40

40. All abdominal sternites without median combs or only one small comb on one sternite. Last abdominal tergite of variable shape (trapezoidal with convex, straight or slightly concave hind margin, subtriangular, or short and slightly convex). N and Central America, S Palaearctic, Oriental region, Africa, some species almost cosmopolitan by human dispersal (7) .... ***Ctenolepisma*** Escherich, 1905 stat. nov.
– Several abdominal sternites with median bristle-combs 41

41. Praetarsal claws normal, empodium smooth. Last abdominal tergite trapezoidal, with its hind margin slightly convex, straight or slightly concave. S Eurasia and Africa .... ***Sceletolepisma*** Wygodzinsky, 1955 stat. nov.
– Praetarsal claws thin and very long, empodium rugose. Last abdominal tergite short, rounded subtriangular, with its hind margin clearly convex. Southern N America .... ***Leucolepisma*** Wall, 1954

42. Each praetarsus with two claws (of similar or different size), without empodium or very reduced 43
– Each praetarsus only with a single claw. SW Africa ....***Nebkhalepisma*** Irish, 1988

43. Each coxa with one or more transverse bristle-combs. Inner process of coxite IX also with one or more transverse bristle-combs, frequently multiseriate and/or with a large number of macrochaetae. Deserts of S Palaearctic: Sahara, Arabia .... ***Hyperlepisma*** Silvestri, 1932
– Coxae lacking transverse bristle-combs. Inner process of coxite IX without transverse comb or with a small comb with few macrochaetae. Namib desert ....***Gopsilepisma*** Irish, 1989

44. Abdominal sternites without median bristle-combs. SW Africa ....***Ornatilepisma*** Irish, 1988
– Several abdominal sternites with a median bristle-comb (8) 45

45. Urotergite X trapezoidal, with its hind margin straight or slightly concave 46
– Urotergite X subtriangular, with its hind margin convex, more or less rounded (Fig. 11G–H). S Palaearctic and S Africa, some species domestic, almost cosmopolitan by human dispersal (9) .... ***Thermobia*** Bergroth, 1890

46. Abdominal sternites I and II bare; abdominal sternite III with only one median comb. Apical article of labial palp with five sensory papillae. S Africa .... ***Psammolepisma*** Irish, 1988
– Abdominal sternites I and II with one median comb; abdominal sternites II and III with 1+1 lateral bristle-combs. Apical article of labial palp with three sensory papillae. Mongolia (10) ....***Asiolepisma*** Kaplin, 1989

Comments to the key

(1) Parameres are not described for *Paracrotelsa*, where only the female sex was described by Uchida (1949).

(2) The genus *Apteryskenoma* s. str. has not been included due to its poor original (and only available) description. If it fits with the previous options of this key (i.e., thoracic sternites reduced and covered by coxae, males with thin paramera, ventral abdominal segments with at least 2+2 combs of macrochaetae), it differs from *Desertinoma* in having six papillae arranged in a single row.

(3) The fossil genera attributed to this subfamily are included here because of the absence of a setal collar; antennal sensilla and scales of legs are not clearly visible in preserved specimens.

(4) Antennal sensilla cannot clearly be seen in the fossil specimen of *Protolepisma*, but the paramera are large, almost attaining the apex of the inner process of the coxite IX.

(5) Recent genetic and morphological phylogenetic studies suggest that the distinction between *Tricholepisma* and *Neoasterolepisma* makes no sense, and that they conform to a single clade. The priority of the name *Tricholepisma* will eventually give this name to the clade, according to ICZN rules.

(6) According to Mendes (1991), *Mirolepisma* and *Prolepismina* should be considered as a single genus.

(7) Heterogeneous group requiring revision, especially of American and some Afrotropical and Oriental species.

(8) Following the description of Silvestri, the genus *Panlepisma* fits here, but the identity of this genus from Argentina is not clear.

(9) This genus is probably heterogeneous and S African species could be separated into a different genus. Specimens recorded in natural habitats of N. America should be revised, since they probably are more related to *Leucolepisma* or to a lineage of the heterogeneous *Ctenolepisma*.

(10) It seems that Kaplin (1989), when describing the new genus *Asiolepisma*, was not aware of the description of the genus *Psammolepisma* by Irish, and unfortunately no discussion comparing these genera was included. We have not seen specimens of *Asiolepisma*, but they seem to be similar to *Sceletolepisma* from neighbouring areas in other characters, so probably *Asiolepisma* derives from some *Sceletolepisma* by losing one urotergal bristle-comb. If this is the situation, *Asiolepisma* probably lacks scales on the tibiae, and we have observed that *Psammolepisma* has scales on this article.

(11) The genus *Acrotelsella* has many undescribed species and is in need of revision. Molecular and morphological studies currently underway have identified two clades within the Australian species currently included under *Acrotelsella*. Females in one clade have simple, primary ovipositors, sheathed on either side by very long extensions of the inner processes of coxites IX; this clade represents *Acrotelsella* s. str. The second clade contains species with secondary ovipositors and shorter inner processes on coxites IX, however the molecular data places *Qantelsella* and *Hemitelsella* within the same clade. Furthermore, *Acrotelsella escherichi* Womersley, 1939 was described as having both elongated inner processes but a secondary type ovipositor.

Discussion

Diversity and distribution of the six subfamilies of Lepismatidae and future challenges

The order Zygentoma is a primitive wingless hexapod group dating back perhaps to the Silurian period (>400 Ma) with extant families diverging in the Triassic (ca 214 Ma) (Misof *et al*. 2014). They are considered to be the sister group of the winged insects. Lepismatidae includes the most encountered species.

Little is known about the mechanisms of Lepismatidae distribution. Airborne dispersal is considered unlikely due to their soft fragile bodies, but they are found on many remote islands. This is especially the case for species of the genus *Heterolepisma* which are known to inhabit the bark of trees and leaf litter. It is presumed that dispersal to these islands is probably by rafting, made easier perhaps because they are long-lived (up to several years) and may not require free fresh water. Dispersal is, however, most likely over land so that the alignment of the continents during the last 200 million plus years has probably had the greatest influence on the evolution and distribution of today's fauna.

All discussion of the diversity and zoogeography must be qualified by the reality that this order has been poorly researched in much of the world. Therefore, we do not have a reliable understanding of the group.

The distribution of peridomestic species is not included in the following maps. Several silverfish species are minor peridomestic pests and a few others are suspected of having been accidentally transported by human activity.

Acrotelsatinae (17 species in 6 genera. North Africa, Central Asia, Australia, Papua New Guinea, Fig. 20)

The subfamily is characterised by the lack of free sternal plates. It displays a relic distribution from a Pangean origin; however, it is surprising that no representatives have yet been found in the Americas. The distribution of the anthropophilic pan-tropical species *Acrotelsa collaris* (Fabricius, 1793) is not included here but the species has been found free-living in the Middle East as well as Hawaii.

Ctenolepismatinae (about 190 species in 20 genera, Fig. 21)

A large and widespread subfamily including several peridomestic pests of minor importance. Different genera dominate in different regions, e.g., *Ctenolepisma* in Africa/Eurasia, *Acrotelsella* in Australia and *Stylifera* as Neotropical. Fossil specimens have been described from 99 Ma Burmese amber and 20–25 Ma Dominican amber.

Much work is still required including collection and examination of existing material within museum collections. This work would benefit from molecular data which is quite limited at the moment, and the use of scanning electron microscopy, particularly of scales and the distribution of sensilla, to establish more robust phylogenies. The genera *Ctenolepisma* and *Thermobia* are under revision, and they will probably be divided into several genera, but not following the criteria of Kaplin (1993). The genus *Acrotelsella* is also under revision; the first results are the works by Smith and Mitchell (Smith 2015; Smith & Mitchell 2022, etc.) based on Australian species and Hazra *et al.* (2023) on an Indian species. The new genus described in this work contains the only known American species of the group.

Heterolepismatinae (40 species in 3 genera, Fig. 22)

Very common in Australia, with many more species awaiting description. Also limited distribution elsewhere except on Indian and Pacific Islands where it is very common. This raises the question of its Gondwanan origin, or perhaps it could be an old Australian subfamily that has spread by rafting. They are superficially very similar in appearance, but molecular data reveal deep divergences between species. The genus *Heterolepisma* is probably polyphyletic. It needs quite a lot of work to decide what

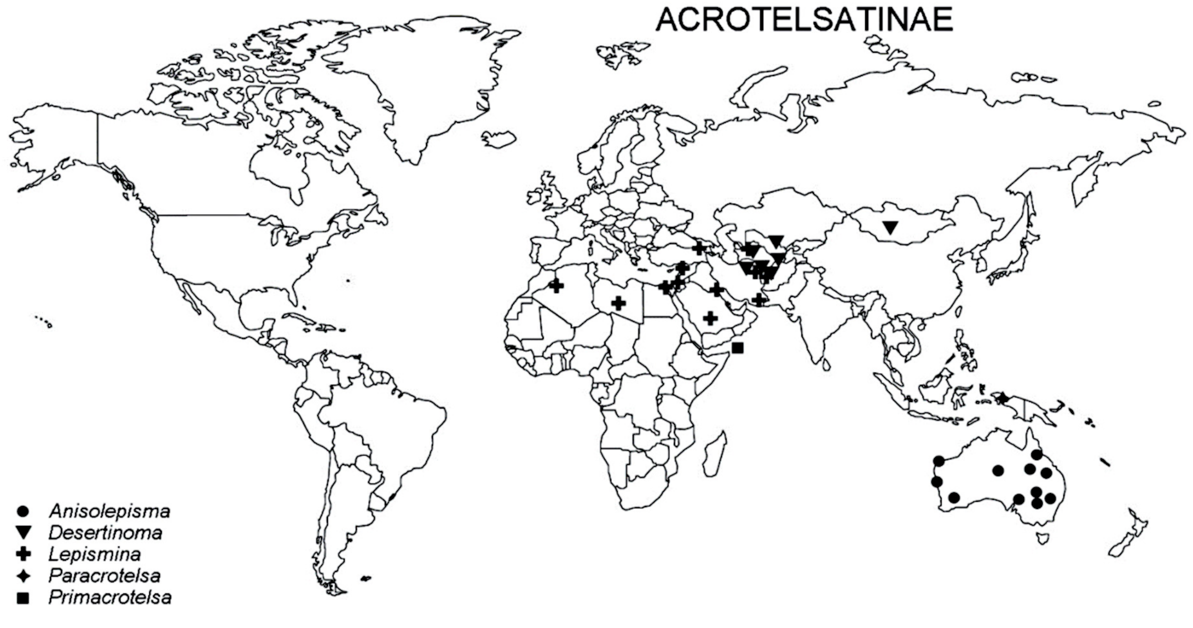

Fig. 20. World distribution of representatives of the subfamily Acrotelsatinae Mendes, 1991.

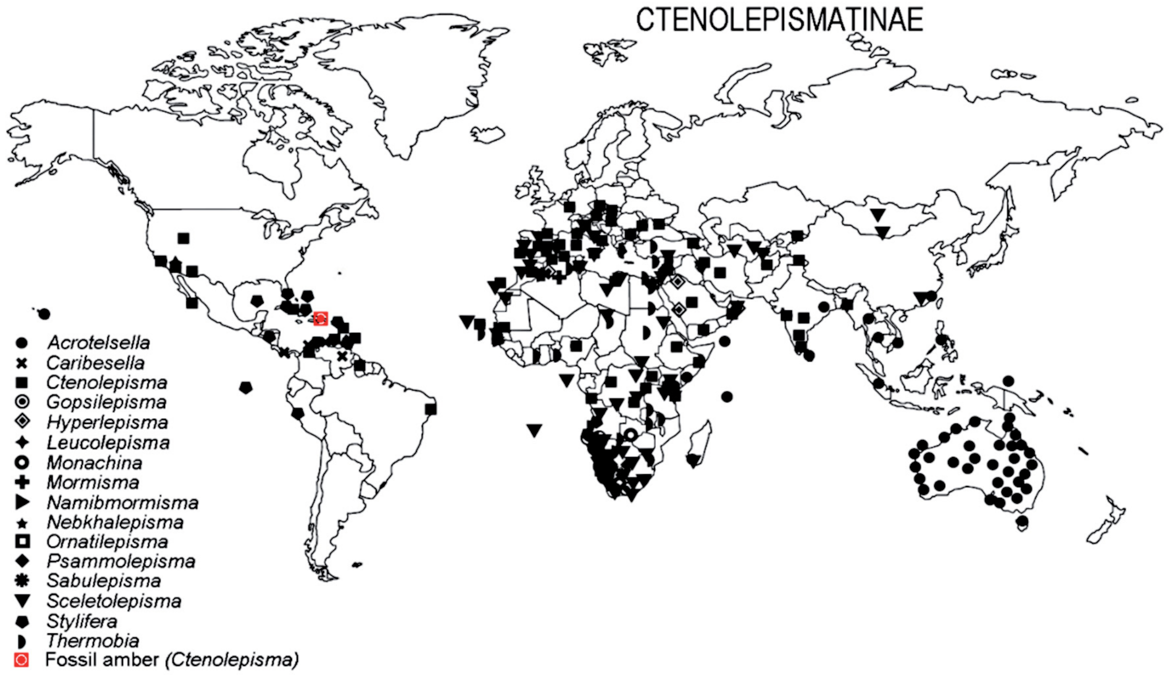

Fig. 21. World distribution of representatives of the subfamily Ctenolepismatinae Mendes, 1991.

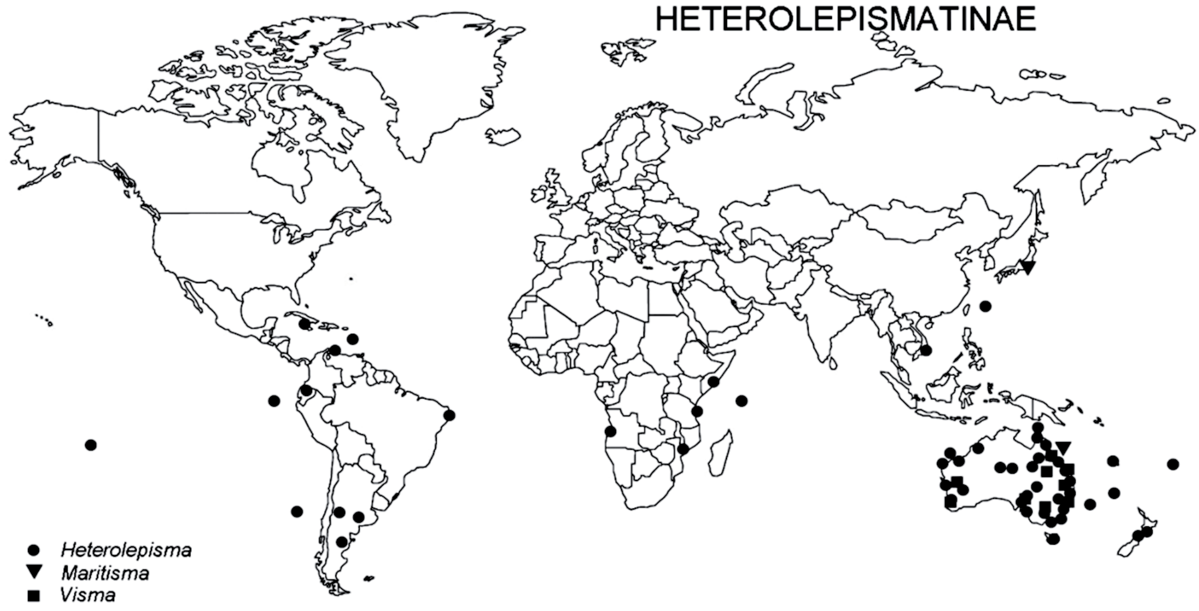

Fig. 22. World distribution of representatives of the subfamily Heterolepismatinae Mendes, 1991.

characters are of phylogenetic importance and we need to obtain specimens of the Argentinian type species of *Heterolepisma* to define the true *Heterolepisma*.

Lepismatinae (79 species in 8 genera, Fig. 23)
Most common in Africa, Europe and Eurasia but also in North America and Australia. This family probably has quite ancient Pangean origins. Fossil specimens described from 99 Ma Burmese amber and 38–50 Ma Baltic amber. Some citations of *Lepisma wasmanni* Moniez, 1894 from South America have not been included due to the suspicion that they were transported by man. Most genera were updated by Mendes (1988) and a key for Mediterranean species associated with ants is given by Robla *et al*. (2023). The status of *Neoasterolepisma* and *Tricholepisma* is under revision, since it has been proven that the genus *Tricholepisma* is not a natural group. Mendes (1991) included *Allacrotelsa* in Lepismatinae, but the position of this genus is not clear.

Mirolepismatinae (3 species in 2 genera, Fig. 24)
Disjunct distribution: Cape Verde Islands, Peru, USA. Poorly understood, possibly introduced to Cape Verde Islands and Peru.

Silvestrellatinae (7 species in 4 genera, Fig. 25)
Afrotropical (Democratic Republic of Congo, Gambia, Namibia, Senegal, South Africa, Sudan), Neotropical (Brazil, Peru, Suriname), Oriental (Sri Lanka, India?), Palaearctic (Cape Verde Islands, United Arab Emirates). Poorly understood, early or mid-Gondwanan.

Problems and opportunities for the future

There is a lack of information due to the very limited interest shown in the Zygentoma. This is understandable because they are not of great economic or health importance. They are also difficult to work with, due to several factors including the numerous adult instars, and it takes many years of experience to be confident in making taxonomic decisions. Luis F. Mendes, who dedicated all his work

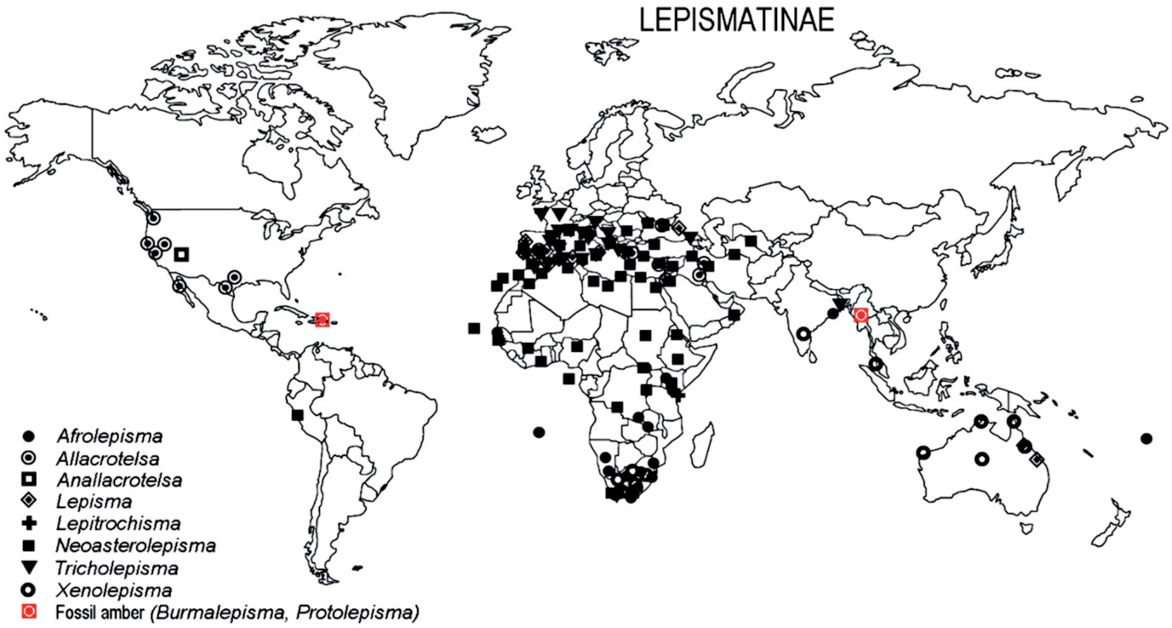

Fig. 23. World distribution of representatives of the subfamily Lepismatinae Latreille, 1802.

Fig. 24. World distribution of representatives of the subfamily Mirolepismatinae Mendes, 1991.

Fig. 25. World distribution of representatives of the subfamily Silvestrellatinae Mendes, 1991.

to basal hexapods, has recently passed away and most of current workers are only part time. We need more people, preferably on continents where insufficient work has been carried out, especially both North and South America and Asia but indeed, there are significant discoveries to be made everywhere. Some recent interest from workers in India and China will hopefully evolve into a better understanding of the fauna in these regions.

We need more sampling efforts in regions where little is known (especially North and South America, Asia). At least some of the material collected should be preserved in 100% ethanol so that molecular data can be obtained, even if this means more brittle specimens. However extra sampling means extra demand on the shrinking base of expertise.

It is understandable but a bit disconcerting to morphologists, that publications are beginning to appear based on molecular data only, without reference to morphology. Given the poor state of knowledge of this order and the lack of expertise around the world, this is likely to occur more often. It is therefore important that we attempt to establish a molecular basis for a wide range of named species with well understood morphology, making it easier to place newly discovered material within the current knowledge framework.

Conclusion

Lepismatidae are an ancient and widely distributed family of Zygentoma; however, our knowledge of them, their phylogeny and zoogeography are hamstrung by the lack of attention paid to these insects.

Acknowledgements

This summary of current knowledge is based on the efforts of many people. All Zygentoma taxonomists have contributed, as have the many collectors and museum curators who facilitate our work. Special thanks are given to Carmen Bach de Roca, who provided the specimens of *Caribesella impudica* collected in Venezuela, and to María del Puerto Barroso Lucena, who helped with the study of some specimens of this silverfish.

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Supplementary material

Supp. file 1. Additional information. https://doi.org/10.5852/ejt.2024.943.2587.11787

Excel file with two sheets:

Sheet 1. List of all the genera of Lepismatidae Latreille, 1802 with literature references. For each genus, the type species is indicated, as well as the literature references of the main taxonomic actions corresponding to each one (original descriptions, redescriptions, etc.).

Sheet 2. Detailed bibliography of Sheet 1.

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