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On some species of African Ctenolepismatinae Escherich, 1905 (Zygentoma: Lepismatidae) preserved in the entomological collection of the Museum für Naturkunde der Humboldt Universität (Berlin)

Rafael Molero-Baltanás[1]*, Carmen Bach de Roca[2] and Miquel Gaju-Ricart[1]

[1] Departamento de Zoología, Universidad de Córdoba, 14014 Córdoba, Spain
[2] 13th Mestral St, Matadepera, 08230 Barcelona, Spain
* Corresponding author, email: ba1mobar@uco.es

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Abstract

Specimens of insects belonging to the subfamily Ctenolepismatinae (order Zygentoma, family Lepismatidae), most of them previously included in the genus *Ctenolepisma*, preserved in the entomological collection of the Museum of Natural History (Museum für Naturkunde der Humboldt Universität) in Berlin (Germany) have been studied for continuing with the revision of the genus *Ctenolepisma* and related taxa. The species *Ctenolepisma erythraeum* sp. nov. is described on the basis of specimens collected in Eritrea and labelled, probably by Escherich, as a new species but never described until now. The description of two species from Madagascar established by Escherich (1910), *Ctenolepisma howa* and *Ctenolepisma madagascariense*, is updated on the basis of type material belonging to both species, concluding that the first one belongs to the genus *Sceletolepisma* (formerly considered as a subgenus of *Ctenolepisma*), so the current name for this species is *Sceletolepisma howa* n. comb. Some characters of both species are corrected with respect to their original description and some new characters are provided, using in some cases scanning electronic microscopy, in spite of the not very good condition of specimens preserved during more than a century. Some descriptive remarks are also included in this work regarding other species of Ctenolepismatinae: *Sceletolepisma corvinum*, *Sceletolepisma parcespinatum*, *Sceletolepisma terebrans* and *Psammolepisma schultzei*.

Keywords Museum collections | *Ctenolepisma* | new species | *Ctenolepisma erythraeum*

1 Introduction

The genus *Ctenolepisma* was created by Escherich (1905) for including species of silverfish (family Lepismatidae Latreille, subfamily Ctenolepismatinae Mendes) with plumose macrochaetae, last abdominal tergite (urotergite X) with variable shape, but not acute triangular, and a concrete type of dorsal abdominal chaetotaxy that, although not accurately described, consists of bearing 3+3 combs on macrochaetae on the posterior margin of some abdominal tergites (urotergites): one in the infralateral position (on the most lateral part of the dorsal plates that bends ventrally and cannot be seen dorsally), one in the submedian

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position (the closest to the midline of the body) and one on lateral position (outer than the submedian, between this and the infralateral); this distinguishes *Ctenolepisma* from *Thermobia* because in this latter genus no urotergites have 3+3 combs but only at most 2+2, one in the infralateral position and one in the lateral position on each urotergite (Escherich, 1905, Molero-Baltanás et al., 2024a). Further studies have revealed that this taxonomic group represents a jumble of several different lineages of the subfamily Ctenolepismatinae. Some preliminary genetic studies, such as those made with synanthropic species of the genus (Molero-Baltanás et al., 2024b) reveal that *Ctenolepisma* is not a natural group and it should be divided into several genera. Some attempts have been made, although some of them have used inappropriate criteria that do not cluster species in natural groups with evolutive and biogeographic sense, such as that of Kaplin (1993), mostly based on the dorsal chaetotaxy of abdomen. The most meaningful split was made by John Irish, that mainly studying South African taxa, distinguished two subgenera, *Ctenolepisma* s. str. and *Sceletolepisma* (Irish, 1987) characterized by the absence or presence of median combs of macrochaetae on ventral abdominal plates (urosternal combs); both subgenera were raised to the generic level by Molero-Baltanás et al. (2024a). Moreover, some other genera were created sharing similar urotergal chaetotaxy, such as *Gopsilepisma* Irish, 1989, *Nebkhalepisma* Irish 1988, *Swalepisma* Irish, 1988, and some species initially attributed to *Ctenolepisma* were later moved to other genera (for example, *Ctenolepisma schultzei* (Silvestri, 1908) was transferred to *Psammolepisma* Irish 1988).

The entomological collections of natural history museums have an important patrimonial and scientific value. For taxonomists, types of species described more than a century ago and not updated since then are especially interesting. This is the case of several species of the genus *Ctenolepisma* (Zygentoma: Lepismatidae) or attributed to this genus, deposited in the Museum für Naturkünde der Humboldt Universität in Berlin (Germany). One of us (Miquel Gaju) had the opportunity to visit this Museum and apply for the loan of some type material, mainly specimens collected from Africa. This allowed us to re-examine the types of African species of *Ctenolepisma* and related genera on the basis of current taxonomic characters of Lepismatidae that were not used at the time of their description. Only some of them had been re-examined by Irish (1987), but we focus especially on two species from Madagascar that had not been studied since their original description, *Ctenolepisma madagascariense* Escherich, 1910 and *Ctenolepisma howa* Escherich, 1910. We even found some specimens labelled with a scientific name given by Escherich but never published. We provide in this work the results of this study.

Table 1. Specimens of types of African *Ctenolepisma* deposited in the Museum für Natürkunde examined for this work. M means that at least one specimen was dissected and mounted for examination with light microscope. S means that at least some parts of one specimen were observed using SEM. The most relevant results involve the samples marked with bold format.

Collection number	Label of the Museum (scientific name + type)	Current name of the species	Number of specimens examined	M / S
31Z	*Ctenolepisma corvina* Holotypus	*Sceletolepisma corvinum*	1 in bad condition	S (one leg and one cercus)
32Z	*Ctenolepisma erythraea* Cotypus	Not previously described	1 juvenile in bad condition	No
33Z	***Ctenolepisma erythraea* Typus!**	**Not previously described. Used to describe a new species**	1 female and 2 juveniles	M (female), S (two legs, one maxilla, one mandible and one antennae of the female)
34Z	***Ctenolepisma howa***	***Sceletolepisma howa***	1 male and 1 female	M (female), S (two legs, one maxilla and one antennae of the female)
41Z	***Ctenolepisma madagascariensis***	***Ctenolepisma madagascariense***	2 young males and 1 broken specimen	M (male), S (two legs, head)
43Z	*Ctenolepisma parcespinata*	*Sceletolepisma parcespinatum*	1 specimen	S (two legs, one antenna)
50Z	*Ctenolepisma schultzei*	*Psammolepisma schultzei*	3 females and 1 in bad condition	S (female)
57Z	*Ctenolepisma terebrans*	*Sceletolepisma terebrans*	27, most of them with broken abdomen	S (one specimen)

2 Material and methods

All specimens were preserved in alcohol and stored in glass vials covered with cotton; most of them were in relatively good condition considering that they were collected and stored more than one century ago. Nevertheless, the absence of fresh specimens made difficult to observe characteristics that are used currently in the taxonomy of Lepismatidae, such as scales of appendages, trichobothrial areas, etc. The specimens examined are indicated in Table 1, with special focus on those examined in more detail that provided significant results. Some other specimens were examined but discarded because their poor condition. When the condition of the specimens was good enough to see at least one of these traits, one specimen of each vial was dissected and mounted on slide using Tendeiro medium (Molero-Baltanás et al. 2000); they were observed with a light microscope, and for some characters micrographs were taken with a Nikon DS-Fi1 digital camera attached to a Nikon Labophot light microscope. Several line drawings were prepared on the basis of some of these micrographs, using the software GIMP2, version 10.12. In some cases, one complete specimen or only part of it, for example some appendages (this was the option when the number of specimens was low) was prepared for observation by scanning electron microscopy (SEM). For this, selected parts of some specimens were first dehydrated with absolute alcohol and the dehydration was completed with hexamethyldisilazane (Ubero-Pascal et al. 2005); then they were mounted on sample holders (Fig. 1). Finally, they were coated with gold prior to observation. The specimens were examined and photographed using a JEOL JSM 7800 SEM in the microscopy service of the Servicio Central de Apoyo a la Investigación (SCAI) from the University of Córdoba (Spain). All the significant characters observed were annotated and, when possible, photographed. SEM photographs and most micrographs obtained are provided in a Supplementary file, except for those used for the original description of the new species presented in Results section.

All specimens were loaned in 2020 just before Covid-19 pandemic, were studied in 2021–22 and were returned to the Museum with a detailed report. The abbreviation MNHU is going to be used in the following sections to refer to the entomological collection of the Museum Für Naturkunde der Humboldt Universität.

3 Results

3.1 Description of new species

***Ctenolepisma erythraeum* sp. nov.**
(Figs 1–6)

Studied material. Holotype: ERITREA, Asmara, 14.i.1906, one female, under stones, Escherich col. Museum MNHU, entomological collection, code SESAM-Kat.Nr:33Z. Labelled as *Ctenolepisma erythraea* Escherich. Previously preserved in alcohol 70% and now mounted on slide, except for some pieces for SEM (Fig. 1A, Table 1). **Paratypes**: same locality and date, 2 juveniles (in the same vial as holotype, with code SESAM-Kat.Nr:33Z, in alcohol 70%) and another specimen from Nefassit, 4.iv.1906, on stones, Escherich

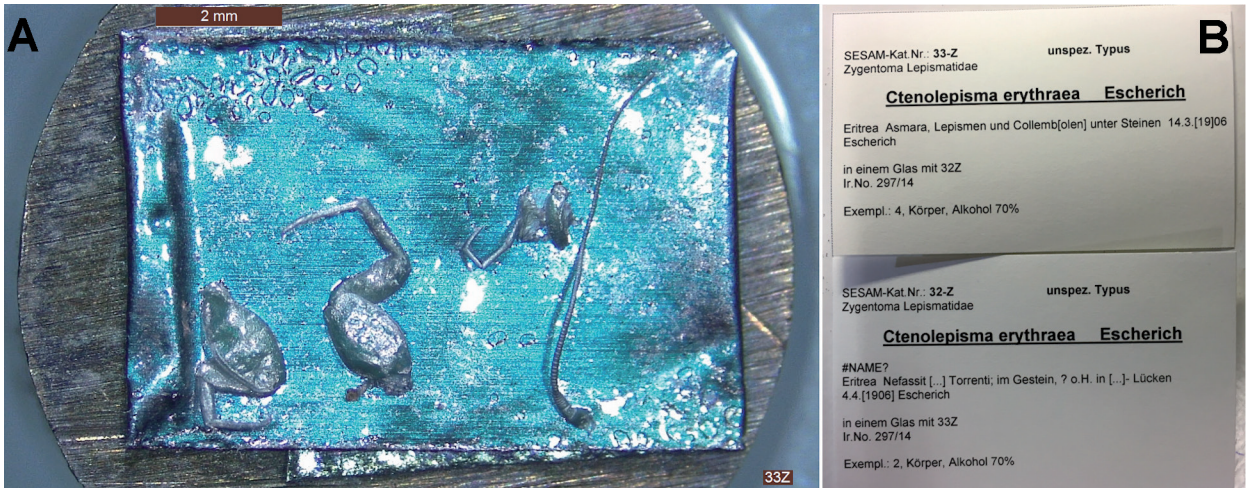

Figure 1. Studying specimens of the Museum für Natürkunde Der Humboldt Universität in Berlin. (**A**) A sample of appendages of *Ctenolepisma erythraeum* sp. nov., holotype, mounted on a stub and coated with gold for SEM observation. (**B**) Labels of the Museum für Natürkunde corresponding to the vials including specimens of *Ctenolepisma erythraeum*. Although the authorship of Escherich is indicated after the scientific name, the description of this species was never published. The vial with the code 33-Z contained the specimen considered as holotype in this work.

(with code SESAM-Kat.Nr:32-Z) in another vial. The numbers of specimens do not coincide with those presented in the labels of the Museum (Fig. 1B); one specimen is missing in each vial (perhaps due to using previously one specimen for microscopy studies and not available in the loaned samples?).

Diagnostic characters: Scales covering the body, scapus and coxae typical, rounded-orbicular to sub-rectangular, with abundant parallel thin rays. Acute lanceolate scales observed on the basal part of maxillary palp, femora, tibiae, styli and caudal filaments. Arrangement of trichobothria on mesonotum

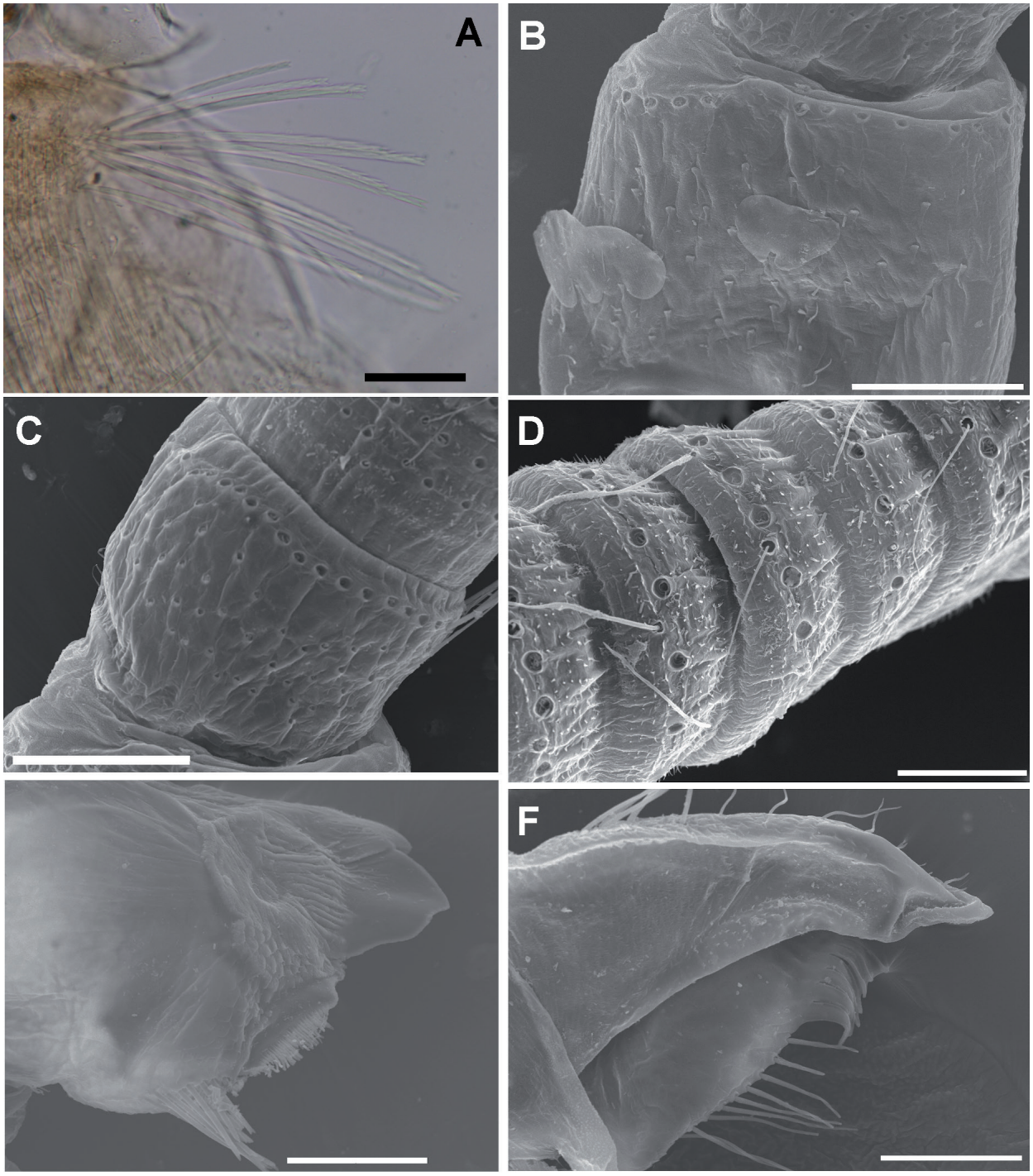

Figure 2. *Ctenolepisma erythraeum* sp. nov., holotype. (**A**) Micrograph of feathered macrochaetae of thorax. (**B**) SEM photograph of the antennal scapus. (**C**) Id., antennal pedicel. (**D**) Id., some annuli of the antennal flagellum. (**E**) Id., apex of mandible showing incisive and molar areas. F: Apex of maxilla, showing galea and lacinia. Scale bars of SEM images (4–8): 0.1 mm, except for Fig. D: 45 µm.

and metanotum as in *C. lineatum* (Fabricius, 1775). Prosternum apically truncate, similar in shape to that of *C. lineatum*. Urotergite I with 1+1 combs of macrochaetae, urotergites II–VII with 3+3 combs, urotergite VIII with 2+2 combs, urotergite IX bare. Urotergite X short, convex, subtriangular, similar to that of *C. lineatum*, with 1+1 combs. Urosternites III–VIII with 1+1 lateral combs. Two pairs of very long abdominal styli; the styli IX are about 2.5 times longer than the length of the inner process of the coxite IX.

Description: Body length of the holotype: 8.3 mm. Antennae broken, the maximum length preserved is 7 mm, but they are probably longer than the body length. Caudal filaments also broken; the maximum preserved length of a cercus is 6.5 mm. Epidermic pigment faint, but perhaps it was more intense and it has been partly lost during more than 100 years of being stored in alcohol. Macrochaetae plumose (Fig. 2A).

Head: Cephalic chaetotaxy similar to other *Ctenolepisma* s.str. Although scales have not been detected in the scapus of the antenna mounted on slide, the image of scanning of the scapus shows rounded orbicular scales and only one subapical row of setae (Fig. 2B), and the pedicel lacks setae; it is covered by setae and has a subapical row of macrochaetae (Fig. 2C). Long trichoid sensilla and trichobothria visible on antennal flagellum (Fig. 2D). Mandibles typical, with a dense field of macrochaetae, although only their insertions are visible; the apical part is shown in Fig. 2E. Galea and lacinia of the maxillae as in Fig. 2F, the lacinia with six lamellate processes and 8–9 thin setae. Last article of the maxillary palp about 7 times longer than wide (Fig. 3A). The penultimate article (N-1) of the maxillary palp is about 1.15 times longer than the antepenultimate (N-2); the fourth article counting from the apex (N-3) has some lanceolate scales (Fig. 3B). The last article of the labial palp is somewhat widened at its apical part; it is about 3–3.5 times wider apically than basally (Fig. 3C). Five papillae are clearly visible, arranged in one row, on the apical part of the last article, but the presence of a sixth and even of a seventh papilla cannot be discarded. There are also some basiconic sensilla inserted on the outer side of the apical article but the total number is difficult to discern because there is a lot of dirt on the surface of this article. The antepenultimate article is also widened distally, about 3 times wider on its distal part than on its basal part.

Thorax, dorsal: Dorsal scales of the thorax seem to be homogeneous, not clearly polymorphic regarding the density of their ribs. Pronotum with 8–9 lateral combs on each side, with 1–3 macrochaetae each (Fig. 4A); the arrangement of trichobothria is not clearly visible. Pronotal collar typical, with anterolateral row consisting of plumose setae. Mesonotum with 9–10 lateral combs on each side, with 2–4 macrochaetae each; a trichobothrium is visible associated with the last

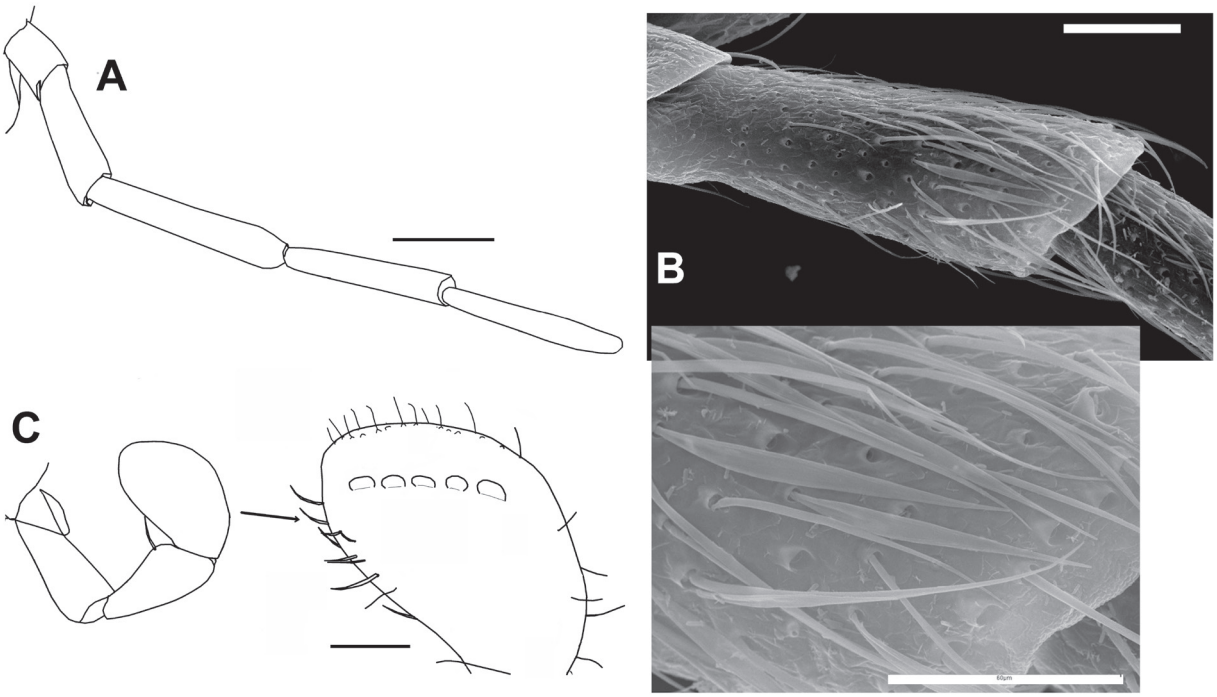

Figure 3. *Ctenolepisma erythraeum* sp. nov., palps of holotype. (**A**) Maxillary palp; scale bar: 0.2 mm. (**B**) SEM images of the fourth article of the maxillary palp (starting from its apex) showing some lanceolate scales; the image below shows a magnification of the scales (scale bars of both images: 60 µm). (**C**) Labial palp, with a detail on the right of the apical article showing five papillae arranged on a single row; scale on the drawing on the right: 0.1 mm.

lateral comb and a similar insertion has been detected in the penultimate lateral comb (Fig. 4B), so it seems that the arrangement of trichobothria on this notum is similar to that of *C. lineatum* (anterior on N-1 comb and posterior on N comb). A long trichoid sensillum is visible on the posterolateral corner of this notum (Fig. 4C). Metanotum with 9+9 lateral combs, each one with 1–4 macrochaetae (the penultimate comb has only one macrochaeta); insertions of trichobothria are visible on similar positions as in mesonotum. On all the three nota, the posterior combs have 4 or 5 macrochaetae; a preserved macrochaeta has about one third of the length of the notum (Fig. 4D).

Thorax, ventral: The shape of the prosternum is difficult to see, but its posterior margin is somewhat truncate, slightly concave (Fig. 4E); it has 5+5 combs of macrochaetae, the anterior combs have 5–7 macrochaetae arranged in a more or less straight row and the posterior

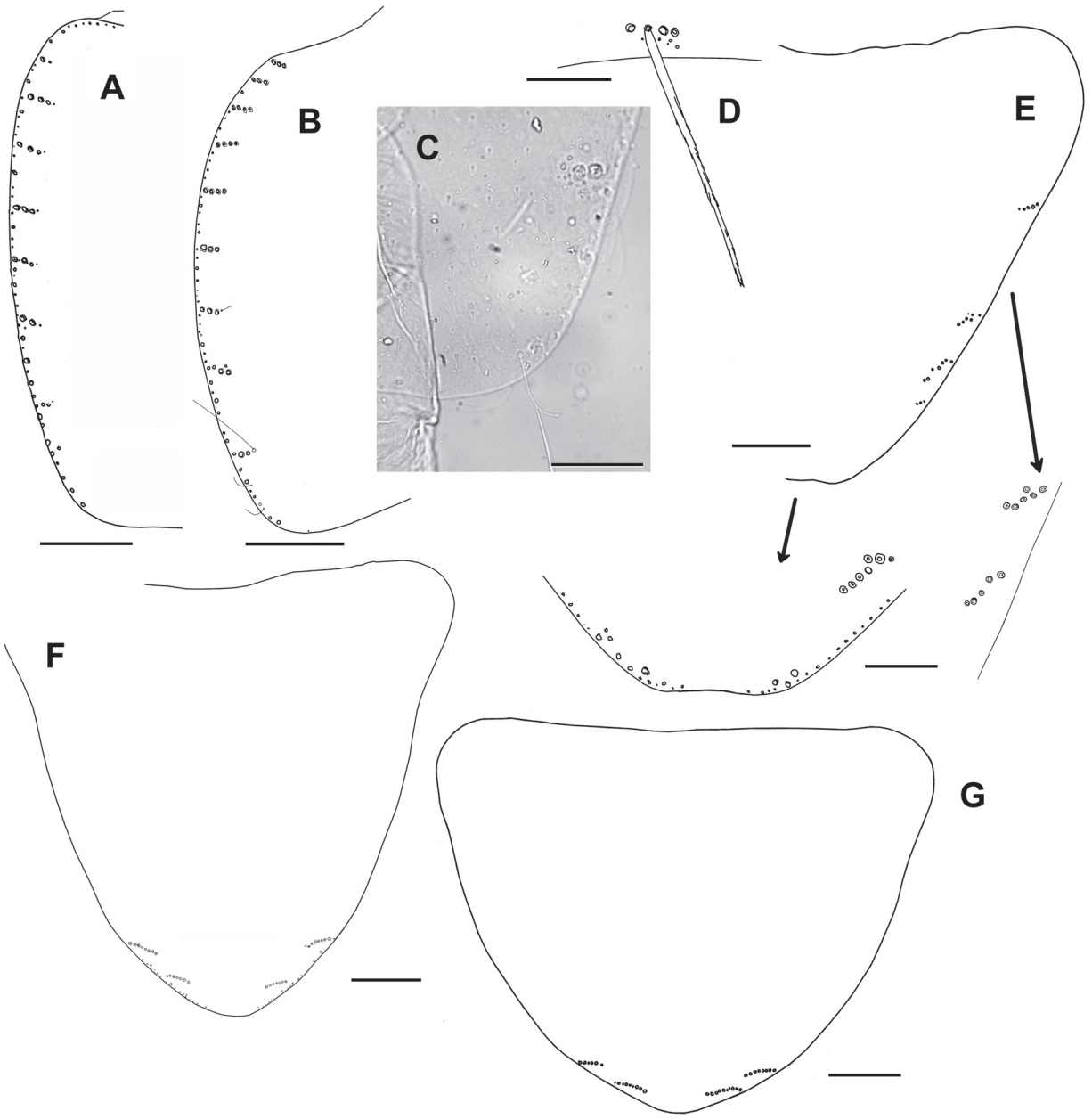

Figure 4. *Ctenolepisma erythraeum* sp. nov., thorax of holotype. (**A**) Left lateral margin of the pronotum. (**B**) Left lateral margin of the mesonotum. (**C**) Micrograph of the right posterior corner of the mesonotum, showing a curved and long trichoid sensillum. (**D**) Posterior comb of the metanotum, showing a preserved macrochaeta. (**E**) Prosternum, with details of insertions of lateral combs of macrochaetae (right) and posterior margin with a subapical comb (below). (**F**) Mesosternum, showing the position of 2+2 subapical combs. (**G**) Metasternum, showing the position of 2+2 subapical combs. Scale bars: 0.25 mm, except for 14, 15 and magnified details of Figure E: 0.1 mm.

ones more irregularly arranged, the antedistal combs with about 10 macrochaetae. The shape of the mesosternum and the metasternum is shown in Figs 4F and 4G, they have a more convex posterior margin and 2+2 combs of macrochaetae. In the mesosternum, all combs bear 8–9 macrochaetae and in the metasternum, the anterior combs have 6–8 and the posterior ones have 9–10 macrochaetae; the distance between the posterior combs is about 1.8 times the width of a comb. The metasternum is wider than long, its ratio length/width is about 0.77.

Legs: Coxae with rounded orbicular scales similar to those covering the body. Femora and tibiae with lanceolate scales (Fig. 5A), those of tibiae narrower; those of femur about 100–130 µm long x 13–20 µm wide and those of tibiae 75–105 µm long x 7–14 µm wide. Protibiae (Fig. 5B) about 3.25 times longer than wide and 1.6 times longer than the tarsomere I of the first leg, with at least 2 dorsal and 2 ventral macrochaetae. Mesotibiae about 3.6 times longer than wide and 1.5 times longer than the tarsomere I of the second leg, with at least 3 dorsal and 2 ventral macrochaetae. Metatibiae (Fig. 6A) about 4.2 times longer than wide and 1.4 times longer than the tarsomere I of the third leg, with at least 2 dorsal and 2 ventral macrochaetae. Tibial spurs and macrochaetae shorter than the width of the corresponding tibia. Tarsomeres II and III similar in length, about one third of the length of the corresponding tarsomere I. Tarsomeres IV slightly longer than the corresponding tarsomere III. Pretarsal claws small.

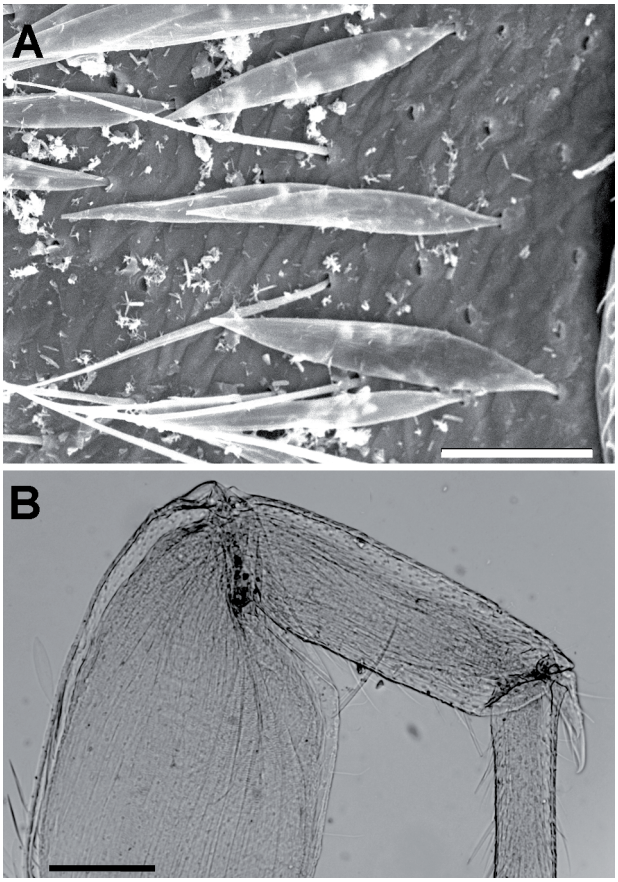

Figure 5. *Ctenolepisma erythraeum* sp. nov., legs of holotype. (**A**) SEM photograph of lanceolate femoral scales; scale bar: 50 µm. (**B**) Micrograph of the protibia, showing the basal part of the first tarsomere and the distal part of the femur; scale bar: 0.2 mm.

Abdomen, dorsal: Urotergite I with 1+1 combs consisting of 5 macrochaetae. Urotergites II–VII with 3+3 combs; the infralateral combs (A) bear 6–8 macrochaetae and the lateral (B) and submedian combs (C) bear 4–5 macrochaetae (Fig. 6B). Urotergite VIII with 2+2 macrochaetae; the infralateral comb with 7–8 macrochaetae and the other comb has 5 macrochaetae (Fig. 6C). Urotergite IX bare. Urotergite X subtriangular, short and convex, similar in shape to that of *C. lineatum*, with 1+1 subapical combs of 8–9 macrochaetae, in the holotype it is damaged (probably due to moulting process of the specimen).

Abdomen, ventral: Urosternal combs difficult to observe in the holotype because the specimen is moulting. Urosternites I and II without combs, urosternites III–VIII with 1+1 combs of about 8–12 macrochaetae, the distance between the lateral combs about 5.2–6 times the width of a comb (Fig. 6D). Two pairs of styli associated to the abdominal segments VIII and IX. Coxites VIII and IX as in Figs 6E and 6F. Inner process of the coxite IX of the female (holotype) about 1.9 times longer than wide on its base and about 2.8 times longer than the outer process. Styli IX about 3.1 times longer than the inner process of the coxite IX and about 1.5 times longer than the styli VIII. Narrow lanceolate scales are visible on the basis of the styli IX (Fig. 6G). Ovipositor long, about 3 mm long in the holotype, with about 44 divisions, surpassing the apex of styli IX about 1.55 times their length (Fig. 6E). Caudal filaments with trichoid sensilla, trichobothria, chaetic sensilla and narrow lanceolate scales (Fig. 6H).

Remarks: *C. erythraeum* sp. nov. is the only African species of *Ctenolepisma* s.str. with a short convex subtriangular urotergite X and 3+3 combs of macrochaetae on urotergites II–VII. It is very similar to *C. lineatum* but has only 2 pairs of styli. Before the redescription of *C. lineatum* by Molero Baltanás et al. (2012), species with these characteristics were considered to belong to *C. lineatum*, but currently they are considered as a few species (this is the case of *C. nicoletii*, *C. almeriense*, etc.). But the lanceolate type of scales on appendages and its distribution in *C. erythraeum* sp. nov. is similar to that of *C. lineatum* (although these scales are not observed on the maxillary palp of the European species) and very different from the aforementioned forms with two pairs of styli. Table 2 presents some characters distinguishing *C. erythraeum* sp. nov. from *C. lineatum* and *C. nicoletii* (this one as representative of the taxa with two pairs of styli with abdominal chaetotaxy similar to that of *C. lineatum*).

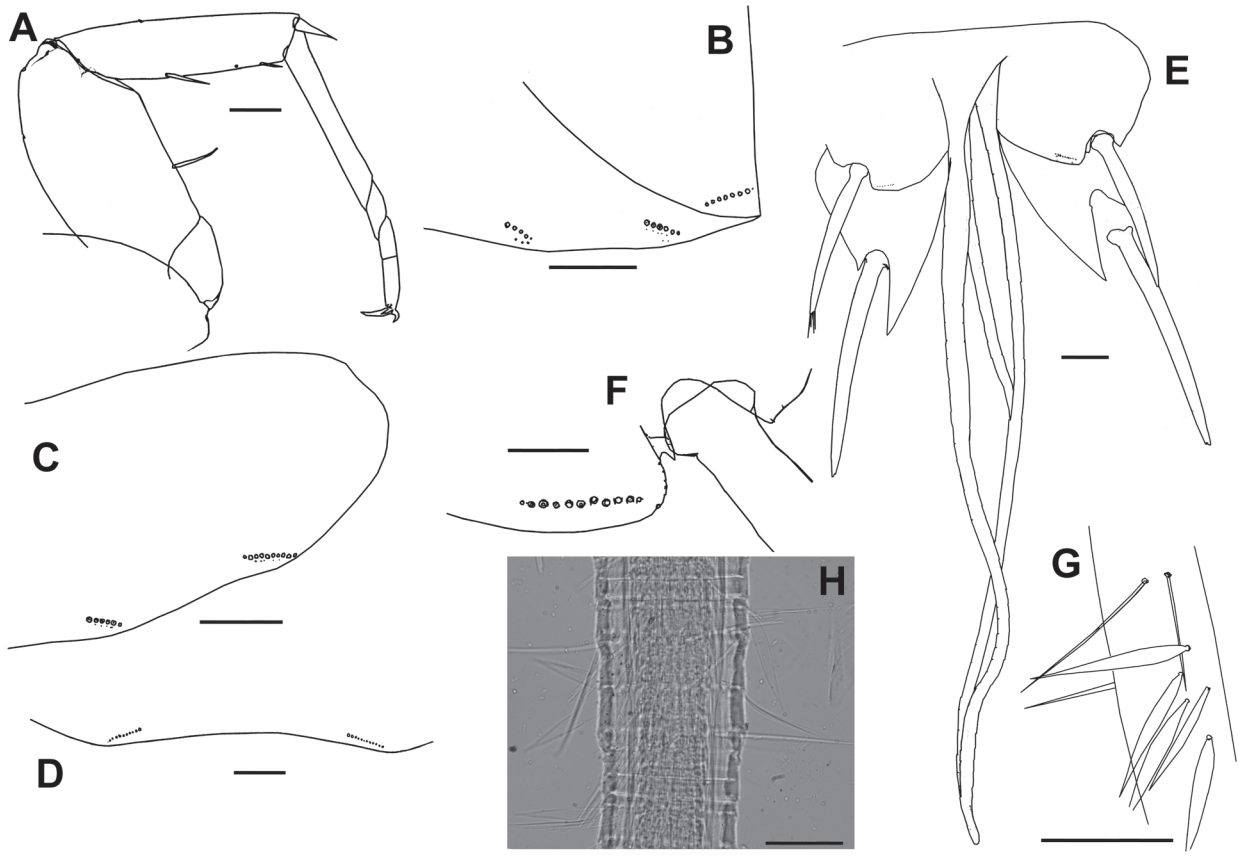

Figure 6. *Ctenolepisma erythraeum* sp. nov., holotype. (**A**) Hind leg. (**B**) Bended right lateral part of the hind margin of the urotergite V, showing the insertions of macrochaetae of three combs. (**C**) Lateral part of the right hind margin of the urotergite VIII, showing the insertions of macrochaetae of two combs. (**D**) Hind margin of the urosternite. (**E**) Coxites, styli and ovipositor as observed in the mounted specimen. (**F**) Hind margin of the coxite VIII showing the insertions of the comb and the base of the stylus VIII. G: Median part of the stylus IX showing acute lanceolate scales. H: Micrograph of some divisions of the cercus showing the presence of some lanceolate scales. Scale bars of Figures A–E: 0.25 mm; scale bars of Figures F–H: 0.1 mm.

Table 2. Comparison of diagnostic characters of *Ctenolepisma erythraeum* sp. nov. and related previously described species.

Character	*Ctenolepisma erythraeum* sp. nov.	*Ctenolepisma lineatum*	*Ctenolepisma nicoletii*
L/W protibiae	3.25	2.2–3	2.5–3.5
Number of macrosetae of posterior combs of prosternum	9–10	2–5	4–11
Number of macrosetae of mesosternal combs	8–9	2–6	3–12
Number of macrosetae of antedistal combs of metasternum	9–10	2–7	3–12
Ratio distance between posterior combs / width of a comb on metasternum	1.8	3.5–12.5	1.7–7
Number of pairs of styli	2	3	2
Femoral scales	Lanceolate acute	Lanceolate acute	Subtriangular, truncate
Posterior margin of prosternum	Widely truncate	Truncate, slightly concave	Convex or slightly truncate

3.2 Descriptive notes and remarks on other examined species

Ctenolepisma madagascariense Escherich, 1910

Ctenolepisma madagascariense Escherich, 1910
Ctenolepisma madagascariensis Escherich, 1910: 535 (Fig. 7; Figs S1–S5)

Studied material. Unspecified type material: MADAGASCAR, Imanombo, no date, two males and one specimen with broken abdomen (indetermined sex), Museum MNHU, entomological collection, code SESAM-Kat.Nr: 41-Z. Labelled as *Ctenolepisma madagascariensis* Escherich, 1910, unspez. Typus. Preserved in alcohol 70%; one male mounted on slide, except for some pieces for SEM (Table 1).

Descriptive notes: The dissection of one specimen allows widening the description of this species in some characters (for example, shape and chaetotaxy of thoracic sternites; see Figs 7A–7C) that were not mentioned by Escherich (1910), although some other characters cannot be properly described due to the imperfect preservation of the specimens. Scales have not been observed on appendages, except for coxae and femora, which bear rounded scales. The scape also has round scales (Fig. S1).

Head: The chaetotaxy of the head, including clypeus and labrum, is similar to that of *C. ciliatum*; a trichobothrium has been observed close to the compound eye (Fig. S2). The apical article of the labial palp is only a bit widened in its distal part; it has five papillae arranged in a row (observed with SEM, see Fig. S3, but difficult to distinguish in the palp mounted on slide).

Thorax: On the anterolateral angles of the pronotum some small scales with fine and dense ribs can be observed; the remaining parts of this notum seem to be covered with bigger scales, also with fine parallel ribs. Pronotal collar with two rows of macrochaetae (most of them are lost, and only their insertions are observed). Some short macrochaetae of the anterolateral row are preserved and seem to be smooth, not pectinate. Insertions of different sizes can be seen on the lateral margins of nota; the bigger ones are grouped in combs of 1–5 macrochaetae (on the pronotum, the maximum number of macrochaetae observed per comb is 3). On one side of the pronotum there are 6 combs. The last lateral comb has a trichobothrium (posterior trichobothrial area) on its inner end; the anterior trichobothrium is not visible.

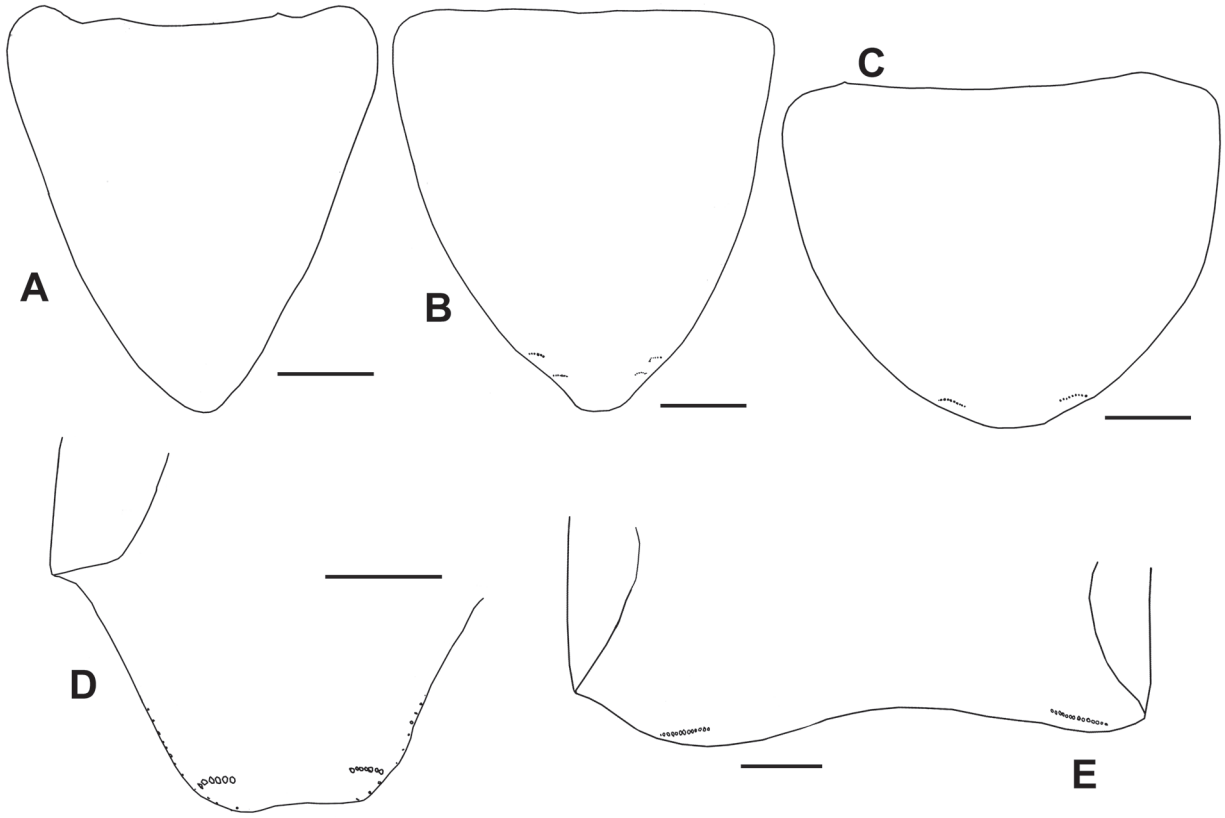

Figure 7. *Ctenolepisma madagascariense* Escherich, 1910. (**A**) Shape of the prosternum. (**B**) Mesosternum, showing the position of 1+1 combs. (**C**) Metasternum, showing the position of 1+1 combs. (**D**) Urotergite X. (**E**) Urosternite IV. Scale bars: 0.25 mm.

Posterior combs of 7–9 macrochaetae. The mesonotum has 11–12 lateral combs and the metanotum 9–10 of these combs. Prosternum (Fig. 7A) and mesosternum (Fig. 7B) subtriangular, about as long as wide or slightly longer (ratio length/width about 1.05); the metasternum (Fig. 7C) is shorter and wider (ratio length/width about 0.75) and with a more rounded apex. The prosternum is slightly shorter than the mesosternum and 1.1 times longer than the metasternum. The chaetotaxy of the thoracic sternites is difficult to discern, especially on the prosternum; on this sternite, an antedistal comb of 5 macrochaetae is observed on one side; the mesosternum has 2+2 very close antedistal combs of 6–7 macrochaetae and the metasternum 1+1 antedistal combs of 9–10 macrochaetae. The distance between the metasternal combs is about 3.3 times the width of a comb.

Legs: Ratio length/width of tibiae: about 2.65–2.75 for protibiae, about 2.85 for mesotibiae and about 3.5 for metatibiae. The tibial spurs of the protibiae are big, its length is more than 1/3 of the length of the tibia (Fig. S4); the size of these spurs is not so big in the other legs (about 30% of the length of the tibia in the second legs and less than 1/4 of the length of the tibia in the third legs). In the second and third legs, the first tarsomere is longer than the sum of the lengths of the three remaining tarsomeres; in the first legs, not clearly longer than this sum. The second and the third tarsomeres are a bit shorter than the fourth. Pretarsal claws smooth, the empodium small and less than half the length of the lateral claws (Fig. S5).

Abdomen: Urotergite I with 1+1 combs of macrochaetae (the number of macrochaetae per comb is difficult to see: it seems to be more than 8 and less than 14). The urotergites II–V seem to have 3+3 combs and the VI–VIII 2+2 combs, but they are difficult to see in the mounted specimen; when visible, they coincide with the original description. The infralateral combs bear 8 macrochaetae and the lateral and sublateral (submedian) comb bear 5–6 macrochaetae. Urotergite IX bare, urotergite X trapezoidal with 1+1 combs of 6–7 macrochaetae; this last abdominal tergite is relatively long (the ratio length/ width is about 0.52) and its hind margin is straight, slightly concave (Fig. 7D). The ventral part of the abdomen is damaged (perhaps someone dissected the genital part and this and the coxites are not clearly visible). Only the first five abdominal sternites are well preserved; the urosternites I and II lack chaetotaxy and the other three sternites have 1+1 lateral combs consisting of 9–14 macrochaetae (Fig. 7E); on the urosternite V, the distance between the lateral combs is about 5.2 times the width of a comb.

Remarks: Irish (1987) listed *C. madagascariense* as *incertae sedis*, since the information available on this species (that provided in its original description) was not sufficient to assign it or not to *Sceletolepisma*. Since we have verified that it lacks median urosternal combs and shows a trapezoidal urotergite X, *C. madagascariense* belongs to the genus *Ctenolepisma* s.str. and not to *Sceletolepisma*. It belongs to a group of African and Eurasian species sharing a urotergite X with trapezoidal shape. Considering that native insects of this group are not found in South Africa, it is likely that this species is more related to species of *Ctenolepisma* native to coastal countries of Indian Ocean, including India.

Sceletolepisma howa (Escherich, 1910)

Ctenolepisma howa Escherich, 1910: 536.
(Fig. 8; Figs S6–S18).

Studied material. Unspecified type material: MADAGASCAR, Andranovory (SW Madagascar), no date, one male and one female, under stones, Escherich col., Museum MNHU, entomological collection, code SESAM-Kat.Nr: 34-Z. Labelled as *Ctenolepisma howa* Escherich, 1910, unspez. Typus. Preserved in alcohol 70%; the female mounted on slide, except for some pieces for SEM (Table 1).

Descriptive notes: The microscopic study of one specimen allows widening the description of this species in some characters (for example, shape and chaetotaxy of thoracic sternites; see Figs 8A–8C) overlooked by Escherich (1910), and correcting some other characters that were not properly described. The most relevant correction concerns ventral abdominal chaetotaxy: despite the bad condition of the specimen dissected, median urosternal combs are visible on abdominal segments II–VI, which is in contradiction with Escherich's description, who mentioned the presence of median combs only on urosternites II and III. The actual arrangement of ventral combs of the abdomen is 0/1/1+1+1/1+1+1/1+1+1/1+1+1/1+1/1+1/ − . The studied specimens are more intensely pigmented than *C. madagascariense*; they are brown in alcohol.

Head: The cephalic chaetotaxy does not seem significantly different to other *Sceletolepisma*; periocular macrochaetae are abundant (Fig. S6). The antennal scape has rounded scales. Mandibles typical. Maxillary palp long slender, the apical article about 8 times longer than wide, slightly shorter than the penultimate; the antepenultimate article about 6 times longer than wide and about 1.2 longer than the last article. Labial palp with the last article somewhat widened apically, about 3 times wider at its distal half than at its base (Fig. 8D), the sensory papillae cannot be clearly seen in the mounted specimen.

Thorax: Most dorsal scales are lost, a small one with crossed ribs has been observed on the pronotum. This dorsal plate has 8–9 lateral combs consisting of

2–4 macrochaetae (usually 3); the posterior combs are more separated between them than the anterior ones. One trichobothrium has been observed associated to the last lateral comb (Fig. S7). Pronotal collar not clearly visible, the anterolateral row is long on both sides of the anterior margin of pronotum. Mesonotum with 11+11 lateral combs similar to those of pronotum; another trichobothrium occurs on the last lateral comb. Metanotum with a lot of dirt, their combs not clearly visible. Prosternum subtriangular, as long as wide or slightly longer, with the posterior margin relatively acute, with 2+2 subapical combs of 4–5 macrochaetae each; more anterior combs have not been observed (Fig. 8A). Mesosternum similar in shape but the posterior margin is a bit more rounded, with 1+1 subapical combs of 10–11 macrochaetae each; these combs are separated by a distance about 2 times greater than the width of a comb (Fig. 8B, Fig. S8). Metasternum wider (ratio length/width about 0.75), with a more rounded posterior margin, with 1+1 combs of 11–12 macrochaetae each; the ratio distance between the combs / width of a comb is similar to that of mesosternum (Fig. 8C, Fig. S9).

Legs: The legs of the available specimens are broken; in some of them only coxae are preserved. Coxal scales rounded, orbicular (Fig. S10). No scales have been observed on other articles, although femora seem to have scales (detected sockets different to those of setae). SEM observation has revealed that there is a strong contrast between the density of setae on the inner side of tibiae (Fig. S11) compared with the outer side, where insertions are scarce (Fig. S12). Protibiae 2.7–2.8 times longer than wide. A mesotibia about 3.2 times longer

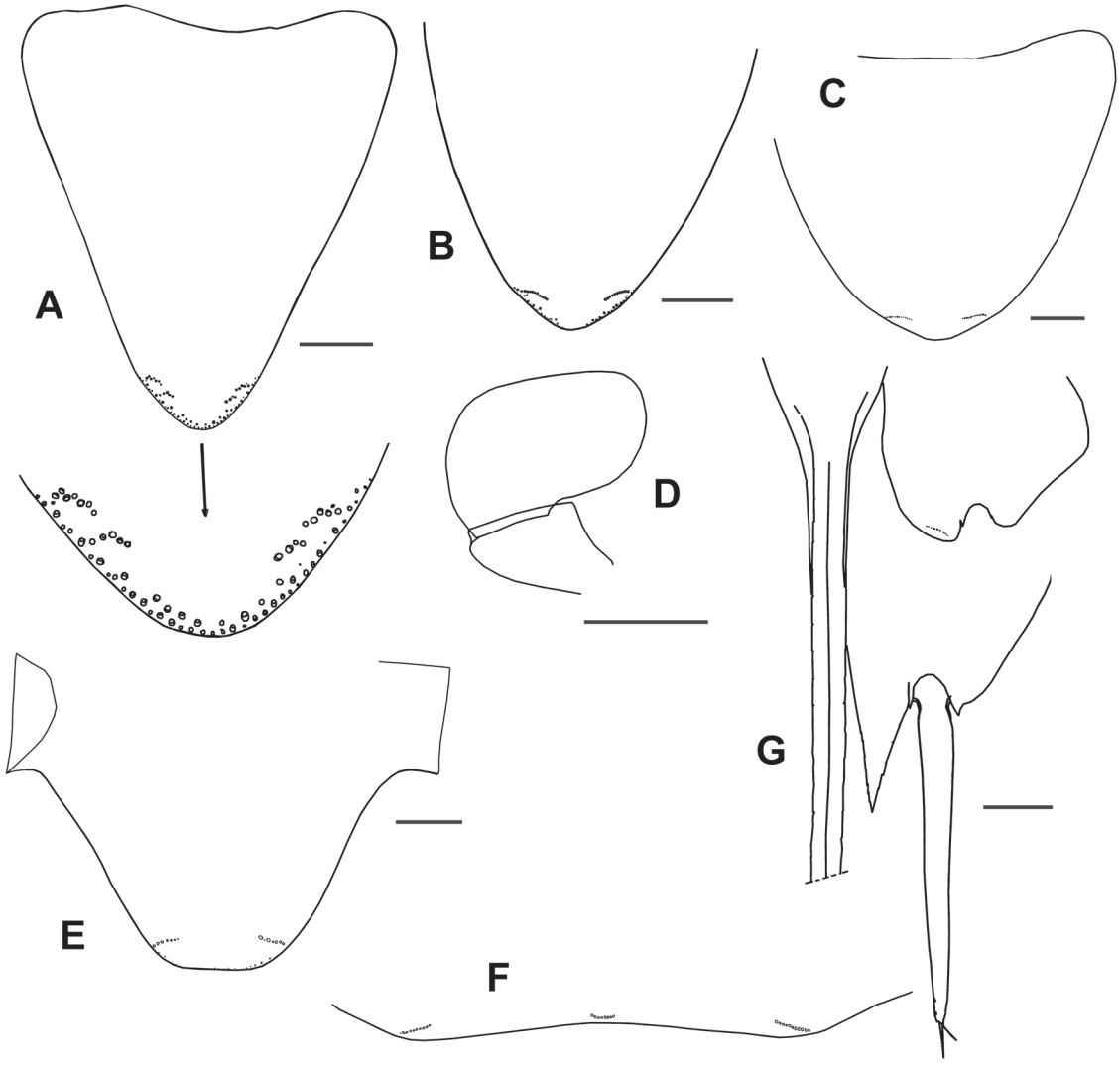

Figure 8. *Sceletolepisma howa* (Escherich, 1910). (**A**) Prosternum, showing below a detail of the apical posterior margin and its chaetotaxy. (**B**) Hind part of the mesosternum. (**C**) Metasternum. (**D**) Shape of the apical article of the labial palp. (**E**) Urotergite X. (**F**) Hind margin of the urosternite V showing a median comb and 1+1 lateral combs. G: Coxites VIII and IX, stylus IX and broken ovipositor. Scale bars: 0.25 mm.

than wide. Tibial spur of protibiae about 0.26–0.27 times the length of the corresponding tibia (Fig. S13). Tibial spur of the mesotibia about 0.23 times the length of the tibia (Fig. S14). In the first legs, the first tarsomere is shorter than the sum of the lengths of the three remaining tarsomeres; in the second legs, slightly longer than this sum. The fourth tarsomere is a bit longer than the third and about as long as the second tarsomere. Pretarsal claws smooth, the empodium shorter and thinner than the lateral claws (Fig. S15).

Abdomen, dorsal: Dorsal chaetotaxy of abdomen difficult to discern in the mounted specimen. Urotergite I with 1+1 infralateral combs. Urotergites II–VII with 3+3 combs; the number of macrochaetae per comb is difficult to see; the infralateral combs of the urotergite III have 5 macrochaetae and the infralateral combs of urotergites IV and VII consist of 7 macrochaetae, the lateral combs have 5 macrochaetae in these urotergites and the submedian combs (comb C, the closest to the midline of body) have 4 or 5 macrochaetae. Urotergite VIII with 2+2 combs of macrochaetae. Urotergite X trapezoidal, as long as in *C. madagascariense* or slightly longer (Fig. 8E); in the mounted specimen the ratio length/ width is about 0.59. Its hind margin is straight and bears 1+1 combs of 7 macrochaetae.

Abdomen, ventral: Urosternite I apparently bare. Urosternite II with a median comb of about 13 macrochaetae (Fig. S16). On urosternites III and IV the median comb is difficult to see but urosternites V, VI and VII show median combs of 8, 9 and 6 macrochaetae (Fig. 8F). The urosternites III–VII have 1+1 lateral combs of 8–11 macrochaetae. Coxites VIII also with one lateral comb of 9 macrochaetae (Fig. S17). Two pairs of abdominal styli. Inner process of the coxites IX about 1.75 times longer than wide at its base and about 3.25 times longer than the corresponding outer process. Styli IX long, about 2.7 times longer than the inner process of the coxite IX (Fig. 8G). The ovipositor of the mounted specimen is broken and only its basal part is preserved; the preserved part, ending at a level between the apex of the coxite IX and the apex of styli IX, has 16 divisions, but it is probably much longer.

Remarks: All the characters examined confirm that this species should be included in *Sceletolepisma*. Some characters not previously described have been observed in the mounted specimen (relatively better preserved than those belonging to *C. madagascariense*) including the sclerotized structures of the proventriculus (Fig. S18).

Sceletolepisma corvinum (Silvestri, 1908)

Ctenolepisma corvina Silvestri, 1908: 293.
(Figs S19–S20).

Studied material. Holotype: SOUTH AFRICA, Steinkopf, no date, one female, L. Schultze col., Museum MNHU, entomological collection, code SESAM-Kat. Nr:31-Z. Labelled as *Ctenolepisma corvina* Silvestri, 1908. Preserved in alcohol 70%, except for one leg and one cercus that have been studied by SEM.

Remarks. The SEM study of the leg has revealed that the tibiae are devoid of scales, the femur has rounded scales at least on the dorsal margin of the inner side (Fig. S19). Very few insertions of scales are observed on coxae (Fig. S20). This information can be added to the redescription presented by Irish (1987).

Sceletolepisma parcespinatum (Silvestri, 1908)

Ctenolepisma parcespinata Silvestri, 1908: 292.
(Figs S21–S26).

Studied material. Holotype: SOUTH AFRICA, Klein-Namaland, Steinkopf, vii-1904 ("04.Jul" indicated in label), L. Schultze col., one male, Museum MNHU, entomological collection, code SESAM-Kat.Nr:43-Z. Labelled as *Ctenolepisma parcespinata* Silvestri, 1908 (a synonym was also indicated in the label: *Sceletolepisma parcespinata*). Preserved in alcohol 70%, except for one antenna and two legs that have been studied by SEM.

Remarks. The SEM study of some appendages has also revealed that tibiae of this species lack scales (Fig. S21), and femora are covered by rounded scales with very thin parallel ribs (Fig. S22). The scapus has insertions of scales (Fig. S23) and the pedicel only insertions of setae (Fig. S24). Some trichoid, coeloconic and basiconic sensilla are observed on the antennal flagellum (Fig. S25); one of these types, with rounded shape, is similar to the type F present in *Lepisma saccharinum* (Adel, 1984) and named as Silvestri's sensillum by some authors. The labial palp has 5 papillae arranged in a single row (Fig. S26). This information represents a significant supplementary information to the redescription given by Irish (1987).

Sceletolepisma terebrans (Silvestri, 1908)

Ctenolepisma terebrans Silvestri, 1908: 291.
(Figs S27–S35).

Studied material. **Co-Types:** BOTSWANA, Kalahari, Seherelela-Kue (Severelela in Kokur in label), x.1904

("Okt.[19]04" in label), L. Schultze col., about 29 specimens, most of them with the abdomen broken and the posterior part missing (in the label they are indicated as Co-Typus, but this status is discussed by Irish (1987)), Museum MNHU, entomological collection, code SESAM-Kat.Nr:57-Z. Labelled as *Ctenolepisma terebrans* Silvestri, 1908. Preserved in alcohol 70%, except for one that has been prepared for study by SEM.

Remarks. Irish (1987) also examined this material consisting of incomplete specimens and commented that some of these specimens could correspond to other species of *Sceletolepisma* (probably *S. pluriseta*); both species are probably very closely related so the following descriptive remarks, although attributed to *S. terebrans*, should be considered with caution and fresh complete specimens should be used to confirm them. The characters observed on legs, antennae, and palps are very similar to those described for *S. parcespinatum*. On antennae, the scapus bears rounded scales and the pedicel has only setae (Fig. S27). Trichoid, coeloconic and basiconic sensilla types B and C have been observed with SEM on the flagellum, as well as insertions of chaetic sensilla (Figs S28–S31); some basiconic sensilla type B are longer than others suggesting two related types (compare the one shown in Fig. S29 with the one in Fig. S31). Two B basiconic sensilla of the short type are also observed on the outer side of the apical article of the labial palp close to a basiconic sensillum type C (Figs S32, S33); this article bears the typical five papilla arranged in a single row (Fig. S32). The preserved dorsal scales of thorax are heterogeneous in shape and in the density of their parallel ribs (Fig. S34); this has been observed in other species of *Ctenolepisma* and *Sceletolepisma*, but a thorough study of fresher specimens is required to assess the differences or similarities in this character between different taxa. As in other *Sceletolepisma*, the scales of femora of the specimens attributed to *S. terebrans* are rounded orbicular, similar to those of coxae, and tibiae lack scales (Fig. S35).

***Psammolepisma schultzei* (Silvestri, 1908)**

Ctenolepisma schultzei Silvestri, 1908: 294.
(Figs S36–S40).

Studied material. Unspecified type material: SOUTH AFRICA, Klein-Namaland, Steinkopf, 1904, L. Schultze col., three females and one specimen in bad condition, Museum MNHU, entomological collection, code SESAM-Kat.Nr:50-Z. Labelled as *Ctenolepisma schultzei* Silvestri, 1908 (a synonym was also indicated in the label: *Psammolepisma parcespinata*, its currently valid name). Preserved in alcohol 70%, except for one female that has been prepared for study by SEM.

Remarks. This species was considered by Irish (1988) as belonging to a separate genus different from *Ctenolepisma* considering mainly its different urotergal chaetotaxy which seems to be more related to the genus *Thermobia*. The results of the observation by SEM of a specimen of this species is not conclusive regarding the question of whether this species is more closely related to *Sceletolepisma* or to *Thermobia*, because it shares with both genera the presence of rounded scales on the scapus (Fig. S36) and the femora (Fig. S37), similar to those covering the body, while antennal pedicels (Fig. S38) and tibiae (Fig. S37) lack scales. The antennal flagellum has a type of sensillum that can be interpreted with light microscopy as a trichobothrium, but it is different to typical trichobothria inserted on caudal filaments (width of the hair, structure of the base; see Fig. S39). These long hairs, probably corresponding to long trichoid sensilla, have not been observed either in *Sceletolepisma* or *Thermobia* and can be interpreted as a trichobothria-like sensilla, perhaps derived from a trichoid sensillum, similar to those found in the genus *Anisolepisma* Paclt, 1967 (Smith, 2016). On the ventral side of femora and tibiae, apart from insertions of macrochaetae or spines, some very long and thin setae, similar to trichoid sensilla, have been detected (Fig. S37). The dorsal orbicular scales of the thorax are, as in *S. terebrans*, very heterogeneous in shape and density of ribs; scales with very few and separated ribs are abundant (Fig. S40).

4 Discussion

Examining some specimens with SEM has revealed, in spite of the non-optimal state of specimens with more than a century preserved in alcohol, that all studied *Ctenolepisma* and *Sceletolepisma* with trapezoidal urotergite X lack scales on tibiae and modified scales on femora; this pattern of distribution and shape of scales has also been observed in some synanthropic species of *Ctenolepisma* and *Sceletolepisma* with this type of urotergite such as *C. longicaudatum* Escherich, 1905 and *S. villosum* (Fabricius, 1775) (Molero-Baltanás et al., 2024b) and also in some free-living Palaearctic species of *Sceletolepisma* and *Ctenolepisma* with the same type of urotergite X found from Portugal to India such as *C. ciliatum* (Dufour, 1831), *C. armeniacum* Molero-Baltanás et al., 2020, *C. iranicum* Molero, Kahrarian & Gaju, 2016, *C. venkataramani* Hazra et al., 2022, *C. udumalpetense* Hazra et al., 2022, *S. guadianicum* (Mendes, 1992), *S. sagartianum* (Molero,

Kahrarian & Gaju, 2016), *S. kermanshanum* (Molero, Kahrarian & Gaju, 2016), etc. We have also observed this pattern in specimens of *Ctenolepisma* attributable to *C. mauritanicum* (Lucas, 1846) deposited in the Berlin Museum (Museum MNHU, entomological collection, code SESAM-Kat.Nr: 64-Z, labelled as *Ctenolepisma transcaspica* Escherich) and to Palaearctic species of *Thermobia* (*T. domestica* (Packard, 1873), *T. aegyptiaca* (Lucas, 1840) and *T. smithi* Raphel et al., 2024) but not in species of synanthropic *Ctenolepisma calvum* (Ritter, 1910), *C. rothschildi* Silvestri, 1907 or in the recently described *C. phantasma* Molero-Baltanás et al., 2025 (confused with *C. calvum*), or in *T. vallaris* Irish, 1988, that have modified subtriangular scales on their femora (data of *T. vallaris*: own observation, previously unpublished). Other species with modified scales on femora and bearing also modified scales on tibiae are those belonging to the group of *Ctenolepisma* with short subtriangular urotergite X, such as the new species *C. erythraeum* sp. nov. This group includes species as *C. lineatum* (Fabricius, 1775) (the type species of the genus *Ctenolepisma*,), *C. algharbicum* Mendes, 1978, *C. almeriense* Molero-Baltanás et al., 2005, *C. nicoletii* (Lucas, 1846), etc., so this suggest that the genera *Ctenolepisma* (as currently understood, i.e., excluding *Sceletolepisma*) and *Thermobia* need a thorough revision and that further studies could conclude that they should be split in several groups at the generic level. This could be against the nomenclatorial stability demanded by some database managers, but a classification that responds to authentic phylogenetic criteria should be given priority.

Online supplementary material

Supplementary Figures with Figs S1 to S40, illustrating additional morphological details.

Acknowledgement

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References

Adel, T. (1984). Sensilleninventar und Sensillenmuster auf den Antennen von Thermobia domestica und Lepisma saccharina (Insecta: Zygentoma). *Braunschweiger Naturkundliche Schriften, 2* (1): 191–217.

Escherich, K. (1905). Das System der Lepismatiden. – Zoologica (Stuttgart), 43: 1–164. https://doi.org/10.5962/bhl.title.7909

Escherich, K. (1910). Lepismatiden von Madagaskar, den Comoren und Ostafrika. In V.A.Voeltzkow (Ed.), Reise in Ostafrika 2. (pp. 535–538). E.E. *Schweizerbartsche Verlagsbuchhandlung, Naegele and Dr. Sproesser, Stuttgart*

Irish, J. (1987). Revision of the genus Ctenolepisma Escherich (Thysanura: Lepismatidae) in southern Africa. *Cimbebasia, Series A 7* (11): 147–207.

Irish, J. (1988). New psammophilous Lepismatidae (Thysanura) from southwestern Africa. *Cimbebasia, 10*: 31–46.

Kaplin, V.G. (1993). On the systematics and phylogeny of the genera Ctenolepisma and Sceletolepisma stat. n. (Thysanura, Lepismatidae). Zoologicheskii Zhurnal, 72 (7): 34–51. [In Russian], English translation in *Entomological Review, 73* (8): 124–140]

Molero-Baltanás, R., Gaju-Ricart, M. & Bach de Roca, C. (2000). On the taxonomic use of the distribution pattern of the antennal asteriform sensilla in Neoasterolepisma and Tricholepisma (Insecta, Zygentoma, Lepismatidae). *Pedobiologia, 44*: 248–256. https://doi.org/10.1078/S0031-4056(04)70045-1

Molero Baltanás, R., Gaju Ricart, M. & Bach de Roca, C. (2012). New data for a revision of the genus Ctenolepisma (Zygentoma: Lepismatidae): redescription of Ctenolepisma lineata and new status for Ctenolepisma nicoletii. *Annales de la Société entomologique de France, 48* (1–2): 66 80. https://doi.org/10.1080/00379271.2012.10697753

Molero-Baltanás, R. Gaju Ricart, M. & Smith, G.B. (2024a). New insights in the taxonomy of Lepismatidae (Insecta, Zygentoma) with an updated key to genera and future challenges. *European Journal of Taxonomy, 943*: 80–126.

Molero-Baltanás, R., Mitchell, A. Gaju-Ricart, M. & Robla, J. (2024b). Worldwide revision of synanthropic silverfish (Insecta: Zygentoma: Lepismatidae) combining morphological and molecular data. *Journal of Insect Science, (2024) 24*(3): 1; ieae045 https://doi.org/10.1093/jisesa/ieae045

Smith, G.B. (2016). Revision of the silverfish genus Anisolepisma (Zygentoma: Lepismatidae: Acrotelsatinae). *Records of the Australian Museum, 68* (6): 269–312. https://doi.org/10.3853/j.2201-4349.68.2016.1662

Ubero-Pascal, N., Fortuño, J.M. & Puig, M.A. (2005). New application for air-drying techniques for studying Ephemeroptera and Plecoptera eggs by Scanning Electron Microscopy. *Microscopy Research and Technique, 68*: 264–271. https://doi.org/10.1002/jemt.20248