# Revision of the Genus *Anisolepisma* (Zygentoma: Lepismatidae: Acrotelsatinae)

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ABSTRACT. The morphology of the enigmatic silverfish genus *Anisolepisma* Paclt is clarified with a redescription of the type species and the description of three new species. The genus is placed within the subfamily Acrotelsatinae and its relevance to the phylogeny and zoogeography of the Lepismatidae discussed. *Paracrotelsa* Paclt is also placed within the Acrotelsatinae.

KEYWORDS. Thysanura; taxonomy; new species; redescription; Paracrotelsa

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Silvestri (1908) described the silverfish Heterolepisma hartmeyeri from a single female specimen collected by the 1905 Hamburg Museum Expedition to south-western Australia. He reluctantly placed the species in the genus Heterolepisma Escherich, 1905 probably because of the smooth macrochaetae and parabolic urotergite X, noting that the species differed from others in the genus by the unusual form of the thoracic sterna. His illustration of the metathoracic sternum showed it as a medial cordiform plate posteriorly fringed with setae, flanked by two small oval sclerites whereas the sternal plates of all other Heterolepisma species are posteriorly free, partially covering the coxae. Silvestri noted the species also possessed a relatively long scape and unique urosternal chaetotaxy (2+1+2 combs instead of 1+1). He illustrated but did not comment on the unique arrangement of papillae on the ultimate article of the labial palp (2+2 in a diamond arrangement). Stach (1933) compared the species of the genus Heterolepisma but expressly excluded H. hartmeyeri

due to these differences. He declined to create a new genus for the species, believing this should be left to the original author. Eventually Paclt (1967), in his review of the Lepismatidae, created the necessary new genus Anisolepisma with a short diagnosis in French, reproducing Silvestri's original illustration of the metathoracic sternum, apparently without examination of the type specimen. Mendes (1982), in his unpublished thesis, repeatedly comments on the uncertainty surrounding this species, its unusual characters and the inadequacy of the original description to answer fundamental questions regarding its placement. Irish (1990) makes similar remarks in his unpublished thesis, listing Anisolepisma as one of the poorly known, monotypic genera in need of revision. Mendes (1991), in his review of the phylogeny of the Lepismatidae, expressly excluded Anisolepisma (as well as Paracrotelsa Paclt, 1967, Panlepisma Silvestri, 1940, Apteryskenoma s.str. Paclt, 1967) from his analysis due to the paucity of adequate detail.



Further Australian material belonging to this genus has since been collected or found within museum collections and it was possible to borrow the holotype of *Heterolepisma hartmeyeri* allowing the genus to be redefined including the description of three new species This paper will redescribe the genus *Anisolepisma*, placing it within the Acrotelsatinae Mendes 1991, a subfamily previously represented in Australia only by the introduced *Acrotelsa collaris* (Fabricius, 1793) (Watson & Li, 1967). It also places the genus *Paracrotelsa* Paclt, 1967 within the Acrotelsatinae.

In most cases, only small numbers of each species have been collected so it is difficult to be certain of the degree of intraspecific variability, especially between adult and immature stages. The generally inadequate collection of silverfish in Australia and the widespread occurrence of this genus (see map Fig. 1), suggests more species exist than have so far been found.

# Materials and methods

Most specimens were collected by the author. These specimens were photographed in the field using a Ricoh CX2 digital camera before being placed into 75% ethanol. Locality coordinates collected were taken using a hand held Garmin eTrex®10 GPS, map datum WGS84. A leg was later removed from some specimens, placed into 100% ethanol and stored at 4°C, should DNA sequencing become available. Pigment pattern was recorded and specimens measured and prepared using the methods outlined in Smith (2013), with the exception of the holotype of Heterolepisma hartmeyeri, which was measured on the prepared slides. The specimen used for scanning electron microscopy was put through an ethanol dehydration series then critical point dried using a Leica EMCPD300. It was mounted on a pin and gold sputter-coated using an Emitech K550 Gold Sputter-coater and imaged using a Zeiss EVO LS15 SEM with a Robinson backscatter detector.

Roman numerals are used to indicate abdominal segment number. The following abbreviations are also used: AMS, Australian Museum, Sydney; *asl*, above sea level (in metres); H+B, head and body length (in millimetres); HW, head width (in millimetres): *IICT*. Instituto de Investigação Científica Tropical, Jardim Botânico Tropical/Zoologia, Lisbon, Portugal (previously referred to as CZL); *L/W*, length to width (ratio); MUSA, Museo di Entomologia "Filippo Silvestri", Università degli Studi di Napoli Federico II, Portici, Italy (a unique centre within the museums of the Dipartimento di Agraria [previously the Instituto di Entomologia Agraria, Portici-IEA]); NSW, New South Wales; NT, Northern Territory; NTM, Museums and Art Galleries of the Northern Territory, Darwin, Australia; PI, PII, PIII, legs of pro-, meso- and metathorax respectively; OLD, Queensland; OM, Queensland Museum, Brisbane, Australia; SA, South Australia; SAMA, South Australian Museum, Adelaide, Australia; SEM, scanning electron micrograph; VIC, Victoria; WA, Western Australia; WAM, Western Australian Museum; ZMB, Leibniz Institüt für Evolutions- und Biodiversitätsforschung, Museum für Naturkunde, Berlin, Germany.

All illustrations are of the holotype except where indicated by a specimen number in brackets in the key to the illustration. The term *macrochaetae* refers to the larger stronger bristles, setae to smaller thinner bristles (usually simple), setulae to the very small, usually straight setae and *cilia* to the curly thin hairs, often associated with the combs, setal collar or notal margins. Antennal segmentation uses the terminology introduced in Smith (2015b) i.e. annulus for the smallest individual unit. *interval* for the collection of annuli forming a repeated pattern where the most distal annulus usually carries trichobothria and is referred to as a T-annulus. Nomenclature of the antennal sensillae follows that of Mendes (1986a) and the types of basiconic sensillae follow the designation of Adel (1984). Numbering of the macrochaetae and trichobothrialike hairs of the nota follow the system of Molero-Baltanás *et al.* (2010) (e.g.,  $m_0$ ,  $m_{-1}$ ,  $m_{-2}$  or  $tr_0$ ,  $tr_{-1}$ , etc) where  $N_0$  is the most posterior submarginal macrochaeta or trichobothrium, N<sub>-1</sub>, N<sub>-2</sub> etc refers to corresponding chaetotaxy sequentially in the anterior direction. Note that there are usually one or two large posteriorly-directed macrochaetae in the posterolateral corner of each notum but these macrochaetae are located on the margin and are not included as numbered submarginal macrochaetae which are somewhat upwardly-directed.

Holotypes and some paratypes of new species are lodged with the museum of the state within which they were collected. Some paratypes are held in the AMS and IICT as indicated in the material examined. One slide of the holotype of *Heterolepisma hartmeveri* was borrowed from and returned to MUSA. It was in poor condition and held one antenna, one labial and one maxillary palp, half of the metanotum, a leg (PIII), urotergite VI and urosternite VI. The remainder of this specimen was held in alcohol at ZMB and, with permission from Dr J. Deckert, was dissected and mounted on two slides and returned to this museum. Other specimens were borrowed from the AMS and QM. Where museum specimen numbers have not been allocated, the specimens have been given a number (e.g., gbs003081) which refers to the unique specimen number allocated in the author's specimen data base.

Climate data summarized in Table 5 was obtained from the Australian Bureau of Meteorology website (BOM, 2016).

# **Systematics**

Family Lepismatidae Latreille, 1802 Subfamily Acrotelsatinae Mendes, 1991

# Paracrotelsa Paclt, 1967

This genus was erected by Paclt for the species Acrotelsa niimurai Uchida, 1949 from Irian Java (Indonesia) without explanation. Paclt's diagnostic characters did not match the illustrations of Uchida in respect to the thoracic sternites. Mendes (1991) excluded this genus from his analysis of the subfamily arrangement due to the lack of certain critical information in the original description but considered it probably close to Acrotelsa. Since then Kaplin (1992) has defined Desertinoma and Mendes (2004) defined Primacrotelsa and the new material allows a better understanding of Anisolepisma. In contrast to Paclt's diagnosis, the illustrations in Uchida (1949) clearly show that the thoracic sterna of Paracrotelsa have the same form as the aforementioned genera. There are also 2+2 combs on some urosternites (III-VI). This arrangement places Paracrotelsa within the Acrotelsatinae even though information on other characters such as the paramera and antennal sensillae are missing.

## Anisolepisma Paclt, 1967

Heterolepisma Escherich, 1905: 51 pro parte. Anisolepisma Paclt, 1967: 27. Type species: Heterolepisma hartmeyeri Silvestri, 1908 (original designation; grammatically neuter).

Diagnosis. Macrochaetae smooth. Cephalic chaetotaxy with well-developed anterior bushes on frons and U-shaped row behind the antennae, clypeus proximally with 1+1 short combs as well as a transverse row of setae, labrum with simple setae. Pedicel long with dark scales; distal intervals of antennae with basiconic sensillae and trichobothria. Ultimate article of labial palp with four papillae of the aufgelöst type arranged in a diamond configuration. Pronotum with 1+1 isolated sub-anterior setal tufts, lateral margins with four to six submarginal macrochaetae and four or five long trichobothria or trichobothria-like hairs (see final discussion), posterior margin glabrous. Meso- and metanota also with three to seven submarginal macrochaetae and three or four long trichobothria-like hairs, posterior margins with 1+1 macrochaetae or 1+1 trichobothria-like setae. Thoracic sternites reduced, not free and largely covered by coxae of legs. Pretarsus complete, empodium smooth. Urotergite I with 2+2 small combs, urotergites II–VII with 3+3 small combs, urotergite VIII with 3+3 or 2+2 small combs, urotergite IX glabrous or with infralateral setae. Urotergite X rounded with small 1+1 apical combs. Urosternite I with small medial comb, urosternite II with 1+1 or 1+1+1 small combs, urosternites III–VIII with 2+2 or 2+1+2 small combs. Styli present in one pair in both sexes. Ovipositor short, with fine setae only. Parameres long and thin, not segmented, lacking obvious glandular region.



Figures 2–5. Anisolepisma spp. appearance when live (2) A. aquilonaridum n. sp. ex Bladensburg National Park, Qld; (3) A. aquilonaridum ex Cobar, NSW; (4) A. subpectinum n. sp. Mount Chambers Gorge, SA; (5) A. pigmentum n. sp. Ormiston, West MacDonnell Ranges National Park, NT.

## Description

Photographs of three species and SEM's of *Anisolepisma aquilonaridum* n. sp. from Bladensburg are used to illustrate the description of the genus but they are not of the type species.

Appearance and body size: Small to medium sized silverfish (7–11 mm), elongate, not strongly tapered. Generally with evenly dark or mottled scales above and light lateral margins to the nota (Figs 2–5). Dark scales on pedicel often conspicuous on live specimens. Antennae and terminal filaments shorter than H+B.

Pigmentation: Present, faint to quite dark.

*Macrochaetae*: Smooth not pectinate, with bifurcated apices (Fig. 6), hyaline or yellow-brown.

*Scales*: Multiradiate and of variable shape, the rays not or only slightly surpassing the distal margin of the scale (Fig. 7), located on frons and clypeus, often all articles of the mouthparts, the body, most articles of the legs, the styli, as well as the scape and pedicel of the antennae. Absent from the terminal filaments.

*Head*: Exposed, eyes small, dark composed of about 12 or 13 ommatidia; head chaetotaxy (Figs 8, 9) consisting of 1+1 large subrectangular bushes of about 40–80 evenly spaced macrochaetae located anteriorly on distinct rounded bulges of the frons above the suture with the clypeus, lacking macrochaetae along lateral margins above antennae, posterior to each antenna is a roughly U-shaped line of macrochaetae with the base of the U along the margin of the frons and a short line sub-perpendicular to the margin on each side of the head just behind the base of the antenna ending with a very long thin trichobothria-like seta, the other longer arm of the U extends above the eye; clypeus with line of simple setae well behind the anterior margin and 1+1 short combs of one to five macrochaetae just below the suture with the frons, with a transverse band of scales between the line of setae and the short combs, extending up between the 1+1 combs of macrochaetae onto the frons; labrum with numerous long, simple setae in two transverse bands (Fig. 9). -Pedicel comparatively long relative to scape in both sexes (2/3-1) (Fig. 9). Most distal preserved antennal annuli without specialized sensillae, but with several basiconic sensillae (types B & C) (Figs 10, 11). -Mandibles with strong incisor region, molar region different on either side of head with one mandible having a distinct comb along the full length of the molar area and the other having no comb, or at most only a few "lamellae" and usually also, at the posterior end of the molar region, a short laterally directed triangular process (possibly composed of "lamellae" fused together), as well as a group of several short, apically bifurcate macrochaetae at the posterior end of the molar region and a strong bush of macrochaetae on the outer side of the mandible. --Maxillae with galea longer than lacinia, lacinia with two strong apical teeth and a similar subapical tooth, several lamellate processes including two rounded or truncated lamellae at the level of the apical teeth, and a row of several simple setae; apical article of maxillary palp usually with a curved basiconic sensilla (type C) (not always visible depending on the orientation of the palp) and often some basiconic sensillae (type B) (Fig. 12). —Labium short and broad, prementum with rows of stout setae at the base of the glossae and paraglossae, postmentum with a short medial row of about three to seven stout setae (or more likely two shorter



Figures 6–7. Anisolepisma aquilonaridum n. sp. ex Bladensburg Q (6) macrochaetae, anterior bush of frons; (7) scales of urotergite.

rows each of one to four setae that almost join in the middle) and one to two lateral setae on each side near the margins; labial palp short, apical article subrectangular to subovate, longer than wide, with four papillae of the "aufgelöst" type arranged in a diamond configuration in the centre of the article rather than apically, with one or two short curved basiconic sensillae (type C), one on outer margin at level of diamond the other proximal to the diamond and remote from the margin, without other specialized sensillae (Fig. 13). *Thorax*: Pronotum (Fig. 14) lacking setal collar, with 1+1 small isolated tufts of strong erect macrochaetae radiating from anterior patches that are surrounded by scales and remote from the anterior margin near or mediad to the sides of the head; each side with three to six large submarginal suberect macrochaetae and similar subposterior-directed macrochaetae in the posterolateral corners on the margins, as well as many short thick setae, margins also with four or five medium length to extremely long trichobothria or



Figures 8–9. *Anisolepisma aquilonaridum* n. sp. ex Bladensburg Q(8) head and anterior margin of pronotum, showing pronotal isolated anterior tuft (pb); (9) head, and base of antennae, anterior view.

trichobothria-like setae (Figs 14–16). Posterior margin glabrous. —Meso (Fig. 17) and metanota with four to six strong submarginal macrochaetae and shorter stout setae spaced along margins plus three or four trichobothria (or trichobothria-like hairs), the most anterior about half way along the margin laterad and slightly forward of a large submarginal macrochaetae, the second about <sup>3</sup>/<sub>4</sub> way along

the margin, laterad of the next submarginal macrochaeta, the third insertion resembles that of a submarginal macrochaeta and may contain either a long trichobothria-like seta or a macrochaetae, the last  $(tr_0)$  is further from the margin and slightly more posterior. Posterior margins with 1+1 single long thin macrochaetae or single long trichobothria-like setae.

Prothorax with very well-developed presternum (Figs 18,



Figures 10–11. Anisolepisma aquilonaridum n. sp. ex Bladensburg  $\Im$  (10) T-annulus of distal region of antenna showing trichobothria (tr) and basiconic sensillae type B (bsB); (11) mid annulus of interval showing basiconic sensillae type B (bsB) and C (bsC). Note also pattern of fine hair-like cuticular "setae".

19). Thoracic sterna not free and largely covered by the coxae. Prothoracic sternum distinctly visible as a raised triangular area anteriorly between the coxae of PI with a central tuft of radiating, erect, apically bifurcate macrochaetae; meso- and metathoracic sterna with raised region medially with the anterior lateral edges of this raised region extended slightly outwards resulting in a flat cordiform surface which permits the coxae insert a little under the edges; lateral margins of raised cordiform region with rows of simple and (at posterior end) apically-bifurcate macrochaetae in distal two thirds, these raised regions are largely concealed by the coxae of the legs of the preceding segment.



Figures 12–13. Anisolepisma aquilonaridum n. sp. ex Bladensburg Q (12) apical article of maxillary palp showing basiconic sensillae (*bsB* and *bsC*); (13) last article of labial palp showing four aufgelöst papillae (*lpp*) and basiconic sensillae C (*bsC*).

Legs stout with strong macrochaetae on femora and tibia (Fig. 18); PI with some setae on the precoxa. —Coxa of PI with a comb of macrochaetae near external "shoulder" and sometimes with one or two shorter combs of setae distal to this "shoulder" comb, all coxae with a single marginal row of strong macrochaetae along most of or parallel to the external lateral margins, all coxae with a comb of two setae on or near the inner margin about  $\frac{1}{2}$ — $\frac{3}{4}$  distally. —Trochanter with

narrow portion articulating with coxa with abrupt change in width along the inner margin (this abrupt change often appears to lead to a buckling of the outer margin in slide mounted specimens giving the appearance of a pseudosegmented trochanter). —Femur with distal group of strong spines as well as several strong and long spines along the posterior margin. Tibia with two pairs of strong spines dorsally and several spines on or near the ventral margin; tibial spur with setae. —Tarsus four-segmented although segmentation may not be distinct, stronger setae ventrally and distally on each article except last. —Pretarsus of two simple lateral claws and a smooth medial empodial claw (Fig. 20).

*Abdomen*: Posterior margins of urotergite I with 2+2 small combs (lateral and submedial, lacking sublateral). Urotergites II–VII with 3+3 small combs. Urotergite VIII with 3+3 or 2+2 small combs (lacking sublateral). Urotergite IX glabrous or with infralateral setae on each side. — Urotergite X rounded with marginal setae and small 1+1 combs submarginally in posterolateral corners.

Urosternite I with small medial comb (Fig. 20). Urosternite II with 1+1 or 1+1+1 small combs. Urosternites III–VII (VIII in  $\bigcirc$ ) with 2+2 or 2+1+2 small combs. Urosternite VIII in female divided into separate coxites each with two combs. Styli (Fig. 21) only present in one pair in both sexes (IX only) with several long strong setae ventrally along their length similar to two larger setae at apex and a long macrochaeta on face of coxite IX internal to each stylus.

Ovipositor (Fig. 22) of primary type (without modified setae or cuticular processes), thin and tapered or expanded distally, pseudoarticulated but difficult to discern, with short to very long and always very thin setae. Coxites IX of  $\bigcirc$  with longer but not very long inner processes; coxites IX of  $\bigcirc$  with long thin setae on inner (dorsal) face. —Penis typical for family. —Parameres almost as long as the inner process, with long thin setae on inner and mediad surfaces but often also with stronger setae subapically on the outer ventral surface, lacking obvious glandular region.

Anal region with well sclerotized epiproct and paraprocts. Cerci and median dorsal appendage with a few shorter basal divisions which become significantly longer from about the fifth division with increasing numbers of transverse rows of setae, those at the most distal end of each division much more robust than the rest, divisions with numerous short and long straight trichobothria (or trichobothrial-like setae) as well as long thin hairs with distinctly curled/hooked ends.

# Anisolepisma hartmeyeri (Silvestri, 1908)

#### Figs 25–73

Heterolepisma hartmeyeri Silvestri, 1908: 51. Anisolepisma hartmeyeri (Silvestri).—Paclt, 1967: 27.

**Type material**. Holotype  $\bigcirc$  (parts of specimen) (gbs001866 MUSA) WA: Northampton, approximately 20.80°S 115.44°E, Michaelsen-Hartmeyer Expedition 1905, slide badly affected by fungal growth, with one antenna, a maxillary palp, a labial palp, right half of metanotum, urotergite VI, one PIII; rest of specimen (gbs001867 ZMB) (originally in alcohol now on two slides).

*Other material examined*: ♀ (HW 0.88) (AMS K260970, K260971 on two slides) WA: 35 km N. of Kellerberrin, McQueens Rd, 31°22'56.60"S 117°39'27.31"E, mid April, 1996, A. Noack, hand collected from log.

**Diagnosis**. Distinguished from other species of the genus by the presence of 3+3 combs on urotergite VIII, three trichobothria-like setae on each side of the the meso and metanota, a glabrous urotergite IX and the presence of medial combs on urosternites I–VII in  $\bigcirc$  or I–VIII in  $\bigcirc$ .

### Description

Appearance: Body elongate with thorax only slightly wider than abdominal segment I, the following abdominal segments remain about the same width up until the fifth segment after which they slowly taper posteriorly to about  $\frac{2}{3}$  the width of the thorax. Antennae incomplete, >0.4 H+B in Kellerberrin specimen. Scale pattern when live unknown. Silvestri described the species as reddish above and silvery below with reddish antennae and terminal filaments, however the Kellerberrin specimen in alcohol is brown dorsally and creamy grey below with brown-pigmented antennae and terminal filaments.

*Body size*: H+B length about 6.6 mm, thorax width 1.8 mm; antennae 3.5 mm (about  $\frac{1}{2}$  H+B) and terminal filaments >2.3 mm (>35% H+B) (>40% in Kellerberrin specimen).

*Pigment*: Cuticular pigment not easy to distinguish in holotype (possibly due to the time the type specimen has been stored in alcohol (>100 years); some areas of legs and articles of palps appear darker possibly due to pigment. Pigment in Kellerberrin specimen also not strong, (16 years in alcohol before mounting) but head with some pigmentation around eyes; antennae evenly pigmented, becoming darker distally, maxillary palp pigmented in last four articles with more in second article, becoming lighter distally, laterally on pronotum especially anteriorly, laterally on meso and meta nota, legs evenly light brown with no obvious pigmentation, urotergite X very slightly darker around margins, styli IX slightly pigmented and ovipositor comparatively dark.

*Scales*: Variable in size and shape, rounded or ovoid, with numerous parallel rays (Fig. 23), that do not extend beyond the margin. Brown or hyaline.

*Macrochaetae*: Smooth, apically bifid (Fig. 24). Other setae with minute delicate apical bifurcations or simple. Hyaline or yellow/brown.

*Head*: Wider than long (Fig. 25) with scales above; chaetotaxy well developed, frons with isolated 1+1 anterior groups of about 70-80 strong, apically bifurcate macrochaetae each posteriorly with three small cilia. Lacking macrochaetae along lateral margins directly above base of antennae. A U-shaped line commences behind the antenna with a short line of five to seven macrochaetae subperpendicular to the margin which terminates in a long thin trichobothria-like seta, the line of setae continues back along the margin of the head before turning up and back over the eves, terminating in two small cilia. Clypeus with 1+1 combs of three to four strong macrochaetae near frons and a line of simple setae well behind the anterior margin, of which two setae are more than twice the length of the other, and a band of scales between this line and the combs. Labrum with numerous simple setae in two irregular transverse rows. Eyes dark, not prominent, composed of about 12 ommatidia. -Antennae incomplete, scape (Fig. 26) slightly longer than wide, pedicel not much shorter than scape (about  $\frac{3}{4}$ ). Each annulus/interval from about the fifth subdivided into two very similar annuli with a trichobothrium subapically on the most distal annulus, the annuli within an interval becoming ever more obvious and longer and by about the ninth subdivide again; each annulus in distal portion of antenna (Fig. 27) with basiconic sensillae (types B and C) distally. —Mandibles (Figs 28–30) with well-developed incisor region and molar regions, the latter on one side with a comb of raised spinelike lamellae, a group of about four to six apically bifurcate macrochaetae on the margin proximal to the molar region

and a bush 50+ setae and macrochaetae externally. ---Maxilla (Figs 31–33) with galea longer than lacinia (however the galea on one of the two maxillae of the Kellerberrin specimen is about equal in length to its lacinia, probably an artefact of mounting), galea (Fig. 32) with small apical lobe, lacinia with two strong apical teeth and a similar subapical tooth as well as two subapical truncated hyaline process, several lamellate processes and a row of four simple setae. Palp of medium length, apical article about four times longer than wide and 1.2 times longer than penultimate article, with a large curved basiconic sensilla (type C) (Fig. 33). -Labium (Fig. 34) short and broad, prementum anteriorly immediately behind glossae medially with 2+2 setae and 1+1 rows of about eight strong setae laterally, postmentum with a short medial row of three to four strong setae and 1+1 groups of two setae laterally; palps of holotype short but not well preserved, apical article almost twice as long as wide, subrectangular (Fig. 35), obliquely angled to penultimate article, with four papillae of the "aufgelöst" type arranged in a diamond configuration in the centre of the article and, at least on the Kellerberrin specimen, two curved basiconic sensillae (type C).

Thorax: Slightly wider than head or abdomen, subparallel sides. Pronotum (Fig. 36) without setal collar but with numerous scales that extend forward over the "neck", with 1+1 closed tufts of four to six erect macrochaetae of unequal size and two cilia on the disc behind the anterior margin mediad of the eyes (Figs 37, 38); lateral margins (Fig. 39) with roughly evenly spaced shorter, apically bifurcate setae and some cilia, five widely spaced larger submarginal apically bifurcate macrochaetae ( $m_0-m_{-4}$  in Fig. 39), as well as three to five long trichobothria-like setae (tr<sub>0</sub>-tr<sub>.4</sub> in Fig. 39). The status of two of these trichobothria-like setae is uncertain (tr<sub>-2</sub> and tr<sub>-4</sub>) as only insertion points remain. At the position marked  $tr_2$  (just anterior to macrochaeta  $m_1$ ) on the left side of the holotype there is a small marginal insertion point that appears to be that of a trichobothrium but could be a cilium; this insertion could not be seen on the right side and was absent on both sides of the Kellerberrin specimen, suggesting there is no trichobothrium in this position in A. hartmeyeri but a trichobothrium is distinctly present in the same location in the following species. The insertion point (marked as  $tr_4 m_3$ ) could be that of a thick trichobothria-like seta or a macrochaeta in both the holotype and Kellerberrin specimens (lost in all specimens). Of the definite trichobothria, the most anterior  $(tr_3)$  is found near the middle of the margin just anterior to the large macrochaeta  $(m_{2})$ , the next  $(tr_{1})$  is while the next two  $(tr_{1})$  $tr_0$ ) are closer together near the posterolateral corner,  $tr_1$ being in front of and tr<sub>0</sub> more posterior and mediad of the last macrochaeta  $(m_0)$  which lies closer to the margin than the other submarginal macrochaetae. There is some variability in this marginal chaetotaxy e.g., the submarginal macrochaeta  $m_{2}$  (and its insertion socket) is completely absent on the left side of the Kellerberrin specimen and the trichobothria-like hair just anterior to this macrochaeta is located slightly more anteriorly than on the holotype. Posterior margin glabrous. —Mesonotum and metanotum (Figs 40–46) laterally similar to pronotum except with only three trichobothria-like hairs, one (tr<sub>-2</sub>) located about midway along the margin and very close to macrochaeta  $(m_2)$ , the next  $(tr_1)$  about  $\frac{3}{4}$  the way along the margin laterad of a large submarginal macrochaeta  $(m_1)$  and the last  $(tr_0)$  in the posterolateral corners posterior

to the insertion of  $m_0$  and further from the margin. Posterior margin with 1+1 posterior macrochaetae (Figs 45, 46) each associated with a small marginal seta and one or two cilia.

Presternum of prothorax large, clearly visible extending across the body anterior to the coxae and sternum (Fig. 47). —Prothoracic sternum not free (Fig. 47), partially concealed by coxae, anterior medial region raised into a triangular plateau with tuft of about 15 radiating macrochaetae (21 in Kellerberrin specimen). —Meso- and metasterna (Figs 48, 49) with medial part raised into cordiform section against which or slightly under which the anterior part of the medial edge of the coxae can fit, without a medial tuft of setae and with a few small setulae anteromedially; the more posterior portion of the lateral margins of mesosternum with eight to nine, metasternum with nine to ten marginal setae, the raised section dropping off to merge with a rounded part of the sclerite on each side.

Legs not particularly long (Figs 47, 48, 50); tibia L/W ratio of legs PI 2.3, PII 2.5-2.6, PIII 3.4; tarsi L/W ratio PI 4.5–6.8, PII 5.8–6.2, PIII 6.1–7.5. —Precoxae of prothorax each with two or three setae and some cilia, the more medial seta the largest. -Coxae of all legs with numerous rounded hyaline scales, more noticeable on the margins on slide material, a row of long setae along the external margin and a small comb of two setae on the ventral face about  $\frac{2}{3}-\frac{3}{4}$  distally, remote from the margin on PI but closer to the margin on PII and PIII. Coxa of PI also with external proximal "shoulder" comb of five to six strong macrochaetae (Fig 47) on the ventral surface and a comb of two setae distal to the "shoulder" comb, distal internal apex with several stronger setae covering the articulation with the trochanter. -Trochanter of all legs appearing subdivided into two halves with the more distal part much wider than the narrower part connecting with the coxae, however this is believed to be an artefact as it is not seen in whole specimens (of other species) and only appears on slide material when the leg folds up so that the coxa covers the femur. -Femur with scales more obvious on leading edge, with several strong, robust spines and some quite long but not so thick macrochaetae along posterior margin especially on, and distal to, the distinct lump on this margin; apically with three or four short very robust spines over the articulation with the tibia. -Tibiae all well scaled with some strong and some robust spines along the posterior margin (i.e. one pair near half way, another pair three quarters along and one much longer subdistally) as well as two pairs of strong stout macrochaetae on outer margin and the usual apical spur, the latter having several fine setae near its base (Fig. 52). - Tarsus (Fig. 53) with four articles, the basal article being almost as long as the other three together and the only article clearly distinct from the following articles which are almost completely fused together; tarsus with numerous setae, those on the ventral side, especially subapically on each article being a little stronger than the rest; scales present at least on basal article. —Pretarsus (Fig. 54) with long thick fairly straight outer claws that narrow and curve apically, medial empodial claw smooth and short.

*Abdomen*: Urotergite I (Fig. 55) with lateral and submedial combs of two macrochaetae plus a marginal seta and a cilium at the external end of each comb and, in the case of both sublateral combs of the Kellerberrin specimen, another anteriorly between the insertions. Urotergites II–VIII (Figs 56–59) with 3+3 combs, the lateral combs with two to three,

Segment	Urotergite			Urosternites			
-	Lateral	Sublateral	Submedial	Lateral	Submedial	Medial	
Ι	2		2			2	
II	2-3	2	2		2-3	2	
III	2-3	2	2	2-3	3	2	
IV	3	2	2	3–4	3–4	2	
V	3	2	2	4	3–4	2	
VI	3	2	2	4	4	2	
VII	3	2	2	4	3–4	2	
VIII	3	2	2	3	2-3	<b>—(</b> ?d)	
IX	0					( 0)	

Table 1. Number of macrochaetae per bristlecomb Anisolepisma hartmeyeri (Silvestri).

the sublateral and medial combs each with two macrochaetae. all combs associated with a single long thin marginal seta and one to three small cilia, one located at the exterior end of each comb and another anteriorly between the more medial or both macrochaetae insertions. All urotergal macrochaetae lost on the holotype, the one present in the outer combs of urotergite VII in the Kellerberrin specimen (Fig. 58) is of the typical apically bifurcated form and about one third the length of the respective tergite, the marginal setae are about half as long as this macrochaeta, the marginal setae on the holotype are noticeably longer than the same on the Kellerberrin specimen. Urotergite IX glabrous. - Urotergite X (Fig. 60) parabolic, about  $1\frac{1}{2}-1\frac{3}{4}$  times as long as broad at base with long and shorter setae on the margins, with 1+1 combs in posterolateral corners each of two stronger macrochaetae and two cilia (Fig. 61).

Urosternite I (Fig. 62) with medial comb of two macrochaetae plus one small seta on margin between them (Fig. 63), Kellerberrin specimen with only two small setae. Urosternite II (Fig. 64) with 1+1+1 combs, all of two macrochaetae and without marginal setae or cilia, one submedial comb on Kellerberrin specimen with a small third macrochaeta on one of the lateral combs as well as a marginal seta on both lateral combs (Fig. 65). Urosternites III-VII (Fig. 66) with 2+1+2 combs, the lateral combs with two to four macrochaetae and sometimes a marginal seta or cilia, the submedial with two to four macrochaetae and sometimes a marginal seta and the medial combs with two macrochaetae only. Coxites VIII separated into two separate coxites in female each with two combs, the lateral comb of three macrochaetae, one marginal seta and a cilium on the outer end of the comb, the sublateral comb with two or three macrochaetae and one to two submarginal setae and, on one side only, a cilium on the outer end of the comb; the Kellerberrin specimen has one or two marginal setae on outer combs and two or three on inner combs as well as a cilium. All macrochaetae lost on urosternites of holotype, those still present on Kellerberrin specimen were one quarter to one half the length of the respective urosternite. —Styli (Fig. 67) present as one pair (IX only).

Coxite IX in  $\bigcirc$  (Fig. 67) with a single strong macrochaeta on each side at the inner base of the stylus, the internal process narrow, acute apically, about 2.6 times longer than the external process (3.6 in Kellerberrin) and 1.6 times as long as broad at its base (Kellerberrin 2.6 times longer than wide at base), reaching to about  $\frac{2}{3}$  (Kellerberrin  $\frac{3}{4}$ ) the length of the stylus, with several strong setae along both the external and internal margins; external process of coxite IX short, triangular, both processes with a thumb-like process at the base on the margin adjacent to the stylus, external margin of outer process with a few strong setae subapically and along external margin.

Ovipositor of primary type, slightly shorter than internal processes in type specimen, with very inconspicuous secondary segmentation; slightly longer than the internal process in the Kellerberrin specimen, almost reaching to apex of stylus (Fig. 68); more apical divisions of both anterior and posterior valves with long thin setae.

Epiproct and paraprocts strongly pigmented/sclerotized (Fig. 69) the former developed into a strong flat forked process over the base of the median dorsal appendage, the latter with a subcylindrical terminal process and a more distal subtriangular mediad process. -Cerci (Figs 70, 71) incomplete in both specimens (>0.35 H+B in holotype, >0.4 H+B in Kellerberrin specimen), divisions from sixth or seventh longer than wide, forming divisions of two annuli by eighth and further subdividing by the tenth or eleventh; trichobothria on inner side of each division, with some long thin hooked hairs of similar thickness to the trichobothria. as well as smaller and larger setae and macrochaetae. Median dorsal appendage (Figs 72, 73) also incomplete (>0.4 H+B) with long basal division followed by shorter division, becoming longer than wide by about the fourth divisions and subdivided by sixth and further subdivided by eighth or ninth, with numerous trichobothria as well as long thin hooked hairs and smaller and larger setae and macrochaetae. Male unknown.

**Biology**. The Kellerberrin specimen was hand collected from a log.

# Anisolepisma aquilonaridum n. sp.

## Figs 2-3, 6-18, 20-22, 74-113, 191

**Type material**. Holotype  $\bigcirc$  (HW 0.95) (QM T234162 on two slides) QLD: Bladensburg National Park (near Winton), 22.54617°S 143.05459°E 232 m asl, 10.iv.2011, Graeme Smith. Paratypes:  $1 \diamondsuit$  (HW 0.93) (QM T234163 on two slides), same data as holotype;  $1 \oiint$  (HW 0.75 mm) (AMS K377712 in 80% ethanol), same data as holotype; 1 juvenile  $\bigcirc$  (HW 0.88) (AMS K377713 in 80% ethanol), same data as holotype; 1 juvenile  $\bigcirc$  (HW 0.70) (authors collection in 100% alcohol), same locality as holotype, 8.viii.2013, Graeme and Louise Smith;  $1 \clubsuit$  (HW 1.00) (used for SEM), same data as previous;  $1 \oiint$  (HW 1.05) (AMS K377714 in 80% alcohol), Bladensburg National Park, Skull Hole 22.55789°S 143.00044°E 204 m asl, 8.viii.2013,



Figures 14–15. Anisolepisma aquilonaridum n. sp. ex Bladensburg  $\bigcirc$  (14) left side of pronotum from above showing the left isolated anterior pronotal tuft (*pb*) and the long, thin trichobothria-like setae (*tls*) and a submarginal macrochaeta (*sm*); (15) idem, from side, showing long, thin trichobothria-like setae (*tls*) and a submarginal macrochaeta (*sm*) as well as the comb in the anterior lateral corner of the coxa of PI (*Plcc*).

Other material examined: QLD:  $1^{\circ}_{\circ}$  (HW 1.0) (AMS K261122, K261123 on two slides), c. 25 km N. Augathella, 25.58235°S 146.60162°E 396 m asl, 14.viii.2013, Graeme Smith. WA:  $1^{\circ}_{\circ}$  (HW 0.96) (WAM E89191 on two slides) North West Cape, 6 km south Exmouth 22.000°S 114.1167°E 10 m asl, 27.ix.2008, Graeme Smith;  $1^{\circ}_{\circ}$  (HW 0.96) (IICT in 80% ethanol), same data as previous;  $1^{\circ}_{\circ}$  (HW 0.79) same data as previous (WAM E89192 on two

slides); 1 juvenile  $\bigcirc$  (HW 0.70) (AMS K377715 in 80% ethanol) North West Cape, Shot Hole Canyon Road, 1st major creek crossing, 22.05°S 114.083°E 20 m asl, 27.ix.2008, Graeme Smith; 1 juvenile  $\bigcirc$  (HW 0.74) (IICT in 80% ethanol), same data as previous;  $1\bigcirc$  (HW 0.83) (WAM E89193 on three slides), Barrow Island, 20.79761°S 115.4408°E, 15.iii.2006, S. Callan, R. Graham (three slides), GP7 pitfall trap. NSW:  $1\bigcirc$  (HW 1.13) (AMS K260968



Figures 16–17. Anisolepisma aquilonaridum n. sp. ex Bladensburg  $\Im$  (16) pronotum, detail of insertions of trichobothria-like seta (*tls*) and submarginal macrochaetae (*sm*); (17) posterior corner of mesonotum showing long, thin trichobothria-like setae ( $tr_0$ ,  $tr_1$  and  $tr_2$ ) and the insertion of a submarginal macrochaeta ( $m_0$ ).

K260969 on two slides), east of Narromine ( $32.24117^{\circ}S$  148.36373°E 250 m asl), 22.v.2012, Graeme Smith); 1 $\bigcirc$  (HW 0.98) (AMS K377716 in 80% ethanol), same data as previous; 1 $\bigcirc$  (HW 1.08) (AMS K261044 K261045 on two slides), east of Cobar (31.51990°S 146.02925°E 246 m asl) 22.v.2012, Graeme Smith; 1 juvenile  $\bigcirc$  (HW 0.78) (AMS K261042 K261043 on two slides), 74 km west of Wilcannia, Spring Creek rest area (31.72279°S 142.68649°E 199 m asl), 21.v.2012, Graeme Smith.

**Diagnosis**. Distinguished from other species of the genus by the presence of only 2+2 combs on urotergite VIII, the presence of five trichobothria-like hairs on each side of the pronotum and four on each side of the meso and metanota, the glabrous urotergite IX and the presence of medial combs on urosternites I–VII (in  $\mathcal{Q}$ ) or I–VIII (in  $\mathcal{J}$ ).



Figure 18. Anisolepisma aquilonaridum n. sp. ex Bladensburg Q (18) head, presternum (ps), prothoracic sternum and tuft (pst), mesothoracic sternum (mss) and legs. Note that the meso and metathoracic sterna are almost completely covered by the legs and scales and only a small part of the mesothoracic sternum is visible.



Figure 19. Anisolepisma pigmentum n. sp. (19) light microscope image showing pronotal tuft (pb), wide presternum (ps), the prothoracic sternal tuft (pst), mesosternum (mss) and metasternum (mts).



Figures 20–21. Anisolepisma aquilonaridum n. sp. ex Bladensburg  $\bigcirc$  (20) tarsus and pretarsus of PIII, and medial comb of urosternite I; (21) stylus IX and base of cercus.

## Description

This description is based on material from the type locality only. Where differences were noted in specimens from other localities, the differences are shown in square brackets.

*Appearance*: Small to medium silverfish with elongate body (Fig. 2) with thorax only slightly wider than abdominal segment I, following abdominal segments remain about

the same width up until about the fifth abdominal segment after which they slowly taper to about  $\frac{2}{3}$  times the width of the thorax in segment IX. Antennae and terminal filaments incomplete but probably considerably shorter than H+B. Scale pattern in live specimens (Figs 2, 3) dark mottled silver with white lateral margins to the nota, dark scales on pedicel and legs and with antennae, terminal filaments and tarsi pinkish brown.



Figure 22. Anisolepisma aquilonaridum n. sp. ex Bladensburg  $\stackrel{\bigcirc}{\rightarrow}$  (22) ovipositor.

*Body size*: H+B length up to about 8.5 mm; HW 1.05 mm [Narromine AMS K260968 1.13]; thorax: length up to 2.55 mm (0.28–0.35 times H+B [Barrow WAM E89193 0.27 H+B]); width up to 1.65 mm [Narromine AMS K260968 1.70]; antennae and terminal filaments incomplete in all specimens from type locality, longest remaining portion of antenna in types >0.63 times H+B (Narromine AMS K377716 complete or almost complete at 0.47), of cerci >0.85 times H+B [Narromine AMS K260969 and K377716 complete or almost complete at 0.44–0.48] and median dorsal appendage >0.54 times H+B [Narromine AMS K260969 complete or almost complete at 0.48].

Pigment: Generally brown or yellowish brown; the pigment appears to fade over time (a few years) in weakly pigmented specimens on slides [specimens from North West Cape and Barrow Island were much less pigmented (almost absent in some specimens) than those from Bladensburg while those from Augathella and NSW showed more pigment but the basic distribution patterns were similar]. Some pigment present around the eyes, antennae with light even pigmentation becoming more pigmented distally, narrow lighter region around joints between articles; ultimate article of maxillary palp with little pigment, penultimate and third articles more strongly pigmented and less so on the second article where it is strongest distally, basal article lacking pigment; labial palp pigmented lightly on ultimate and penultimate articles; nota with light pigment along lateral margins strongest anteriorly; coxae with light pigment only along outer margin; trochanter with little pigment, only at outer distal end; femora with light pigment over much of surface but denser along posterior margin especially on the bulging area and more distally; tibia with some pigment over much of surface but slightly darker distally, tarsal articles with some pigment, more so on basal articles; styli pigmented, urosternites IX pigmented, more so around the stylus insertion and along the outer margin of the inner

process; terminal appendages quite darkly pigmented however terminal filaments appear almost pinkish white in live specimens; ovipositor with overall light brown pigment.

*Scales*: Quite variable in shape, dorsal scales on alcohol preserved specimens appear dark brown, ventral scales clear, those on legs, pedicel, scape, basal four articles of maxillary palp, penultimate article of labial palp and clypeus brown or clear. Scales on slide material appear dark brown/black or clear, rounded or ovoid, with numerous parallel rays that do not or only minutely extend beyond the margin of the scale (Figs 7, 74, 75).

*Macrochaetae*: Bifid apically or simple, hyaline or yellow/ brown (Figs 6, 76).

Head: Wider than long, with scales above; chaetotaxy well developed (Figs 8, 9 and 77), frons with isolated 1+1 anterior groups of about 70-80 strong, apically bifurcate macrochaetae located on bulges of the anterolateral corners (fewer macrochaetae on smaller specimens) [50-90 on specimens from North West Cape depending on specimen size]; a distinct hollow exists between these bulging rounded corners; lacking macrochaetae along lateral margins above antennae; behind each antenna and before the eyes is a U-shaped group of setae, the anterior arm of this group terminates in a long, thin trichobothria-like seta and the longer posterior arm extends over the eye. Clypeus with 1+1 combs of three to four macrochaetae [Narromine AMS K260968 five] near the anterior combs of the frons and a line of simple setae (two of the setae much longer than the others as seen in Fig. 8) well behind the anterior margin and a band of scales between the combs and the line. Labrum with numerous simple setae in a transverse subposterior band and a line of six fine setae subapically. Eyes dark, composed of about 12 or 13 ommatidia. —Antennae incomplete, scape slightly longer than wide, pedicel not much shorter than scape (0.65-1.00), both of which are covered in scales below the subapical rosette of setae. Each annulus/interval from



Figures 23–35. *Anisolepisma hartmeyeri* (Silvestri) holotype  $\bigcirc$  (23) dorsal scale and lateral comb of urotergite I; (24) two macrochaetae of mandible; (25) head (AMS K260970); (26) base of antenna; (27) antenna, most distal surviving annuli showing basiconic sensillae type B (*bsB*) and type C (*bsC*); (28) mandible, left; (29) mandible, right; (30) idem, incisor and molar regions; (31) maxilla, only large setae shown; (32) apices of galea and lacinia; (33) ultimate article of maxillary palp with basiconic sensilla type C (*bsC*); (34) labium; (35) ultimate article of labial palp showing four "aufgelöst" papillae (*lpp*) and basiconic sensillae type C (*bsC*). Scale bars = 0.1 mm.



Figures 36–49. *Anisolepisma hartmeyeri* (Silvestri) holotype  $\bigcirc$  (36) pronotum; (37) idem, left enclosed tuft of macrochaetae; (38) idem, right enclosed tuft; (39) idem, left lateral margin with numbered macrochaetae ( $m_0 - m_{-4}$ ) and trichobothria-like hairs ( $tr_0 - tr_{-4}$ ); (40) mesonotum; (41) idem, left lateral margin; (42) metanotum, left half; (43) idem, right half; (44) idem, left lateral margin; (45) idem, insertion of left posterior macrochaeta; (46) idem, right posterior macrochaeta insertion; (47) prothoracic sternal region and PI; (48) mesothoracic sternum and PII; (49) metathoracic sternum. Scale bars = 0.1 mm.



Figures 50–67. *Anisolepisma hartmeyeri* (Silvestri) holotype  $\bigcirc$  unless indicated by specimen number (50) PIII; (51) PI, anterior comb of coxa; (52) PIII, tibial spur; (53) PIII tarsus; (54) PIII pretarsus; (55) urotergite I, right half; (56) urotergite III, right half; (57) lateral comb of urotergite VII (AMS K260971); (58) sublateral comb, urotergite III; (59) submedial comb, urotergite III; (60) urotergite X; (61) idem, posterolateral corner; (62) urosternite I; (63) idem, medial comb and scale; (64) urosternite II; (65) idem, lateral comb (AMS K260971); (66) urosternite IV; (67) coxites VIII and IX with styli and ovipositor. Scale bars = 0.1 mm.



Figures 68–73. Anisolepisma hartmeyeri (Silvestri) holotype  $\bigcirc$  unless indicated by specimen number (68) coxites IX with styli and ovipositor (AMS K260971); (69) paraprocts and epiproct (AMS K260971); (70) cercus, basal divisions; (71) idem, most distal surviving divisions; (72) median dorsal appendage, basal divisions; (73) idem, most distal surviving divisions. Scale bars = 0.1 mm.

about the sixth subdivided into two very similar annuli with a trichobothrium subapically on the most distal annulus, the annuli within an interval becoming ever more obvious and longer and by about the ninth subdivide again; each annulus in distal portion of antenna (Figs 10, 11, 78) with basiconic sensillae (types B and C) distally, the arrangement of which is not yet well established but the type C sensillae appear to occur only in the annuli of the basal half of an interval, the type B sensillae are more numerous occurring on most annuli but numerous on the most distal annulus of an interval; the apical annulus of each interval appears to have one or two subapical trichobothria above and another below, at least until the eleventh interval after which it appears to revert to one above and one below and at least two longer thin hooked setae on each subarticle. -- Mandibles (Figs 79-81) with well-developed incisor and molar regions, the molar region on one side with pronounced comb which is lacking on the other molar, a group of four to seven apically bifurcate stout macrochaetae beyond the molar region [North West Cape E89191 and E89192 with seven to eleven. Narromine AMS K260968 with eleven], and a bush of >100 macrochaetae and setae externally (fewer on smaller specimens). ---Maxilla (Fig. 82) with galea longer than lacinia (although in the holotype (T234162) one lacinia is longer than the galea but this is believed to be an artefact of preparation), lacinia with two large apical teeth and a pre-apical tooth almost as large

as those apically, and several lamellate processes, the most distal two of which are truncate or rounded and lie parallel to and extending beyond the apical teeth of the lacinia; proximal to the lamellae is a row of four to seven thin, simple, delicately apically bifurcate setae, apical article of maxillary palp (Fig. 12) 3.4–5.5 [North West Cape AMS K377715 3.2] times longer than wide (more elongate in larger specimens) with a basiconic sensilla (type C) which is not always visible depending on the orientation of the palp on the slide as well as a basiconic sensilla (type B), penultimate article similar in length or slightly shorter than ultimate article. third article with few stout setae subapically, second article with rosette of stronger setae [Narromine AMS K260968 setae are longer, less robust and less rosette-like]; articles (except ultimate) with some small round scales on the outer margin, especially basally. -Labium (Fig. 84) short and broad, prementum with rows of strong setae at the base of the glossae and paraglossae, postmentum with short medial row of three setae (possibly better interpreted as two shorter rows of one and two together) [North West Cape specimens 4–7 setae] and 1+1 lateral groups of one to two [Narromine AMS K260968 three] lateral setae; there are fewer setae in all groups in smaller specimens; labial palp short, apical article rounded subrectangular (Figs 13, 85), longer than wide (L/W 1.29–1.77) [Narromine AMS K260968 1.82] subequal in length to penultimate article, with four papillae



Figures 74–85. *Anisolepisma aquilonaridum* n. sp. holotype  $\bigcirc$  unless indicated by specimen number (74) scale from urosternite; (75) scale from posterior margin of metanotum; (76) macrochaeta from mesonotum; (77) head; (78) antennae, most distal surviving intervals (T234163); (79) mandible, distorted outer margin; (80) apex of mandible; (81) apex of other mandible; (82) maxilla, only larger setae shown; (83) idem, apices of galea and lacinia (T234163); (84) labium, most setae of palps omitted; (85) idem, ultimate article of palp. Scale bars = 0.1 mm.



Figures 86–93. *Anisolepisma aquilonaridum* n. sp. holotype  $\bigcirc$  unless indicated by specimen number (*86*) right margin of pronotum with macrochaetae ( $m_0 - m_{-4}$ ) and trichobothria ( $tr_0 - tr_{-4}$ ) numbered; (*87*) right margin of mesonotum; (*88*) metanotum (T234163) showing extreme length of trichobothria-like setae (tr); (*89*) right margin of metanotum; (*90*) presternum, precoxae and prosternum (T234163); (*91*) mesosternum and PII (AMS K377712); (*92*) metasternum; (*93*) PI. Scale bars = 0.1 mm.

of the "aufgelöst" type arranged in a diamond configuration in the centre of the article rather than apically (see comment on aberrant individual in the discussion section), with two short rounded basiconic sensillae (type C), penultimate article with some stronger setae on the bulge, all articles with scales visible on the margins especially basally.



Figures 94–105. Anisolepisma aquilonaridum n. sp. holotype  $\bigcirc$  (94) PIII; (95) urotergite I; (96) urotergite II; (97) idem, lateral comb; (98) idem, sublateral comb; (99) idem, submedial comb; (100) urotergite X; (101) sublateral comb of urosternite III; (102) submedial comb of urosternite III; (103) urosternite I; (104) urosternite II; (105) urosternite III. Scale bars = 0.1 mm.

*Thorax*: Pronotum (Figs 14–16, 86) without setal collar but with numerous scales that extend forward over the "neck", with 1+1 closed tufts on the disc behind the anterior margin mediad of the eyes, each of seven to nine erect macrochaetae in two irregular sub-parallel rows with two or three cilia at the posterior end (Figs 14, 86); lateral margins fringed with shorter and longer, stout, apically bifurcated setae; anterior corners with three or four medium sized apically bifurcated setae followed by

five larger submarginal macrochaetae at intervals ( $m_0-m_{.4}$ in Fig. 86). The arrangement of these macrochaetae is not very consistent, for example  $m_{.3}$  is missing from the right side of the pronotum of T234163 but is clearly present on the left side and the most posterior macrochaeta ( $m_0$ ) is missing from the left margin of a specimen from North West Cape (E89191) but present on the right. Five very long trichobothria-like setae are found at intervals along the lateral margins, the most anterior trichobothria-like seta



Figures 106–113. Anisolepisma aquilonaridum n. sp. holotype  $\bigcirc$  unless otherwise indicated by specimen number (106) coxites VIII, IX, ovipositor and styli of  $\bigcirc$ ; (107) coxites IX of  $\eth$  and stylus (T234163); (108) coxites IX, penis and parameres of  $\eth$  from Barrow Island (E89193); (109) paramere (T234163); (110) epiproct, paraprocts and base of median dorsal appendage; (111) base of cercus; (112) most distal surviving division of cercus; (113) most distal surviving divisions of median dorsal appendage. Scale bars = 0.1 mm.

(tr<sub>-4</sub>) is located about  $\frac{1}{4}$  the way along the margin anterior to macrochaeta m<sub>-2</sub>, the second (tr<sub>-3</sub>) about half way along the margin anterior to macrochaeta m<sub>-1</sub>, the next (tr<sub>-2</sub>) is anterior to macrochaeta m<sub>0</sub> and the last two (tr<sub>-1</sub>, tr<sub>0</sub>) are fairly close together near the posterolateral corner (Fig. 86). Posterior margin glabrous but also with numerous dense overlapping scales that make it difficult to discern the margin of the nota in whole specimens. —Mesonotum (Figs. 17, 87, 88) lacking anterior tufts, almost as long as pronotum along mid-line, with four (rarely five) submarginal macrochaeta

 $(m_0-m_{-3})$  and four long trichobothria-like hairs  $(tr_0-tr_{-3})$ , the first trichobothrium  $(tr_{-3})$  about half way along the margin on the margin just before submarginal macrochaeta  $m_{-1}$ , the next  $(tr_{-2})$  close to the margin just in front macrochaeta  $m_0$ , and the last two  $(tr_{-1}, tr_0)$  away from the margin close to each other in the posterior corners. In one specimen (holotype) an additional submarginal macrochaeta socket  $(m_{+1})$  occurs on the left posterior corner just behind and mediad of tr\_1; this macrochaeta socket was not seen on the right side nor on the slide mounted paratype T234163. Posterior margins

with 1+1 sublateral single insertion sockets (Fig. 89), each associated with a smaller seta closer to but not on the margin and a cilium; these sockets appear quite small and it is not possible to tell if they are for setae or trichobothria-like hairs) [it was not possible to discern new setae forming under the old cuticle in a specimen from North West Cape which was about to moult (AMS K377715) although the marginal setae were visible, suggesting that these insertion points may be for trichobothria-like hairs, but on a specimen from (AMS K260968) there was a distinct strong macrochaeta about <sup>1</sup>/<sub>4</sub> the length of the mesonotum]. —Metanotum (Fig. 89) slightly smaller than mesonotum but with similar chaetotaxy.

Presternum of prothorax (Figs 18, 90) large, clearly visible extending across the underside of the head anterior to the coxae and sternum, about 3.7-4.0 times as wide as long. -Prothoracic sternum not free, partially concealed by coxae (Figs 18, 90), anterior medial region of sternum raised into a triangular ridge with triangular field of about 20 simple or apically bifurcate macrochaetae [Barrow WAM E89193, North West Cape E89191 and E89192 with 28-32, Narromine AMS K260968 with 35, Cobar AMS K261044 with 23]. - Mesosternum (Fig. 91) and metasternum (Fig. 92) also not free but raised and cordiform such that the anterior internal margins of the coxae can fit against the outer edges of the medial part of the sternum with the coxae covering the oval-shaped lower rounded lobes; the distal  $\frac{2}{3}$  of the lateral margins of the raised cordiform area with 10-11 setae along each lateral margin and a few minute setae anteromedially; surface covered with hyaline scales. -Metasternum similar but slightly wider.

Legs not particularly long (Figs 91, 93, 94); tibia L/W ratio of legs PI 2.5-3.6 [North West Cape E89191 3.7], PII 2.8-3.1 [2.6-3.2], PIII 2.7-3.3; tarsi L/W ratio PI 4.5-6.0 [Wilcannia AMS K261042 4.3], PII 5.1-6.4, PIII 6.0-7.0 [North West Cape E89192 and Narromine AMS K377716 both 7.2]. Precoxa with a macrochaeta and zero to two small setae and a cilium. -Coxa of prothoracic leg (Fig. 93) with comb of five long macrochaetae on each "shoulder" [Narromine AMS K260968 seven macrochaetae], a shorter comb of two macrochaetae below it and a line of long erect macrochaetae and shorter setae along exterior margin, rounded scales dorsally which are especially noticeable on anterior margin as well as a comb of two long thin setae on the dorsal face about half way along the coxa near to the medial margin and several setae apically covering the articulation with the trochanter. -- Trochanter probably without scales. -- Femur with scales, more obvious on leading edge, with several

strong spines and longer macrochaetae along posterior edge, apically with insertion points suggesting at least two or three strong spines over the articulation. —Tibia well scaled especially above and along lateral margins, with very robust stout macrochaetae near posterior margin (two pairs plus a more distal single macrochaeta which is longer than the apical spur, as well as other strong setae especially distally; two pairs of stout macrochaetae on outer margin and some strong setae distally near usual apical spur which has several long fine setae in basal half. - Tarsi (Fig. 20) with four articles (although very difficult to discern the suture between the last two); scales present at least dorsally on the basal article and probably basally above on all articles except perhaps the most distal of PI and PII. - Pretarsus (Fig. 20) with long thick straight outer claws that narrow and curve apically, short, thick, smooth, medial empodial.

All urotergal macrochaetae lost from dissected type specimens but some of the marginal setae still present [macrochaetae mostly intact on Narromine specimen AMS K260969 where they are quite long, almost half the length of the respective tergite]. Urotergite I (Fig. 95) with lateral and submedial combs of two strong macrochaetae [AMS K261045 from Cobar with one or two macrochaetae] both with one or two cilia and one or two quite long thin marginal setae. Urotergites II-VII (Fig. 96-98) with 3+3 combs, the lateral combs (Fig. 97) on segments II-III with two [two or three in specimens from Cobar, North West Cape and Narromine] and those on IV-VII with two to three macrochaetae as well as a marginal seta and two or three cilia, the sublateral (Fig. 98) and submedial combs (Fig. 99) each with two macrochaetae [North West Cape and Narromine specimens sometimes with only one macrochaeta], a single small marginal seta and one to three cilia. Urotergite VIII with 2+2 combs, the lateral comb of three macrochaetae [North West Cape specimens two or three] and submedial comb of two macrochaetae also with a single marginal seta and two or three cilia. Urotergite IX glabrous. --Urotergite X parabolic (Fig. 100) 0.51–0.57 times [North West Cape specimens 0.43–0.54] as long as wide with several strong and some finer setae on margin, with 1+1 combs of two or three strong macrochaetae, associated with up to two cilia, in posterolateral corners.

Only one urosternal macrochaeta preserved on dissected type specimens, which is apically slightly bifurcate and less than one third the length of the corresponding sternite (III) (Fig. 101); medial macrochaetae intact on specimen used for SEM (Fig. 20) about one third to one half the length of

Segment	Lataral	Urotergite	Submodial		Lataral	Urosternites	Modial	
	Lateral	Sublateral	Submediai		Lateral	Submedial	Iviculai	
Ι	2	_	2 [1-2]			—	2	
II	2	2	2			3 [2-4]	2	
III	2	2	2	-	2–3 [2–4]	3 [2–5]	2	
IV	2-3	2 [1-2]	2		3 [3-4]	3-4 [3-5]	2	
V	3 [2–3]	2 [1-2]	2		3 [2-5]	3-4[2-5]	2	
VI	3 [2-3]	2 [1-2]	2 [1-2]		3 [2-4]	3 [2-5]	2	
VII	3 [2-3]	2	2		3 [3-4]	3 [2-5]	2 [1-2]	
VIII	3 [2–3]		2		3 [2–3]	3 [2–4]	$2(\sqrt[3]{only})$	
IX	0							

**Table 2**. Number of macrochaetae per bristlecomb—Anisolepisma aquilonaridum n. sp. from Bladensburg [wider range if found on non-topotypic specimens].

the corresponding sternite [macrochaetae mostly intact on the Narromine specimens where they are longer, almost half that of the respective sternite]; marginal setae also guite long but much thinner than macrochaetae (Fig. 102). Urosternite I (Fig. 103) with medial comb of two macrochaetae plus two or three marginal setae [North West Cape zero to two marginal setae] on small medial bulge on posterior margin. Urosternite II (Fig. 104) with 1+1+1 combs, the submedial combs each of three macrochaetae [North West Cape three or four, Narromine and Cobar two] and a marginal seta [marginal setae often absent in specimens from North West Cape and Cobar], the medial comb of two macrochaetae and two marginal setae [often absent in North West Cape and Cobar specimens]. Urosternites III–VII (Fig. 105) in ♀ (III–VIII in  $\bigcirc$ ) with 2+1+2 combs, the lateral combs with two to three macrochaetae [North West Cape of three to five, Narromine and Cobar of two to three] macrochaetae, the submedial combs with three to four macrochaetae [North West Cape three to five, Narromine sometimes with only two], a marginal seta and sometimes a cilium and the medial comb with two [Cobar with one or two] macrochaetae and usually a marginal seta.

Coxite VIII in  $\bigcirc$  (Fig. 106) divided into two coxites, each with two combs of three or four macrochaetae [Narromine AMS K260969 of two to four], the submedial comb with two marginal setae, the lateral with one marginal seta and a cilium.

Coxite IX in the Q as in Fig. 106, the internal process acute apically reaching to about  $\frac{2}{3}$  the length of the stylus [about as long as the stylus in North West Cape E89191 and longer than stylus in specimen from Narromine AMS K260969], about 3.8 times longer than the external process [North West Cape E89191 about 4.1, Narromine AMS K260969 about 4.5] and 2.0 times as long as broad at its base [North West Cape E89191 2.6, Narromine AMS K260969 2.1], with several strong setae along external margin and a strong macrochaeta adjacent to and medial of the base of the stylus; external process of coxite IX small, triangular with acute apex, a few strong setae subapically and along external margin. —Ovipositor of primary type with very inconspicuous secondary segmentation; more apical divisions of anterior valves with very long thin setae (Figs 22, 106). In largest specimen observed, the ovipositor only just extends beyond the end of the inner processes [North West Cape E89191 extends beyond by about half the length of the inner process and is about the same length as the inner process in the Narromine specimen AMS K260969].

Coxite IX in the  $3^{\circ}$  as in Figs 107, 108, the internal process acute apically, about 1.9–2.0 times longer than the external process [Barrow WAM E89193 2.1–2.4, Cobar AMS K261045 2.8) and 1.0–1.1 times as long as broad at its base [Barrow WAM E89193 1.0–1.2], with several strong setae along both margins; external process of coxite IX small, triangular with a few strong setae subapically and along external margin. —Penis (Fig. 108) with numerous small rods/setae apically, each set on a protuberance. —Parameres difficult to differentiate from inner process of coxite IX in slide material of holotype (Figs 108, 109), appear to be long, unsegmented, almost as long as the internal process with numerous long fine setae as well as some stronger setae on inner (ventral) surface; see also illustration of Barrow Island specimen WAM E89193 (Fig. 108) for clearer representation.

Styli in one pair (IX only) with several long strong setae

ventrally along their length similar to two larger setae at apex (Figs 21, 106, 107).

Epiproct and paraprocts in both sexes not strongly pigmented/chitinized (Fig. 110) [much more so in specimens from Narromine and Wilcannia, but not Cobar, nor North West Cape nor Barrow], the former developed into a flat, forked process over the median dorsal appendage, the latter with a rounded conical terminal process and more proximal rounded right angled process; cerci with basal division glabrous (Fig. 111), the next division very short with a few small setae and trichobothria and a pointed macrochaeta on the outer face, divisions becoming gradually longer with two annuli, each with a rosette of small setae and trichobothria by the sixth division, three annuli by the eighth, four by the ninth, and six by the thirteenth persisting to the most distal surviving divisions which have both long, strong and smaller, simple setae, trichobothria as well as long fine hooked cilia as shown in Fig. 112. --Medial dorsal appendage similar (Figs 110 and 113) but with shorter divisions of only four annuli in the most distal surviving articles.

Discussion. In spite of the small differences noted especially in pigmentation and the large distances between collection sites (Fig. 1) (about 3,000 km between Barrow Island and the type locality) the specimens from the seven localities listed are considered to belong to the same species. The dissected and mounted specimens from Western Australia were much lighter in colour (pigmentation, sclerotization, scale cover?) than specimens from Bladensburg which were not quite as dark as specimens from NSW, initially suggesting that they were different species. However close examination of specimens including comparing measurement data and details of the chaetotaxy failed to identify any character(s) that would unequivocally support this. Minor differences in numbers of macrochaetae and length of antennae etc (as indicated in the description) were not considered significant. It is possible that the darker colouring of specimens is due to their more recent collection and better condition (slightly larger, collected more recently, less handling damage and less time as slide preparation). Differences in pigmentation between individuals in species of other genera (e.g., *Heterolepisma*) are also sometimes seen to be quite variable even within a single population. Given the small number of specimens available and the difficulty of working with insects that moult often and suffer handling damage easily, molecular data might be required before this question is investigated.

Habitat. All specimens were collected from places with fairly low (<550 mm per year) but highly to extremely variable rainfall with long periods without rain quite common (Table 5). Most Bladensburg specimens were collected by hand from very dry leaf litter on rocky surfaces on a hot exposed ridge in 2011. Another two specimens were collected from the same locality in 2013 and a further specimen from dry leaf litter on soil at Skull Hole about 6 km further west. A total of five specimens were collected by hand in dry leaf litter accumulated in dry creek bed south of Exmouth, WA. The Barrow Island specimen was collected in a pitfall trap. The Wilcannia specimen was collected by hand in dry Casuarina/Allocasuarina(?) leaf litter. Two specimens were collected near Narromine by hand during daylight hours under pieces of old dry wood fallen from a large Eucalypt tree. The specimen from Cobar was found in Acacia leaf litter on red soil.

**Etymology**. From the Latin words *aquilonis* for northern and *aridus* for arid reflecting the distribution of this species across the arid north of Australia.

**Comment**. This species, while close to *A. hartmeyeri*, differs significantly in the chaetotaxy of urotergite VIII and the conversion of the most posterior submarginal macrochaeta on the meso- and metanota to a long, thin trichobothria-like seta.

## Anisolepisma pigmentum n. sp.

# Figs 5, 19, 114-157

**Type material**. Holotype  $\mathcal{S}$  (HW 1.10) (NTM I008585 on two slides) NT: West MacDonnell National Park, Ormiston near Larapinta campsite (23°37.881'S 132°43.342'E 680 m asl), 9.vii.2009, Graeme Smith. Paratype 1 $\mathcal{Q}$  (HW 1.13) (NTM I008586 on two slides), same data as holotype.

**Diagnosis**. Distinguished from other species of the genus by its larger size and heavier pigmentation, the presence of four trichobothria-like setae on each side of the pronotum and three on each side of the meso and metanota, the presence of 1+1 trichobothria-like setae on the posterior margins of the meso and metanota (rather than macrochaetae), the presence of only 2+2 combs on urotergite VIII, the presence of infralateral setae on urotergite IX, the absence of medial combs on urosternites II–VII and the short setae on the ovipositor.

#### Description

*Appearance*: Medium sized silverfish with elongate body (Figs 5, 114) with the thorax only slightly wider than abdominal segment I, the subsequent abdominal segments remain about the same width or become slightly wider up until the sixth abdominal segment after which they slowly taper to about <sup>3</sup>/<sub>4</sub> of the width of the thorax in segment IX. Antennae and terminal filaments not quite complete in both specimens but only about one third H+B. Scale pattern when live (Fig. 5) evenly dark grey with distinct "white" margins along the sides of the thorax, antennae and terminal filaments dark, pinkish grey.

*Body size*: Up to 10.3 mm; HW 1.13 mm; thorax length up to 2.9 mm (or 0.25–0.29 times H+B), thorax width up to 1.85 mm; antennae and terminal filaments not quite complete in both specimens, longest remaining portion of antenna 0.34 times H+B, of cerci 0.29 and of median dorsal appendage 0.33 times H+B.

*Pigment*: Pigment brown and blotchy and distributed densely and extensively over much of the head and body segments, although less on the anterior urosternites. Mouthparts and appendages all pigmented, especially where scales are present (Fig. 19); antennae flagellum evenly pigmented light brown becoming slightly darker distally; pigment quite strong on all articles of labial and maxillary palp except ultimate article of the latter where it is noticeably lighter and more even; mandibles strongly pigmented externally, all articles of legs with quite strong pigment especially in scaled areas, pigment on tarsomeres more confined to patches, especially dorsally, than on other leg articles; styli darkly pigmented; terminal filaments with subtle lighter rings at the joint of divisions but these rings disappear not much beyond the end of the ovipositor to become evenly pigmented brown and darker distally; coxites

IX of female and ovipositor strongly pigmented.

*Scales*: Round or ovoid (Fig. 115), dark brown/black to light brown, some along the lateral margins of the nota appear to be white in alcohol. Scale insertions arranged in conspicuous longitudinal rows on the head and tergites. Scales present on top of head and between anterior bushes, across the clypeus, on the pedicel and scape, all articles of labial palp, all articles of maxillary palp except ultimate article, all tergites and sternites, all articles of legs, and most of the length of each stylus; absent from antennal flagellum and terminal filaments, parameres and ovipositor.

*Macrochaetae*: Bifid apically or simple, hyaline to quite dark brown or almost black (in alcohol).

Head: Very round, slightly wider than long, with scales above; eyes well forward; chaetotaxy (Fig. 116) well developed, frons with isolated 1+1 anterior groups of about 30-40 strong, apically bifurcate macrochaetae above 1+1 single macrochaetae on clypeus, lacking macrochaetae along lateral margins above antennae, behind each antenna is a short row of about three to five macrochaetae sub-perpendicular to the margin terminating in a very long thin, trichobothria-like seta, the row connects along the lateral margin with a long comb of macrochaetae above the eyes extending almost to the posterior margin of the eye (details obscured by eye pigment in Fig. 116). —Antennae almost but not quite complete, pedicel not much shorter than scape (Fig. 116) and both covered in dark scales up to the distal rosette of setae, most distal remaining intervals (Fig. 117) with setae, trichobothria and basiconic sensillae type B and possibly type C but the high level of pigment makes observation difficult. —Mandibles (Figs 118, 119) with well-developed incisor region, the molar region on one side with pronounced comb which is lacking on the other mandible which has a pointed posterior end, laterally; a group of several apically bifurcate and simple macrochaetae beyond the molar region with three short setae and a bush of 70+ macrochaetae externally. —Maxilla (Figs 120–122) with galea longer than lacinia, lacinia with two almost equally long apical teeth and a slightly smaller subapical tooth, seven or eight lamellate processes and a row of six or seven simple setae; apical article of maxillary palp 3.6–4.7 times longer than wide with a simple basiconic sensilla type C subapically; penultimate article similar in length or slightly longer than ultimate article, third article with a few stout setae subapically, second article with rosette of stronger setae; all articles, except ultimate, with some small round scales on the outer margin, especially basally. -Labium short and broad, prementum with rows of strong setae at the base of the glossae and paraglossae as illustrated (Fig. 123), postmentum with two short combs each of two setae and another comb of two setae on each side near the lateral margins; labial palp short, apical article subrectangular to ovoid (Fig. 124), longer than wide, subequal in length to penultimate article, with four papillae of the "aufgelöst" type, with a single short rounded basiconic sensilla type C on outer margin at level of diamond.

*Thorax*: Pronotum (Figs 125–127) with 1+1 closed tufts of about four erect macrochaetae plus two small cilia (Fig. 126); some stout, apically bifurcated macrochaetae on the anterior corners, then only three submarginal macrochaetae along the margins (as numbered  $m_0-m_{-2}$ ) plus many short lateral marginal setae; four trichobothria at intervals along the lateral margins; only the most posterior being located slightly away from the margin (Fig. 127), posterior margin glabrous with numerous, long, densely overlapping scales.



Figures 114–124. Anisolepisma pigmentum n. sp. holotype  $\stackrel{\circ}{\circ}$  (114) habitus; (115) dorsal scale; (116) head with some macrochaetae illustrated, cross-hatched area obscured by eye pigment; (117) antenna, most distal remaining divisions showing example of basiconic sensilla type B (*bsB*); (118) mandible; (119) idem, molar and incisor regions; (120) maxilla, only large setae shown; (121) idem, lacinia and galea; (122) idem, apical article of palp, showing sensory sensilla (*bsC*); (123) labium; (124) idem, ultimate article of palp. Scale bars = 0.1 mm unless otherwise indicated.



Figures 125–137. Anisolepisma pigmentum n. sp. holotype 3 (125) pronotum; (126) idem, left enclosed tuft; (127) idem, left margin with numbered macrochaetae and trichobothria-like setae; (128) mesonotum; (129) idem, left margin; (130) idem, trichobothria-like seta of left posterior margin; (131) metanotum; (132) idem, left margin; (133) ventral view of head and prothorax (drawn while in alcohol); (134) presternum and sternum; (135) mesothoracic sternal region; (136) metathoracic sternum; (137) PI. Scale bars = 0.1 mm.



Figures 138–150. Anisolepisma pigmentum n. sp. holotype  $3^\circ$  unless otherwise indicated by specimen number (138) part of femur, tibia and tarsus of PII; (139) part of femur, tibia and tarsus of PIII; (140) urotergite III, circle is air bubble, small spots are some of the scale insertion points; (141) sublateral comb of urotergite III(?); (142) urotergite IX, damaged on right hand side; (143) idem, left infralateral comb; (144) urotergite X; (145) urotergite X of paratype  $9^\circ$  (1008586); (146) urosternite I; (147) idem, posterior medial comb; (148) urosternite II; (149) idem, right comb and scale; (150) urosternite VI. Scale bars = 0.1 mm.

—Mesonotum (Figs 128–130) shorter than pronotum with three or four submarginal macrochaetae ( $m_{-1}$  absent on right side of holotype) and two trichobothria-like setae on the lateral margins ( $tr_{-1}$ ,  $tr_{-2}$ ) and a submarginal trichobothrium at each posterolateral corner ( $tr_0$ ) (Fig. 129); posterior margins with 1+1 sublateral trichobothria-like setae associated with a setula and a cilium (Fig. 130). —Metanotum (Figs 131, 132) shorter than mesonotum, with four or five submarginal lateral macrochaetae, the macrochaeta associated with the middle trichobothria-like seta was most often absent; posterior margin with 1+1 trichobothria-like setae as on mesonotum.

Presternum of prothorax very large (Figs 19, 133, 134), about one quarter as long as wide; clearly visible extending across segment between the labium and the coxae and sternum. —Prothoracic sternum (Figs 19, 133,134), with about 50 macrochaetae in medial tuft. —Raised area of meso- and metathoracic sterna heart-shaped of similar length to each other but the latter slightly wider, both with about seven, mostly simple, macrochaetae along the margins (Figs 135, 136).



Figures 151–157. Anisolepisma pigmentum n. sp. holotype  $\mathcal{S}$  unless otherwise indicated with specimen number (151) genital segments of  $\mathcal{S}$ , right side showing stylus, penis and paramere; (152) genital segments of  $\mathcal{Q}$  paratype (I008586), right side showing stylus, one anterior and both posterior gonapophyses; (153) apex of anterior gonapophyses of  $\mathcal{Q}$  (I008586); (154) apex of both posterior gonapophyses (I008586); (155) base of terminal filaments; (156) cercus, most apical surviving divisions (12th and 13th) (I008586); (157) median dorsal appendage, most apical surviving divisions (16th and 17th) (I008586). Scale bars = 0.1 mm.

Legs (Figs 137–139) not particularly long, tibia L/W ratio of legs PI 2.6-3.3, PII 2.5, PIII 3.7-4.5; tarsi L/W ratio PI 5.3-5.5, PII 6.0-6.5, PIII 7.2-7.8. —Precoxae with two or three setae not as comb. -Coxae of PI with transverse comb of seven stout macrochaetae anteriorly near the lateral margin; all coxae with long, strong setae along the lateral margins and a group of short, strong setae apically over the articulation. - Trochanter without strong macrochaetae. -Femora with several long, strong macrochaetae along the posterior margin and a group of short strong macrochaetae apically over the articulation. -Tibia with two pairs of strong spines on or near the lateral margin and several spines on or near the posterior margin, tibial spur with a few setae. —Tarsi distinctly four segmented, stronger setae ventrally and distally on each article except last. -Pretarsus of two simple lateral claws and a shorter smooth medial empodial claw.

*Abdomen*: Urotergite I with 1+1 or 1+2 combs each of a single macrochaetae only each associated with a marginal setula and one or two cilia, the combs seem to be very inconsistent with the lateral combs absent on the holotype

(one possibly due to damage). Urotergite II also inconsistent with one lateral comb absent on the holotype and the other of a single macrochaeta while both lateral combs on the paratype have two macrochaetae but both submedial combs and one sublateral comb is absent. Urotergites III-VII (Fig. 140) with 3+3 combs, the lateral and sublateral combs with two macrochaetae and the submedial of just a single macrochaeta, each comb associated with one or two marginal setulae and one to three cilia. Urotergite VIII with 2+2 combs, the lateral comb of two and submedial of a single macrochaeta plus a setula and cilia (Fig. 141). Urotergite IX (Fig. 142) with infralateral combs of one straight and one curved seta (Fig. 143). —Urotergite X truncated parabolic (Fig. 144) with numerous strong setae along the lateral margins, larger marginal macrochaetae in the corners and some stronger and weaker setae mediad to the corners with an area between these groups lacking setae, with 1+1 combs of two strong macrochaetae near the posterolateral corners, however the urotergite X on the female has only a single larger macrochaeta on the left side, displaced somewhat anteriorly (Fig. 145).

Segment	Lateral	Urotergite Sublateral	Submedial	Lateral	Urosternites Submedial	Medial
Ι	0-1		1			2
II	0–2	0–2	0-1		2	_
III	2	2	0-1	2	2–3	
IV	2	2	1	2	2	
V	2	2	1	2	2	_
VI	2	1–2	1	2	2	_
VII	2	2	1	1-2	2	
VIII	1-2		1	2	2	
IX	1–2 (infr.)					

Table 3. Number of macrochaetae per bristlecomb—Anisolepisma pigmentum n. sp. from Ormiston.

Urosternite I with medial comb of two macrochaetae (Figs 146, 147). Urosternite II with 1+1 combs each of two macrochaetae (Figs 148, 149) associated with a setula and a cilium. Urosternites III–VIII with 2+2 combs (Fig. 150), the lateral combs with two or three macrochaetae, the submedial with two macrochaetae as well as one or two small thin setulae and cilia between the comb and the margin; the macrochaetae are about half the length of the segment. —Styli (Figs 151, 152) in one pair (IX only) with several long strong setae ventrally along their length similar to the large apical setae; with single large macrochaeta on coxite IX mediad to the base of each stylus.

Coxite IX in the ♂ as in Fig. 151, the internal process acute apically, about 2.3 times longer than the external process and 1.2 times as long as broad at its base, with several strong setae along both the external and internal margins; external process of coxite IX small, about as long as wide at its base, triangular with an acute apex, a few strong setae subapically and along the external margin. —Penis with numerous setae apically, each set on a protuberance. —Parameres long, unsegmented, almost as long as the internal process with numerous very long fine setae (Fig. 151).

Coxite IX in the  $\bigcirc$  as in Fig. 152, internal and external processes similar in size and shape to those in  $\bigcirc$ . — Ovipositor (Figs 152–154) noticeably widened apically, with indistinct segmentation, extending (in only specimen available) to about the end of the internal process, apical divisions of both anterior and posterior gonapophyses with sparse fine setae, lacking very long setae.

Epiproct and paraprocts strongly pigmented, the former developed into a flat, forked process over the median dorsal appendage, the latter with an acute conical terminal process and more proximal rounded right angled process (Fig. 155). —Cerci with basal division glabrous (Fig. 155), the next two divisions short with a few small setae, divisions becoming gradually longer with two annuli by the seventh or eighth, each with a rosette of small setae and trichobothria, four by the eleventh or twelfth persisting to the most distal surviving divisions which have both long, strong and smaller, simple setae, trichobothria as well as long fine hooked cilia as shown in Fig. 156. —Medial dorsal appendage similar (Figs 155, 157) but with shorter divisions of only four annuli in the most distal surviving articles.

**Habitat**. Under low *Eucalyptus* (mallee) in 5 cm deep leaf litter on rocky hillside.

**Etymology**. The species is named *pigmentum* due to it having the most conspicuous cuticular pigmentation of any species so far known in the genus.

**Comment**. This species has urotergal and lateral notal chaetotaxy similar to *A. hartmeyeri* but differs from all other known species in the conversion of the posterior macrochaetae of the meso- and metanota to long thin trichobothria-like seta, the complete lack of medial combs on urosternites II–VIII and the presence of infralateral setae on urotergite IX and the quite short setae of the ovipositor.

# Anisolepisma subpectinum n. sp.

#### Figs 158–189

**Material examined**. *Holotype*  $\bigcirc$  (HW 0.94) (SAMA 05-000001 on two slides) SA: Mt Chambers Gorge (30.95281°S 139.22484°E 166 m asl), 15.v.2012, Graeme Smith.

**Diagnosis**. Distinguished from other species of the genus by the 3+3 combs on urotergite VIII, the presence of several basiconic sensillae type B on the apex of the maxillary palp and the absence of medial combs from some urosternites.

## Description

Appearance: Small to medium silverfish with elongate body with thorax slightly wider than abdominal segment I, the following abdominal segments remain about the same width until the sixth abdominal segment after which the abdomen slowly tapers to be about <sup>7</sup>/<sub>3</sub> the width of the thorax in segment IX. Antennae and terminal filaments incomplete. Scale pattern in live specimen mottled silver with light bands on edge of pronotum (Fig. 4) probably due to the overlap of transparent scales along the margins, dark scales on pedicel and dorsal face of tibia of at least PIII; antennae, terminal filaments and tarsi light pinkish brown.

*Body size*: H+B 7.3 mm; HW 0.94 mm; thorax: length up to 1.98 mm (or 0.27 times H+B); width 1.48 mm; antennae and terminal filaments incomplete, longest remaining portion of antenna 0.40 times H+B, of cerci 0.32 and median dorsal appendage 0.30 times H+B.

*Pigment*: Brown and often blotchy; antennae flagellum lightly to moderately pigmented with lighter areas at the distal end of each interval/annulus in basal portion of flagellum, pedicel and scape pigmented; head with light pigment around eyes; apical article of maxillary palp with light pigment, penultimate article with slightly more pigment, mostly distally, third article almost completely pigmented but lighter proximally, second article overall dark brown except for basal ring, basal article without pigment; all articles of



Figures 158–167. Anisolepisma subpectinum n. sp. holotype 3 (158) dorsal scale adjacent to submedial comb of urotergite I; (159) head, cross hatched area obscured by eye pigment; (160) antenna, scape pedicel and basal intervals; (161) idem, most distal surviving intervals showing basiconic sensillae type B (*bsB*); (162) mandible; (163) maxilla, only larger setae of palp shown; (164) idem, apex of galea and lacinia; (165) ultimate article of maxillary palp with basiconic sensilla type C (*bsC*) and type B (*bsB*); (166) labium, damaged anteriorly; (167) idem, ultimate articles of palp with basiconic sensilla type C (*bsC*). Scale bars = 0.1 mm.



Figures 168–178. Anisolepisma subpectinum n. sp. holotype 3 (168) pronotum with outline of some scales overlapping margins left anterior and posterior margins; (169) idem, left enclosed tuft of macrochaetae; (170) idem, left lateral margin with submarginal macrochaetae (numbered m<sub>0</sub>-m<sub>-5</sub>) and trichobothria-like hairs (numbered tr<sub>0</sub>-tr<sub>-2</sub>); (171) mesonotum, damaged right margin; (172) idem, left lateral margin; (173) idem, left posterior comb; (174) metanotum; (175) idem, left lateral margin; (176) prothoracic sternal region and right leg, the displacement of the macrochaetae from the margin is probably an artefact; (177) metahoracic sternum, left; (178) PII. Scale bars = 0.1 mm.



Figures 179–189. Anisolepisma subpectinum n. sp. holotype  $\stackrel{\wedge}{\bigcirc}$  (179) PIII; (180) pretarsus; (181) urotergite VIII; (182) right lateral comb of urotergite IV; (183) urotergite X; (184) left submedial comb of urosternite VIII; (185) urosternite V; (186) urosternite IX, penis, parameres and styli; (187) epiproct and base of median dorsal appendage, from below; (188) paraproct and base of left cercus; (189) cercus, most apical surviving divisions. Scale bars = 0.1 mm.

labial palp with very light pigmentation, thoracic nota with pigment along lateral margins, legs lightly pigmented but darker areas occur on the anterior edge of the femur as well as over the faces near the posterior edge distal to the ventral bulge, tibia evenly but somewhat more darkly pigmented especially distally and along outer or dorsal margin, tarsi with very light even pigmentation; urotergite X pigmented posteriorly, urosternite IX with moderate pigment around stylus insertion and along outer margin of internal and inner margin of external processes, styli well pigmented except at base; parameres and penis with light pigmentation.

*Scales*: Rounded, subrectangular (Fig. 158) or ovoid or sometimes quite irregularly-shaped, with numerous parallel rays that do not extend beyond the margin, dark brown/ black or clear (the latter more so medially on the urosternites and along the margins of the nota), those on legs, basal articles of palps brown or clear, those on pedicel, scape and clypeus, especially in non-mounted material can look almost black; scales on dorsal surface arranged in transverse rows extending well beyond the posterior margins of the tergites. Scales present on top of head, pedicel and scape, on clypeus, basal four articles of maxillary palp mostly in the basal part of each article, on labial palp, tergites and sternites as well as most leg articles except the more apical articles of tarsi on PI and PII, and at the base of the styli. Absent from flagellum and terminal filaments.

*Macrochaetae*: Bifid apically or simple, hyaline or yellow/ brown.

Head: Wider than long; chaetotaxy (Fig. 159) well developed, from with isolated 1+1 anterior groups of about 65–80 strong, apically bifurcate macrochaetae plus two or three cilia, lacking macrochaetae along lateral margins above antennae, a U-shaped row (often more than one macrochaeta wide) starts from a very long thin trichobothria-like seta a short distance onto the frons behind the antennae and runs perpendicular to the margin, turning back along the margin to the eye then running up above the eye to or slightly beyond the posterior level of the eye; clypeus with 1+1 combs of four macrochaetae immediately close to but laterad of the bushes on the frons as well as a row of finer setae (two of which are much longer) across the sclerite about 1/3 its length from the distal suture, the area between the row of setae and 1+1 combs densely covered in dark scales; labrum with area of fine setae across the sclerite about <sup>1</sup>/<sub>4</sub> its length from the suture with the clypeus and another shorter line of finer setae <sup>2</sup>/<sub>3</sub> distally. —Antennae incomplete; pedicel shorter than scape (about  $\frac{2}{3}$  its length), both of which are covered in scales below the subterminal rosette of setae (Fig. 160), with small groups of tiny setulae near the base of both the pedicel and scape; annuli/intervals of flagellum begin to subdivide from fourth interval of flagellum with the subdivisions becoming clearer and the individual annuli longer apically, intervals further subdivide from about the eighth interval with short setae as well as both straight and curly trichobothria-like hairs, the straight trichobothria restricted to the distal end of the most distal annulus in each interval; most distal remaining intervals (Fig. 161) without specialized sensillae but each annulus with a subapical ring of basiconic sensillae type B with occasional type C also present. -- Mandibles (Fig. 162) with well-developed incisor and molar regions, the molar region typical for genus with one side having a comb of raised spines, the other without the comb but with a pointed projection and three short bifurcated setae behind the

molar area; beyond the molar area is a group of one shorter rounded and five or six apically bifurcate macrochaetae and a bush about 90 setae and macrochaetae externally. ---Maxilla (Figs 163-165) with galea longer than lacinia, galea with small apical lobe, lacinia with one or two large teeth and one smaller pre-apical tooth, the apical teeth associated with truncate or rounded lamellate processes; six to seven apically acute lamellate processes and a row of five delicately apically bifurcate setae along the inner margin of the lacinia (Fig. 164), apical article of maxillary palp (Fig. 165) 4.6 times longer than wide with at least one small basiconic sensilla type C as well as a few type B sensillae towards the apex, penultimate article shorter than ultimate article (0.8), third article without obviously stouter setae, second article with distinct rosette of stronger setae well back from apex; scales on all articles except ultimate, usually more obvious proximally. -Labium (Fig. 166) short and broad, prementum with rows of strong setae at the base of the glossae and paraglossae (1+1 medial groups each of two setae, 1+1 lateral lines of seven setae) and postmentum with a short medial row of four setae and single lateral setae; labial palp short, apical article (Fig. 167) 1.5 times longer than wide, slightly longer than penultimate article, with four papillae of the "aufgelöst" type arranged in a diamond configuration near the centre of the article rather than apically, with a short curved basiconic sensilla type C on external margin at level of papillae.

Thorax: Pronotum (Figs 168-170) without setal collar but with numerous scales that extend forward over the neck, with 1+1 closed tufts of six erect macrochaetae in two rows and two or three small posterior cilia on the disc behind the anterior margin mediad of the eyes (Fig. 169); lateral margins (Fig. 170) with some shorter and longer, stout, apically bifurcated setae on anterior corner and along the lateral margins along with some cilia, as well as five submarginal strong apically bifurcate macrochaetae on each side (numbered  $m_0 - m_4$  in Fig. 170); four trichobothria-like hairs (numbered  $tr_0-tr_3$  in Fig. 170) located at intervals along the lateral margins, the most anterior  $(tr_3)$  quite long, located about one quarter the distance along the margin anterior to submarginal macrochaeta  $(m_{-3})$ , the second  $(tr_{-2})$ almost half way along the margin anterior to submarginal macrochaeta ( $m_{-2}$ ), the third ( $tr_{-1}$ ) about  $\frac{7}{8}$  the distance along the margin just anterior to the most posterior submarginal macrochaeta  $(m_0)$  and the last  $(tr_0)$  is a little further from the margin in the posterior corner of the notum  $(tr_0)$ ; posterior margin glabrous with numerous dense overlapping scales that make it very difficult to discern the margin of the nota in whole specimens. - Mesonotum (Figs 171-173) about the same length as the pronotum in the midline, lateral margins with five submarginal macrochaetae on each side (numbered  $m_0-m_4$  in Fig. 172) and three trichobothria-like hairs (numbered  $tr_0-tr_2$ ) the first is very long and located on the margin almost halfway along and associated with submarginal macrochaeta  $m_{2}$ , the second is shorter but also on the margin and associated with macrochaeta  $m_1$ , the last is also apparently shorter and located in the posterolateral corner a small distance from the margin and posterior to a submarginal macrochaeta m<sub>0</sub>; 1+1 macrochaetae on the posterior margin each associated with a marginal seta and two cilia (Fig. 173). - Metanotum (Figs 174-175) slightly shorter than mesonotum but with similar chaetotaxy however the first two trichobothria-like hairs are located slightly more posteriorly.

Presternum of prothorax large, clearly visible extending across segment anterior to the coxae and sternum. — Prothoracic sternum (Fig. 176) not easily visible on slide mount but not free, partially concealed by coxae, anterior medial region of sternum raised into a triangular ridge with triangular field of about 22 insertion sockets. —Mesosternum lost during dissection but observed before dissection to be similar to metasternum. —Metasternum (Fig. 177) also not free and covered by coxae, cordiform with a row of 8–10 long thin simple macrochaetae along or near each lateral margin and six small cilia anteromedially in V-shape; surface covered with hyaline scales.

Legs not particularly long (Figs 174–175), tibia L/W ratio of legs PI 3.0, PII 2.4, PIII 3.1; tarsi L/W ratio PI 5.8, PII 5.9, PIII 6.4. —Subcoxa with a macrochaeta and two cilia. -Coxa of prothoracic leg (Fig. 176) with numerous round scales, a comb of five stout macrochaetae on each "shoulder" and a shorter comb of two macrochaetae below it and a line of macrochaetae running down the outer margin, in the slide mount it appears to run remote from and parallel to the margins however this may be an artefact due to the rolling of the coxae as the slide dried; there is also as a comb of two setae on the dorsal face close to the inner margin about halfway along the coxa. -Coxa of PII and PIII (Figs 178, 179) without shoulder combs and the comb of two setae on the face is more posterior. distal internal apex with several stronger setae covering the articulation with the trochanter. -Trochanter of all legs simple but with tendency to distort if the femur contracts a long way under the coxa on slide mounts giving the erroneous appearance of two distinct parts to the trochanter. —Femora of all legs with scales more obvious on leading edge with three to eight short stout setae distally over the articulation (more on femur of PIII than the anterior legs), posterior ventral margin with four very stout, thick macrochaetae especially near the bulge, as well as several long strong macrochaetae along the whole length. - Tibia well scaled, anterior or dorsal margin with a pair of stout macrochaetae just short of midway and another pair subdistally, ventral margin with three pairs of stout macrochaetae plus other smaller setae, with another stout macrochaeta on the dorsal face, dorsal surface subdistally with a row of setae; apical spur with several long thin setae arising in the proximal half. - Tarsus with four articles with numerous setae, scales appear to be lacking from more apical articles of tarsus of PI and PII but are present on most articles of PIII. -Pretarsus with long thick outer claws that narrow and curve apically, shorter smooth medial empodial claw (Fig. 180).

Urotergite I with lateral combs of two macrochaetae,

a marginal seta and two cilia, the submedial comb, only present on one side in holotype, with two macrochaetae, a thin long marginal seta and a cilium. Urotergites II-VIII (Fig. 181) with 3+3 combs, the lateral combs with two or three (Fig. 182), the sublateral and submedial each with two macrochaetae, a single long thin seta on the margin and one to three small cilia associated with each comb in a regular pattern (one at the distad end of each comb and one between the more distad pair of macrochaetae slightly anterior to the comb and on the more posterior urotergites, another anterior to and between the remaining pair of macrochaetae (urotergite V was lost during slide preparation), on urotergites VI and VII a submedial comb is missing on one side, on VI completely missing and on VII just a single cilium being present. Urotergite IX glabrous. - Urotergite X parabolic (Fig. 183), 0.6 times as long as wide at the base with many strong setae along lateral and posterior margins and combs of two or three macrochaetae plus two cilia in posterolateral corners.

Urosternite I with medial comb of two macrochaetae and a thin marginal seta. Urosternite II with 1+1+1 combs. all of two macrochaetae and a long thin marginal seta, the submedial combs also with one or two cilia. Urosternites III. IV and VI with 2+1+2 combs, the lateral combs with three, the submedial (Fig. 184) with three and the medial with one or two macrochaetae with both lateral and submedial combs associated with one long thin setae marginal seta and a cilium at the laterad end of each comb. Urosternites V (Fig. 185), VII and VIII with 2+2 combs, in the case of V and VII the posterior margin of the urosternite is clearly concave with the medial comb lacking, lateral and submedial combs all composed of three macrochaetae, a long thin marginal seta and a laterad cilium except the right submedial comb of segment VII which has four macrochaetae. - Styli (Fig. 186) in one pair (IX only) with scales at base and several long strong setae ventrally along their length similar becoming stronger distally but not as strong as those at the apex; with single large macrochaeta on coxa mediad to the base of each stylus.

Coxite IX in the  $3^{\circ}$  as in Fig. 186, it was very difficult to discriminate from paramere, the internal process acute apically, about 1.8 times longer than the external process and 1.1 times as long as broad at its base, with several strong setae along external margin; external process of coxite IX small, acutely triangular with a few strong setae subapically and along external margin. —Penis with numerous setae apically, each set on a protuberance. —Parameres difficult

Table 4. Number of macrochaetae per bristlecomb-	-Anisolepisma subpectinum n. sp.	from Mt Chambers
Gorge.		

Segment		Urotergite			Urosternites		
-	Lateral	Sublateral	Submedial	Lateral	Submedial	Medial	
Ι	2		0–2			2	
II	2	2	2	_	2	2	
III	3	2	2	2	3	2	
IV	3	2	2	3	3	1	
V	?	?	?	3	3	0	
VI	3	2	0-2	3	3	2	
VII	3	2	0–2	3	3–4	0	
VIII	3	2	2	3	3	0	
IX	0						

to see as they are obscured by coxites IX but they are long, unsegmented, lying very close to and almost as long as the internal process, with simple setae along the mediad margin and apex and numerous long thin setae on the protected inner side of both the parameres and inner process of coxite.

Epiproct and paraprocts moderately pigmented (Figs 187, 188), the former developed into a strong, flat forked process, the latter with a subcylindrical process and a more distal acutely subtriangular medial process. -Cerci and median filament incomplete but at least 0.3 times H+B. Cerci (Figs 188, 189) with at least 13 divisions, the second division shorter than the first, then gradually becoming longer with the sixth division about as wide as long, second annulus appearing in the fifth division and four annuli per division by the seventh which persists to the most apical surviving article with the annuli becoming increasingly longer. -Median dorsal appendage with at least 12 divisions, the basal divisions much shorter than long but becoming gradually longer with the fifth division about as long as wide, each division subdivided into two annuli by seventh and further subdivided into a total of four annuli by the tenth division.

Female unknown.

**Comment**. This species would appear most closely related to *A. hartmeyeri* based on the dorsal chaetotaxy but differs in the reduced ventral chaetotaxy and the arrangement of sensillae on the maxillary palp.

**Habitat**. A single male specimen was found on soil under rocks in the car park along with a specimen of genus *Heterolepisma*.

**Etymology**. The species is named *subpectinum* in recognition of the reduced number of medial combs on the urosternites.

# Anisolepisma sp.

John Irish identified some specimens of *Anisolepisma* among the Australian material he had borrowed from the University of Queensland collection in the 1980's (Irish pers. comm.). He returned the material (in alcohol) to the museum in the early 90's, and the University collection was later transferred to the QM. Unfortunately, the shipment from Irish was never unpacked and, when finally located, the tubes were found to have dried out and the specimens shrivelled up. Attempts were made to re-hydrate and dissect the specimens with somewhat mixed but nevertheless unsatisfactory results as detailed below.

1 (sex unknown), gbs003081, QLD: "Durrie", 40 mi. E. of Betoota 25.68°S 141.27°E 100 m asl, B. Cantrell (QM on two slides).

The specimen was very dried out and the slides prepared not of much use. The specimen has abdominal combs on the urotergites and urosternites of at least some segments similar to those expected for mid-abdominal segments of *A. aquilonaridum* or *A. hartmeyeri*, but otherwise very little else is certain.

13 gbs003076 QM on two slides. NT: Mount Cavanagh, 15.viii.1959, E. Exley, under stones, rifle range. This specimen dissected reasonably well and a lot of detail could be determined. It has abdominal chaetotaxy similar to *A. pigmentum* except that it appears both urotergites I and II have 2+2 combs whereas urotergite II has 3+3 combs in *A. pigmentum*. Unfortunately the quality of the head and thorax is more affected by the desiccation so no attempt is made here to describe this material. Two other specimens (gbs003077 and gbs003078 QM) remain somewhat shrivelled in 80% ethanol.

## Key to the described species of Anisolepisma Paclt

Urotergite VIII with 3+3 combs each of one to three macro- chaetae	
Urotergite VIII with 2+2 combs of one to three macrochaetae (missing the sublateral)	
Medial combs of two macrochaetae present on all urosternites (I–VII in $\bigcirc$ , I–VIII in $\bigcirc$ ); ultimate article of maxillary palp with a single basiconic sensilla type C	solepisma hartmeyeri (Silvestri)
Medial combs reduced or missing on some urosternites; ultimate article of maxillary palp with one basiconic type C and a few basiconic type B sensillae	A. subpectinum n. sp.
Urosternites III–VII with 2+1+2 combs; pronotum with five, meso and meta nota with four long thin trichobothria-like setae on each side; urotergite IX glabrous	A. aquilonaridum n. sp.
Urosternites III–VII with $2+2$ combs (lacking medial comb); pronotum with four, meso and meta nota with three long thin trichobothria-like setae on each side; urotergite IX with $1-2$ infralateral setae	A niamontum n sn
	Urotergite VIII with 3+3 combs each of one to three macro- chaetae Urotergite VIII with 2+2 combs of one to three macrochaetae (missing the sublateral) Medial combs of two macrochaetae present on all urosternites (I–VII in $\bigcirc$ , I–VIII in $\bigcirc$ ); ultimate article of maxillary palp with a single basiconic sensilla type C

species	location (nearest weather station)	min–max °C	mm	rainfall pattern
A. hartmeyeri	Northampton (Nabawa)	7.4–34.1	445	All year but mostly in winter. Highly variable
	Kellerberrin	5.4-34.0	329	All year but mostly in winter. Highly variable
A. aquilinaridum	Bladensburg (Winton)	8.2-38.2	415	Mostly summer, extremely variable
	North West Cape (Learmonth)	11.4-38.0	266	Mostly summer, extremely variable
	Augathella	4.2-35.0	533	Throughout year, highly variable
	Narromine (Triangie)	3.2-33.3	496	Throughout year, highly variable
	Cobar	3.1-34.1	334	Throughout year but mostly in summer highly variable
	Wilcannia	4.0-36.6	268	Throughout year, extremely variable
A. subpectinum	Mt Chambers Gorge (Balcanoona)	5.3-33.6	225	Throughout year but mostly summer, extremely variable
A. pigmentum	Ormiston (Papunya)	6.4-38.0	286	Mostly summer, highly variable
Anisolepisma sp.	Betoota (Birdsville)	6.6-38.8	165	Throughout year but mostly summer, extremely variable
	Mt Cavanagh (Curtin Springs)	3.7-37.8	237	Throughout year but mostly summer, extremely variable

**Table 5**. Climate data for all collection localities from the Australian Bureau of Meteorology (BOM, 2016). Range of lowest mean monthly minimum–highest mean monthly maximum temperature (*min–max*°*C*); average annual rainfall (*mm*).

#### **Biology**

Most *Anisolepisma* specimens were collected in leaf litter with the exception of the single specimen of *A. subpectinum* collected under a rock, the *A. hartmeyeri* (Kellerberrin) specimen collected from within a decaying log and two specimens of *A. aquilonaridum* (Narromine) which were collected from the under side of a piece of wood. The collection sites were generally exposed to very high temperatures and were extremely dry. On several occasions specimens of *Acrotelsella* sp. or *Heterolepisma* sp. were collected from the same litter or under the same rock/piece of wood. Climate statistics are summarized in Table 5. All species were collected in low rainfall areas (average rainfall 165–533 mm/ year) with high to extreme variability where no significant rain may fall for several months in some seasons.

# Discussion

Mendes (1991) created the subfamily Acrotelsatinae for the genera Acrotelsa Escherich, 1905, Lepismina Gervais, 1844 and "Apteryskenoma" Paclt, 1953, noting the absence of an apical sensilla on the maxillary palp, the long, thin tubuliform paramera lacking a glandular area, the gonapophyses with thin setae only, the absence of a setal collar and the strong reduction of the prosternum. He excluded the genera Panlepisma, Silvestri 1940, Paracrotelsa Paclt, 1967 and Anisolepisma Paclt, 1967 from his analysis due to the inadequate descriptions available for the type species. Since then Kaplin (1992) has removed a group of central Asian species from Apteryskenoma into a new genus Desertinoma and Mendes (2004) described Primacrotelsa from the Yemeni island of Socotra. These two genera, along with Anisolepisma, generally exhibit the key characters noted by Mendes, and are therefore placed within the Acrotelsatinae, but they differ in other characters such as the papillae of the labial palp and the type of macrochaetae. It is therefore necessary to slightly modify Mendes' definition of the subfamily to include these new genera.

#### Acrotelsatinae redefinition

Macrochaetae feathered or smooth; antennae with basiconic sensillae; cylindrical sensilla of apex of maxillary palp distal article missing; anterior border of pronotum largely devoid of setal collar but often with 1+1 isolated pronotal tufts of

macrochaetae or with a small collar occupying about half of the front margin; paramera tubuliform, long and thin, without glandular area with numerous fine setae; gonapophyses with thin setae only and sometimes apically provided with strong sclerotized cuticular teeth; all sterna not free, largely covered by coxae; 2+3 or 2+2 labial palp papillae.

#### Relationships

*Anisolepisma* seems to be very close to *Primacrotelsa* Mendes, 2004 with both genera showing some characters divergent to the rest of the Acrotelsatinae such as the smooth macrochaetae, the absence of bushes on the clypeus and the simple apex to the ovipositor (without cuticular spines).

The genus *Heterolepisma* Escherich, 1905 is generally considered to be the most primitive genus of the Lepismatidae but this "consensus" placed little emphasis on the morphology of the thoracic sterna. A review of the major morphological characters below suggests that this discussion could be re-opened in the light of our increasing knowledge of the order.

Thoracic sterna. It appears that all genera within the Acrotelsatinae lack free thoracic sternal plates which cover the medial base of the coxae. This character is not adequately described for species of Lepismina but the illustration of the ventral aspect Lepismina aurisetosa Wahlgren, 1906 in Schremmer (1964) clearly shows the coxae covering the thoracic sterna. The morphology of the meso and metathoracic sterna of the comparatively common peridomestic species Acrotelsa collaris do not appear to have been published. This arrangement is so contrary to that seen in most Lepismatidae (including *Heterolepisma*) where the medial part of the sterna is developed into a free plate articulating only along the anterior margin and covering much of the internal anterior margins of the coxae, that it could be considered the most obvious defining character of the subfamily.

Mendes (1991) considered the genera *Desertinoma* (as *Apteryskenoma* Paclt without *A. andersonae* Womersley, 1928), *Acrotelsa, Lepismina, Mirolepisma* Silvestri 1938, *Monachina* Silvestri, 1908, and *Prolepismina* Silvestri 1940 as having a strongly reduced prothoracic sternum. In *Prolepismina, Monachina* and *Mirolepisma* the prosternum remains free but smaller in size and not covered by the coxae. This appears to be a reduction of the typical "free" sternite



Figure 190. *Anisolepisma*, schematic representation of mesothoracic sternum with sections at A, B and C shown on right.

of the Lepismatidae. The meso and metasterna are also free and cover the base of the coxae. This is a fundamentally different arrangement to that seen in the Acrotelsatinae where the coxae largely cover the sterna (as in the Tricholepidiidae, Maindroniidae, Nicoletiidae and Protrinemuridae). The medial portion of the sternum is somewhat raised between the anterior mediad corners of the coxae and that of the prosternum bears a medial tuft. In the case of Anisolepisma (and probably, judging from the published illustrations, also Primacrotelsa and Desertinoma) the raised heart-shaped structure of the meso and metasterna have slight concave hollows below the lateral margins into which the anterior median margins of the coxae fit (see schematic representation in Fig. 190). The oval "sclerites" at the base of the heart shaped meso- and metasterna reported in Silvestri (1908) are a continuation of the sternum below the coxa, without any obvious suture separating the raised cordiform medial section from the rest of the sternum.

Could this condition represent a plesiomorphic state for the Lepismatidae? Could the concave hollows beneath the raised cordiform section have become progressively deeper covering more of the coxae until the raised part of the sternum became a free sternum? If the form of the sternum in these genera represented a regression of the sternum, one would expect a decrease in size as in the prothoracic sternum of *Prolepismina*, *Monachina* and *Mirolepisma*, but not necessarily a fusion to the underlying sternal plates.

Macrochaetae. Both Anisolepisma and Primacrotelsa have smooth, apically bifurcate or smooth pointed macrochaetae. They do not have any feathered macrochaetae. In contrast the other genera of the Acrotelsatinae (Acrotelsa, Apteryskenoma, Desertinoma and Lepismina) display various degrees pectination. Smooth macrochaetae are characteristic of the Heterolepismatinae and Lepismatinae although some Ctenolepismatinae (e.g., Mormisma Silvestri, 1938) have "false-smooth" macrochaetae with rounded tips, seen as a secondary modification by Mendes (1988). All other genera have pectinate macrochaetae. Smooth macrochaetae are a feature of the Nicoletiidae, Protrinemuridae and Tricholepidiidae and generally considered to be plesiomorphic, suggesting Anisolepisma and Primacrotelsa are the only two known genera within the Acrotelsatinae to have retained this plesiomorphic character. At least some of the pectinate macrochaetae of *Acrotelsa* resemble the smooth apically bifurcate macrochaetae of Anisolepisma and Heterolepisma but with fine pectinations along the shaft (see Watson & Li, 1967, fig. 2) and different in appearance to the variety of pectinate macrochaetae seen in the Ctenolepismatinae. The pectinations in some Acrotelsatinae may be a parallel development to those of the Ctenolepismatinae.

Cephalic chaetotaxy. Most genera in the Acrotelsatinae, including Anisolepisma, have quite strongly developed anterior bushes on the frons; the exception being *Primacrotelsa* where the cephalic chaetotaxy is greatly reduced, anterior bushes are present but quite small. Mendes (1982) and Irish (1990) consider the plesiomorphic state as one completely lacking bushes with macrochaetae along the margins of the head as in *Heterolepisma*. While small anterior bristle bushes are present on the frons of at least some Maindroniidae, they are lacking in the Nicoletiidae, Protrinemuridae and Tricholepidiidae, where bristles occur scattered over the surface of the frons and often with some stronger bristles along the margins. This offers support to the argument that bristle bushes are apomorphic. However we see a reduction in density of macrochaetae within several genera of the Zygentoma (e.g., Primacrotelsa and also Qantelsella Smith, 2015 which seems to be a reduction in the much denser chaetotaxy observed in the related Acrotelsella Silvestri, 1935). The possibility that the chaetotaxy of Heterolepisma represents a reduction from an earlier bristle bush state should not be discarded.

Furthermore, the illustrations of cephalic chaetotaxy in Mendes (1982) show the shape of the anterior margin of the head and the arrangement of bristlecombs in *Allacrotelsa kraepelini* (Escherich, 1905) (Lepismatinae) is most reminiscent of that of *Anisolepisma*, differing mainly in the absence of a gap in the chaetotaxy on the margin adjacent to the antennae, and the absence of 1+1 combs and scales on the clypeus. Further characters shared with this genus are discussed below.

Antennal sensillae. Anisolepisma, Heterolepisma, Allacrotelsa Silvestri, 1935, Primacrotelsa and Acrotelsa have simple basiconic sensilla type B and type C on the annuli of the more distal intervals of the antennae. They lack specialized sensillae such as the branched asteriform sensory structures seen on the antennae of Lepismatinae (Mendes, 1982; Molero-Baltanás *et al.*, 2000) and the flattened circular poculiform sensillae seen in Hyperlepisma Silvestri, 1932, Mormisma and Qantelsella Smith, 2015. Simple sensillae are probably a plesiomorphic state with neither the Nicoletiidae, Heterolepisma, Anisolepisma nor the more ancient Lepismatinae (Allacrotelsa) having more derived antennal sensillae.

**Sensillae of the maxillary palp**. *Anisolepisma* and *Primacrotelsa* do not have a cylindrical sensilla at the apex of the most distal article of the maxillary palp nor do they have feathered papillae seen on the apical article of the maxillary palp of *Heterolepisma*, nor the asteriform sensillae seen in the Lepismatinae. They have only small basiconic sensillae types B and C. This state seems to be correlated with that of the antennal sensillae.

**Papillae of the last article of the labial palp**. Both *Primacrotelsa* and *Anisolepisma* have papillae of the "aufgelöst" type, which are only four in number and, at least in the case of *Anisolepisma*, arranged in a diamond pattern. The appearance of five papillae on just one of the two palps in the single specimen from Cobar (AMS K261044) (Fig. 191) suggests that the diamond format could be an apomorphy for these genera, having evolved from the 3+2 arrangement by a fusion of the two papillae in the proximal row. The Ctenolepismatinae and Mirolepismatinae



Figure 191. Anisolepisma aquilonaridum n. sp. ex Cobar, aberrant labial palp.

have several (three to more than ten) papillae in a single line while the Heterolepismatinae, Mirolepismatinae and Silvestrellatinae have five papillae in a 3+2 arrangement seen all subfamilies except the Ctenolepismatinae and Mirolepismatinae. The Tricholepidiidae have six papillae in two lines, the Maindroniidae have the 3+2 arrangement and the Nicoletiidae have six papillae arranged in three lines of three, two and one so it is likely that the 3+2 arrangement represents the plesiomorphic state for the Lepismatidae. The genera of the Acrotelsatinae display a wide range of states with the 3+2 arrangement in *Desertinoma* and *Lepismina* and five or six in a single row in *Acrotelsa* and *Apteryskenoma*.

Again it is interesting to note the similar character appearance in *Allacrotelsa* Silvestri, 1935 (Lepismatinae) with regards to the rather unusual shape of the ultimate article of the labial palp in *Anisolepisma* and other Acrotelsatinae; but noting that *Allacrotelsa* has five papillae in two rows.

**Notal chaetotaxy**. *Anisolepisma* and *Primacrotelsa* lack a setal collar, a character shared with some other Acrotelsatinae (*Acrotelsa* and *Apteryskenoma*) however a partial collar covering 50–60% of the anterior margin is present in *Desertinoma* (Kaplin, 1992) and in *Lepismina* there are three marginal tufts. A setal collar is absent from the Lepismatinae, the Silvestrellatinae and some Ctenolepismatinae. In contrast a setal collar appears on all Heterolepismatinae, Mirolepismatinae and some Ctenolepismatinae and strong macrochaetae are found along the anterior margin of the nota in the Tricholepidiidae, Maindroniidae(?) and most Nicoletiidae suggesting the presence of a setal collar character is plesiomorphic.

Anisolepisma, Acrotelsa and Primacrotelsa have 1+1 closed anterior tufts of radiating macrochaetae on the pronotum. Something similar is seen on the pronotum of *Allacrotelsa kraepelini* Escherich, 1905 (Lepismatinae) (as described in Wygodzinsky, 1942) but the tufts are located more laterally and appear to be in contact with the anterior margin. Such tufts are absent from all other genera of the Zygentoma..

Notal trichobothria. Most genera of Zygentoma silverfish have two trichobothria (very long thin sensory hairs) on each side of the thoracic nota (Mendes, 1986b). Anisolepisma has several very similar looking hairs on anterior lateral margins and, in the case of A. *pigmentum*, the posterior macrochaetae of the nota are replaced by trichobothria-like setae. These trichobothria-like setae are very long and thicker than usual (>500 µm and about 2.6 µm or greater in diameter) compared to those described in Mendes (1986b) which are up to 350  $\mu$ m in length and only 1.4  $\mu$ m in diameter. Mendes (2004) reports that the pronotum of Primacrotelsa also has very thin and long (trichobothria-like) macrochaetae laterally although the number is not specified. The presence of long thin trichobothria-like hairs instead of (or perhaps as well as) macrochaetae is reported by Stach (1935) in his redescription of Lepismina aurisetosa Wahlgren, 1806 (Acrotelsatinae). In Anisolepisma these hairs look very much like typical trichobothria except for their extraordinary length but detailed examination of the insertion points and their greater thickness basally suggests that several of them are modified setae. The insertion does not appear to be the evenly rounded hole with dents on one edge as described by Kränzler & Larink (1980) but seem very similar to the insertion sockets of the macrochaetae (compare sockets in Fig. 16). This hypothesis is further supported by the single long thin trichobothrialike hairs on each of the posterior combs of the meso and meta nota of A. pigmentum whereas the other species have a single macrochaeta in these locations. Wygodzinsky (1942) illustrates similar supernumery trichobothria on the pronotum of Allacrotelsa kraepelini (Escherich, 1905) (Lepismatinae) and Anallacrotelsa cricetophila Mendes, 1996 (Lepismatinae) also has three quite long trichobothria (c. 400 µm) on the pronotum.

The long thin trichobothria-like seta seen on the tibia of PIII in some species of some genera e.g., *Acrotelsella* (Ctenolepismatinae), *Heterolepisma* (Heterolepismatinae) and *Primacrotelsa* (Acrotelsatinae) and *Allacrotelsa* (Lepismatinae) (Wygodzinsky, 1961) but not yet seen in any species of *Anisolepisma* is also probably an example of the modification of a seta and such a plastic conversion in form, present in at least half the subfamilies of Lepismatidae, is probably a plesiomorphic character but at present provides little insight into the phylogeny of the family.

**Urotergites I–VIII**. Mendes (1982) considered the 3+3 comb arrangement to represent the most primitive condition. Reductions in the number of combs are common but more so on urotergites I and VIII. Most genera of the Acrotelsatinae have only 2+2 small combs (or single macrochaetae) on urotergite I except *Desertinoma* and *Apteryskenoma* where urotergite I is glabrous or has only 1+1 combs.

The chaetotaxy on the anterior urotergites does not appear to be very stable in *Anisolepisma* with regular instances of combs missing from one side. Mendes (1979) and Molero-Baltanás (2010) also report asymmetry and loss or addition of combs in some rare individual specimens of *Ctenolepisma ciliata* (Dufour, 1831).

Two species of *Anisolepisma* have 3+3 combs on urotergite VIII while the other two have only 2+2 combs, the condition seen in all other Acrotelsatinae and all Heterolepismatinae. **Urotergite IX**. Only one species of *Anisolepisma (A. pigmentum)* has chaetotaxy on urotergite IX in the form of infralateral setae. This is reminiscent of that found in species of *Heterolepisma* and the Nicoletiidae and therefore may be a plesiomorphic character.

**Urotergite X**. The shape of urotergite X is often useful at the genus and species level. The shape of this urotergite in *Anisolepisma* is typical of that found in species of *Heterolepisma*, being rounded with just 1+1 apical combs consisting of two or three macrochaetae, as well as a fringe of marginal setae. Most shapes of urotergite X are represented within the Acrotelsatinae (i.e. rounded in *Anisolepisma*, trapezoidal with concave posterior margin in *Primacrotelsa* and strongly triangular in *Acrotelsa* and *Paracrotelsa*) and is therefore difficult to use as a character to determine the phylogeny of the subfamily.

Irish (1990) noted that the chaetotaxy of the tenth urotergite was a stronger character than its shape. Here again we see a diversity within the Acrotelsatinae with *Anisolepisma* and *Primacrotelsa* having 1+1 combs or single macrochaetae in the posterolateral corners while *Acrotelsa* and *Paracrotelsa* have several combs along each margin of their triangular tenth urotergites. Interestingly, species of *Allacrotelsa* Silvestri, 1935 (Lepismatinae), including the fossil species *Allacrotelsa dubia* (Koch & Berendt, 1854) have a tenth urotergite very similar to *Anisolepisma*, in both shape and chaetotaxy.

**Urosternites**. Anisolepisma shares with Acrotelsa, Paracrotelsa, Primacrotelsa and Desertinoma, the presence of 2+2 combs on urosternites III–VIII. In most species of Anisolepisma there is also a small medial comb on urosternites I–VII (VIII in  $\Im$ ). There is always a medial comb on urosternite I, something that is not found on other Acrotelsatinae but does occur in some species of other subfamilies. Lepismina is unique in that it is the only genus of Lepismatidae to have no urosternal chaetotaxy.

Irish (1990) considered the character state in *Maindronia neotropicalis* Wygodzinsky as representing the plesiomorphic state where most urosternites have 3+3 small combs. In this case the Acrotelsatinae would be closer to the ancestral state than any other subfamily where the combs have been reduced to 1+1 or 1+1+1.

**Parameres**. Males of *Anisolepisma* have tubuliform paramera similar to *Acrotelsa*. Those of the Heterolepismatinae are short and more bulbous, while those in the Lepismatinae are quite variable in their presentation. Paramera have been lost in the Ctenolepismatinae, Mirolepismatinae and Silvestrellatinae. They are present in the Tricholepidiidae and Nicoletiidae and Protrinemuridae as well as the Microcoryphia and should be seen as plesiomorphic.

**Ovipositor**. Females of *Anisolepisma* and *Primacrotelsa* have simple short ovipositors of the primary type which have only simple thin setae apically. Ovipositors in females of *Acrotelsa*, *Desertinoma* and *Lepismina* are also short but apically widened and with apical cuticular spines in addition to the simple setae. Females of *Heterolepisma* and *Anallacrotelsa* also have simple ovipositors of the primary type but those of *Heterolepisma* are very much longer, extending well beyond the apices of the inner coxal processes of urosternite IX. Ovipositors in the Nicoletiidae and Protrinemuridae are also of the primary type with simple

setae and this form is generally considered as plesiomorphic. The development of cuticular spines within some genera of the Acrotelsatinae is a unique synapomorphy within the subfamily.

The position of Anisolepisma and the Acrotelsatinae within the Lepismatidae. The form of the thoracic sterna in the Acrotelsatinae would seem to be fundamentally different to the free sterna of the remaining subfamilies of the Lepismatidae. If it were to be considered as plesiomorphic state rather than an autapomorphy brought about through a reduction of the previously free sterna, then the Acrotelsatinae could be the most primitive subfamily of the Zygentoma. The subfamily possesses many primitive traits such as the presence of parameres, the primary ovipositor with simple setae, the lack of specialized sensillae on the antennae and the more numerous combs of the urosternites. Its dorsal abdominal chaetotaxy, including the presence of infralateral setae on IX, resembles that of *Heterolepisma*, which is considered by most workers as the most plesiomorphic. Other characters such as the occurrence of both smooth and pectinate macrochaetae, the diversity of shapes and chaetotaxy of urotergite X, do not shed any light on this question. An interpretation giving priority to the form of the thoracic sternites creates other difficulties such that the simple cephalic chaetotaxy of both the Heterolepismatinae and Lepismatinae would have to be considered as a regression from having bushes or else constitute a parallel development within the two lines of evolution with fundamentally different thoracic sternal arrangements.

Irish (1990) also commented on the difficulty of interpreting the thoracic sterna in the genera now included within the Acrotelsatinae, noting that reference to other families suggests the state with the coxa lying above the sterna as symplesiomorphic but he could not accept this on holomorphological grounds as it ran contrary to almost all other significant characters he used to create his phylogram.

Finally the number of uncommon characters shared by *Anisolepisma* and *Allacrotelsa* (Lepismatinae) is intriguing. They have similar cephalic chaetotaxy, similar unspecialized sensillae on the antennae, similar shaped labial palps, pronotal tufts, supernumery notal trichobothria and urotergite X. They differ dramatically however in the development of the thoracic sternites, but it raises the question of whether there could be an ancient relationship between these genera. Molecular data may eventually be a useful tool to help resolve this issue.

**Zoogeography of the Acrotelsatinae**. Discussions on the zoogeography of the Zygentoma must be considered as very hypothetical primarily because of the very uneven research activities on the order. While southern Europe, northern and southern Africa, parts of central Asia and parts of Australia have received moderate to strong attention, most of the rest of the world has been very poorly sampled judging from the literature. In addition, anthropophilic/ peridomestic species must be excluded from discussions due the presumed influence of human activities man on their wide distributions.

Being flightless the distribution is likely to be slower than for other groups although several endemic species are known from remote volcanic islands such as Hawaii. Distribution over water has therefore clearly occurred with a few Ctenolepismatinae and Nicoletiinae and several Heterolepismatinae. The subfamily Acrotelsatinae is well known from the Mediterranean to central Asia (six species of *Desertinoma* is reported from Afghanistan, Mongolia, Turkmenistan and Uzbekistan, four species of *Lepismina* from Afghanistan, Egypt, Kuwait, Iran, Israel, Libya, Saudi Arabia, Syria and possibly Turkey? and the monotypic *Primacrotelsa* from Yemen). Another less well known group of genera occurs in the Australia/Pacific region with four species of *Anisolepisma* from Australia, one species of *Paracrotelsa* from Irian Jaya (eastern Indonesia) and a single species of the enigmatic *Apteryskenoma* from the New Hebrides (Womersley, 1928). Given the extensive survey work of Irish in Southern Africa, it would seem that the subfamily does not occur there and it has not yet been reported from the Americas, although this could well be a sampling issue.

Silverfish, being soft bodied, do not preserve well so the fossil record is very sparse and placement of the species into subfamilies difficult. They belong to a very ancient group of insects with their origins in the Silurian or Devonian (450-400 Ma) with the Tricholepidiidae separating from the remaining Zygentoma in the late Triassic (214 Ma) based on molecular clocks (Misof et al., 2014). At this time the continents may have been more or less united in a supercontinent. Mendes and Wunderlich (2013) summarize the fossil record to date. The oldest known Lepismatid fossils date to the Cretaceous (c. 110 Ma) a time when the continents were breaking apart. They are either unplaced ("gen. sp. from Araripe" from Brazilian sandstone) or placed within the Lepismatinae (Myanmar amber). More recent Eocene amber specimens (50–38 Ma) from Baltic belong to the Lepismatinae and the extinct Lepidotrichidae. The first Ctenolepismatinae fossil (Ctenolepisma electrans) dates from the Oligocene (34-25 Ma) in Dominican amber.

It is therefore perhaps premature to explain the current distribution based on such limited data. It is possible that all Lepismatid subfamilies existed before the break-up of the continents and that the current distribution of the Acrotelsatinae represents the relic remains of a widespread subfamily, or could simply be a reflection on the incomplete collection efforts. For example, silverfish of the genus *Lepisma* were believed to be restricted to the Mediterranean region (except the peridomestic *Lepisma saccharina*) however Smith (2015a) recently described a species collected within termite nests in Australia.

The Acrotelsatinae are showing a similar but wider distribution pattern, suggesting an earlier extensive distribution now surviving as relic populations in specialized habitats. The absence of the subfamily from southern Africa, which has been well sampled, and the Americas, which hasn't, conflicts somewhat with any explanation of a distribution through Pangea as Australia/PNG was only joined to Eurasia via Africa and Antarctica in the Permian (c. 225 Ma). In contrast, the Heterolepismatinae have a more or less southern Gondwanan distribution, suggesting a more recent origin.

In summary, the genus *Anisolepisma* appears to be an endemic Australian genus, widespread through Australia in the drier regions. It belongs in the family Acrotelsatinae which has a somewhat disjunct distribution with representatives in PNG, the Solomon Islands, central Asia through the Middle East to southern and eastern Mediterranean countries.

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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: 191–217.
- BOM, 2016. Australian Bureau of Meteorology website. [Accessed March 2016]

http://www.bom.gov.au/climate/data/index.shtml

- Escherich, K. 1905. Das System der Lepismatiden. Zoologica (Stuttgart) 43: 1–164.
- Irish, J. 1990. *Phylogeny of the Lepismatidae (Thysanura), with a Revision of the Southern African Genera*. Ph. D. Thesis (unpublished), Faculty of Science, University of Pretoria. 337 pp.
- Kaplin, V. G. 1992. The bristletails *Desertinoma* gen. n. (Thysanura: Lepismatidae) of the world fauna. *Izvestiya Akademii Nauk Turkmenskoi SSR Seriya Biologicheskikh Nauk* 3: 22–29.
- Kränzler, L., and O. Larink. 1980. Postembryonale Veränderungen und Sensillenmuster der abdominalen Anhänge von *Thermobia domestica* (Packard) (Insecta: Zygentoma). *Braunschweiger Naturkundliche Schriften* 1: 27–49.
- Mendes, L. F. 1979. Note sur quelques malformations rencontrées sur des specimens de *Ctenolepisma* et Asterolepisma (Zygentoma, Lepismatidae). Boletim Sociedade portuguese *Ciência naturales* 19: 95–97.
- Mendes, L. F. 1982. Dados sobre a sistemática evolutiva e a zoogeografia dos Lepismatidae (Zygentoma); Revisão das espécies do género *Lepisma s. latum*. Lisboa: Universidade de Lisboa—Faculdada de Ciências Thesis (unpublished) vol. 2: 317–587.
- Mendes, L. F. 1986a. Sur quelques caracteristiques morphologiques des Lepismatidae (Zygentoma: Insecta). II. Les sensilles spécialisées de l'antennae. In 2nd International Seminar on Apterygota, Sienna Italy 1986, ed. R. Dallai, pp. 217–228. Sienna: University of Sienna.
- Mendes, L. F. 1986b. Sur quelques caracteristiques morphologiques des Lepismatidae (Zygentoma: Insecta). III. Les aires trichobothriales. In 2nd International Seminar on Apterygota, Sienna Italy 1986, ed. R. Dallai, pp. 229–236. Sienna: University of Sienna.
- Mendes, L. F. 1988. Sobre algumas características morfológicas dos Lepismatidae (Zygentoma: Insecta). V. O tipo de macroquetas. Actas do III Congresso Iberico de Entomologia, Lisboa Suppl. 1: 143–148.

- Mendes, L. F. 1991. 1.1. On the phylogeny of the genera of Lepismatidae (Insecta: Zygentoma). In Advances in management and conservation of soil fauna, ed. G. K. Veeresh, D. Rajagopal and C. A. Viraktamath, pp. 3–13. New Delhi Bombay Calcutta: Oxford & IBH Publishing Co. Pvt. Ltd.
- Mendes, L. F. 1996. Some new data on the Microcoryphia and Zygentoma (Insecta) from the United States. *Garcia de Orta, Séries Zoologia, Lisboa* 21(1): 117–126.
- Mendes, L. F. 2004. Zygentoma (Insecta) from the Socotra Archipelago. *Fauna of Saudi Arabia* 20: 357–398.
- Mendes, L. F., and J. Wunderlich. 2013. New data on thysanurans preserved in Burmese amber (Microcoryphia and Zygentoma Insecta). Soil Organisms 85(1): 11–22.
- Misof, B., S. Liu, K. Meusemann, R. S. Peters, A. Donath, C. Mayer, et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346(6210): 763–767. http://dx.doi.org/10.1126/science.1257570
- Molero-Baltanás, R., M. Gaju-Ricart and C. Bach de Roca. 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. http://dx.doi.org/10.1078/S0031-4056(04)70045-1
- Molero-Baltanás, R., M. Gaju-Ricart, C. Bach de Roca and L. F. Mendes. 2010. On *Ctenolepisma ciliata* and a new related species, *Ctenolepisma armeniaca* n.sp. (Zygentoma, Lepismatidae). *Deutsche Entomologische Zeitschrift* 57(2): 243–252.

http://dx.doi.org/10.1002/mmnd.201000021

- Paclt, J. 1967. Thysanura. Fam. Lepidotrichidae, Maindroniidae, Lepismatidae. *Genera Insectorum* 218e: 1–86.
- Schremmer, F. 1964. Ergebnisse der Zoologischen Nubienexpedition 1962. Annalen des Naturhistorischen Museums in Wien 67: 631–650.
- Silvestri, F. 1908. Thysanura. In *Die Fauna* Südwest-Australiens. *Ergebnisse der Hamburger südwestaustralischen Forschungsreise 1905*, ed. W. Michaelsen and R. Hartmeyer, vol. 2, pp. 47–68. Jena: Gustav Fischer.

- Smith, G. B. 2013. A new species of *Heterolepisma* from Barrow Island (Zygentoma: Lepismatidae). *Records of the Western Australian Museum*. Supplement 83: 229–240. http://dx.doi.org/10.18195/issn.0313-122x.83.2013.229-240
- Smith, G. B. 2015a. Australian Lepismatinae (Zygentoma: Lepismatidae). General and Applied Entomology 43: 25–36.
- Smith, G. B. 2015b. New silverfish species (Zygentoma: Lepismatidae) from Barrow Island. *Records of the Western Australian Museum* 30(2): 98–131. http://dx.doi.org/10.18195/issn.0312-3162.30(2).2015.098-131
- Stach, J. 1933. Heterolepisma horni n.sp. und die Zusammenstellung der Arten der Gattung Heterolepisma (Thysanura). Annales Musei Zoologici Polonici, Warszawa 9(22): 341–350 and table XLVII.
- Stach, J. 1935. Die Lepismatiden-Fauna Ägyptens. Annales Musei Zoologici Polonici, Warszawa 11(4): 27–111.
- Uchida, H. 1949. Apterygota aus Neu-Guinea. Insecta Matsumurana 17(1): 38–47.
- Watson, J. A. L., and C. S. Li. 1967. A further pest species of silverfish (Thysanura) from Australia, with a key to the domestic species. *Journal of the Australian Entomological Society* 6: 89–90.

http://dx.doi.org/10.1111/j.1440-6055.1967.tb02121.x

- Womersley, H. 1928. Apterygota from the New Hebrides. *Annals* and Magazine of Natural History (10)2: 56–61, plates V, VI. http://dx.doi.org/10.1080/00222932808672848
- Wygodzinsky, P. 1942. Second contribution towards the knowledge of Diplura and Thysanura from Palestine. *Revista Brasileira de Biologia* 2(1): 29–46.
- Wygodzinsky, P. 1961. Synonymical notes on the Lepismatidae (Thysanura). Pan-Pacific Entomologist 37(4): 213–216.

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