THE AUSTRALIAN SILVERFISH FAUNA (ORDER ZYGENTOMA) – ABUNDANT, DIVERSE, ANCIENT AND LARGELY IGNORED

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Summary

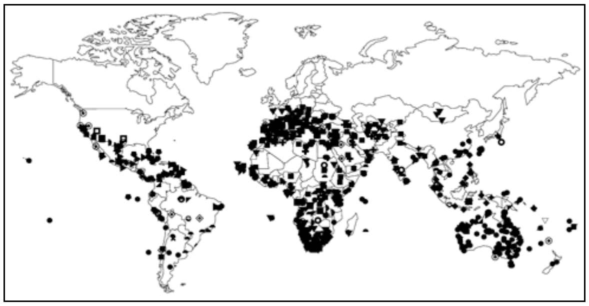
The Australian silverfish fauna is reviewed at the level of genus, based on the literature and almost 1000 additional collection events. The morphology, biology and collection methods for the Zygentoma are briefly reviewed. A key to the genera found in Australia is provided. Seventy species in 23 genera in two of the five extant families have now been described. Of these, six species are introduced cosmopolitan anthropophilic species, although only one of these (*Ctenolepisma longicaudata* Escherich) is common and of only limited economic importance. The fauna demonstrates a high degree of endemism with 88% of described species and 52% of genera known only from Australia. Four (of six) subfamilies of the Lepismatidae are represented by autochthonous species. The lepismatid genera *Acrotelsella* Silvestri and *Heterolepisma* Escherich are very abundant but only a very small percentage of their species have been described; both genera have ranges extending beyond Australia. Within the Nicoletiidae, three of the five subfamilies are represented, many collected from deep subterranean habitats via mining exploration bore holes and many still undescribed. Eight genera of the inquiline Atelurinae belong to a single tribe, the Atopatelurini, with *Wooroonatelura* Smith currently unplaced. Four of these supposedly inquiline genera have been collected from caves or deep subterranean habitats with no obvious host association. The zoogeography of this ancient Order and conservation issues are discussed.

Keywords: Thysanura, key, Lepismatidae, Nicoletiidae, zoogeography

INTRODUCTION

Silverfish belong to an ancient hexapod order, generally considered to be a sister group of the winged insects, diverging from this evolutionary path in the Silurian, some 465-421 Ma (e.g. Grimaldi, 2010 and Misof *et al.*, 2014). Little was known of the Australian fauna, with fewer than 20 species having been described by the Italian entomologist Filippo Silvestri and by Herbert Womersley in the first half of the 20th century (see table 1 for details of species and references). Watson (1970) and Smith & Watson (1991) presented overviews of the Australian silverfish fauna. Most people however are only familiar with the common introduced household nuisance species *Ctenolepisma longicaudata* Escherich. This work examines the composition of the Australian fauna at the level of genus and discusses the zoogeography of the fauna. It reveals a much more diverse fauna than that listed in Smith (1998a) and aims to provide sufficient information for the non-expert to identify species collected in Australia to genus level.

Figure 1. Distribution of extant silverfish (excluding peridomestic species).



Silverfish are widely distributed throughout the warmer parts of the world (Figure 1) however the illustrated distribution also reflects the very uneven research effort in different regions as much as the true distribution. Many areas are poorly documented (e.g. South America and much of Asia) or work is concentrated on a single family only (e.g. subterranean Nicoletiidae in North and Central America).

Karl Escherich wrote the first monograph of the Zygentoma in 1905. Since that time Silvestri (1873-1949) and Petr Wygodzinsky (1916-1987) each described over 100 new species, while more recently Luis Mendes has described a further 130 new species and developed a coherent suprageneric arrangement. Five extant families are now recognised with at least two of these (Tricholepidiidae and Maindroniidae) considered ancient relics with just a single or a few described species with disjunct distributions. The subterranean Protrinemuridae is also poorly known with only ten described species in four genera, distributed from Europe through Asia to South America. None of these three families has yet been found in Australia.

In contrast, the Lepismatidae and Nicoletiidae, each with around 300 described species worldwide, are much more diverse. The lepismatid silverfish have eyes and are usually covered in darker or rarely golden, scales. They are collected under bark, in leaf litter, in soil, under stones, occasionally in the nests of ants or termites and a few species have become peridomestic nuisance pests. Six subfamilies are recognised, four of which occur in Australia. Thirty native Australian species have now been described plus six introduced species.

The Nicoletiidae are eyeless, lack pigment and may be covered in transparent or golden scales. Four of the five recognised subfamilies are known from soil or other subterranean habitats such as caves. Eighteen Australian species are described, belonging to the Subnicoletiinae and Coletiniinae and many undescribed species are held in museum collections. The Atelurinae are generally inquilines, living with ants or termites. Eighteen Australian species have been described with all but one placed within the Atopatelurini Mendes, 2012. The position of *Wooroonatelura* Smith, 2016 is considered uncertain (Table 1).

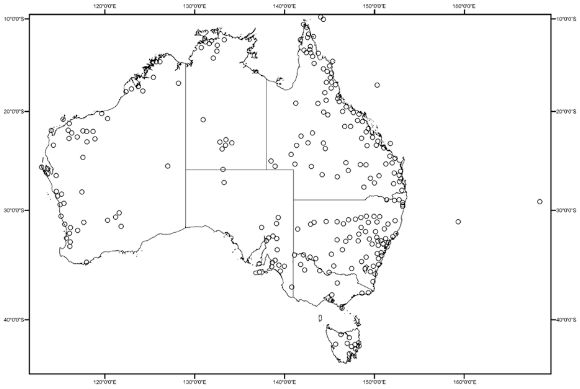
Since the last published review of the Australian fauna (Smith, 1998a), the number of species described has doubled to 72, with the number of genera increasing from 12 to 23 (Table 1). Four of these genera belong to subfamilies not previously recognised as part of the native Australian fauna. The fauna is clearly much richer than previously believed, with a great many undescribed species within museum collections and much of the country still to be adequately surveyed. Considerable work is still required to describe material already available, especially of the genera *Heterolepisma* Escherich and *Acrotelsella* Silvestri, genera that represent about three quarters of all specimens examined during this work. This publication provides a key to the genera present and a short diagnosis of each. It also provides information on the known distribution, habitats and abundance of each genus. The composition and endemicity of the Australian Zygentoma is discussed within the zoogeographic framework introduced by Heatwole (1987).

For clarification, the ordinal name Zygentoma Börner, 1904 is used by all current silverfish taxonomists. This name replaces the deprecated name "Thysanura", now considered as being of no taxonomic value since it was originally created for an order that included, at various times, the silverfish, the Microcoryphia, the Diplura and even the Collembola (see Gaju-Ricart *et al*., 2015).

MATERIALS AND METHODS

Material and records: More than 4000 specimens from about 1000 collection events in Australia were examined (Figure 2). These specimens were collected by the author, by colleagues working on other invertebrate groups (e.g. termites or ants) and conducting environmental surveys (e.g. Barrow Island or Pilbara mining sites in Western Australia) or were available within some museum collections (especially the Australian National Insect Collection in Canberra (ANIC) and Australian Museum, Sydney (AMS)). Published records are also included. All records form part of the author's database, a copy of which is held by the AMS Entomology Department.

Figure 2. Collection event locations (each dot is about 50km in diameter and may include several collection events).



World distribution was established from the taxonomic literature and, while not fully comprehensive, serves as a reasonable approximation of the known distribution within the limits of collection effort. Locality records for the widely distributed anthropophilic species (*Acrotelsa collaris* (Fabricius), *Ctenolepisma longicaudata* Escherich, *Ct. lineata* (Fabricius), *Ct. rothschildi* Silvestri, *Lepisma saccharina* Linnaeus and *Thermobia domestica* (Packard) are omitted as inclusion would only cloud the zoogeographic conclusions. *Nicoletia phytophila* Gervais is also excluded as it was first described from glasshouses at the Paris Museum and may have been transported widely with soil. Similarly *Lasiotheus nanus* (Escherich) is widespread and has probably travelled with the invasive ant species *Pheidole megacephala* (Fabricius). Some marginal cases (e.g. *Hematelura convivens* Escherich in Brazil,

Figure 3. *Ctenolepisma longicaudata* – Sydney, NSW.

Figure 4. *Xenolepisma penangi* – Penang, Malaysia (photo courtesy of Lee Chow Yang).

Figure 5. *Qantelsella louisae* – Bladensburg N.P., QLD.

Figure 6. *Acrotelsella* sp. – Murray Sunset N.P., VIC.

Figure 7. *Australiatelura eugenanae* – Wilsons Promontory N.P., VIC.

Martinique and Cuba, *Bharatatelura malabarica* Mendes in India and Fiji and *Namunukulina funambuli* Wygodzinsky in Brazil, Peru, Sri Lanka and Suriname), where various authors have suggested possible human involvement, are included in the mapped distributions.

Standard abbreviations are used for the states (i.e. New South Wales (NSW), Northern Territory (NT), Queensland (QLD), South Australia (SA), Tasmania (TAS), Victoria (VIC), Western Australia (WA) and National Park (N.P.).

Collection methods: Several methods were used to collect silverfish. The Barrow Island survey (Callan *et al.*, 2011) used unbaited pitfall traps and Winkler sack litter sampling very successfully. Suction sampling of low vegetation collected one species of *Acrotelsella* that only rarely appeared in pitfall traps. Deep subterranean fauna was sampled using leaf litter traps suspended at various depths in mining exploration drill holes or by scaping the walls of the drill holes (Smith *et al.*, 2012, Halse & Pearson, 2014). Cave dwelling species were hand collected. Inquiline species were found under rocks and logs with ants or collected when whole termite nests were sampled.

Figure 8. *Subtrinemura anemone* – Bungonia N.P., NSW.

Silverfish are soft bodied and unable to climb smooth surfaces. Hand collecting is made easier, and damage minimised, by using a small trowel to pick up litter and depositing it in a plastic bowl for careful sorting. Thanotosis (playing dead) can make it surprisingly difficult to find some specimens in the sample. Hand-collecting also allows the specimen to be photographed live, capturing its scale patterns, before it is placed into 70-100% ethanol. Silverfish are much more common in very dry leaf litter, so sampling litter which has accumulated under protection from rain (e.g. under rock overhangs or beneath partially fallen trees) is most productive. Leaf litter caught in the forks of trees or between the fronds of *Macrozamia* plants, where it dries out quickly, can be hand collected and placed into the plastic bowl. Bark sampling with pyrethrum spray (Baehr, 1995) is extremely efficient for some species. Soft bark trees with many cavities (e.g. red bloodwood *Corymbia gummifera*) yielded higher numbers but all bark with cavities is a potential habitat, even if the tree is dead. This method has also been used to successfully sample the lower dead leaves of grass trees (*Xanthorrhoea* sp.).

Molecular data: There are very little molecular data on silverfish in general and Australian silverfish in particular, even though such data could be very useful given the large number of instars and apparent morphological variability. It is however difficult to

Figures 9-22. Morphology 9. typical Lepismatid scale with subparallel ribs, *Heterolepisma buntonorum*, 10. nicoletiid scale with extremely elongated ribs (**r**) arising from a central basal origin and extending well beyond the membrane (**m**), *Wooroonatelura lenta*, 11. lanceolate scale, *Heterolepisma parva*, 12. robust smooth macrochaeta, *Anisolepisma hartmeyeri*, 13. delicately apically bifurcate macrochaeta, *Wooroonatelura lenta*, 14. pectinate macrochaetae, *Hemitelsella clarksonorum*, 15. abiesiform macrochaeta, *Australiatelura tasmanica*, 16. rows of lyriform macrochaetae on apex of tibia, *Ausallatelura ordoarmata*, 17. head with bushes on frons, clypeus and labrum, *Acrotelsella parlevar*, 18. frons of *Ausallatelura ordoarmata*,

19. distal antennal chains showing the trichobothria of each T-annulus (**T-a**) and the specialised asteriform sensillae (**as**), *Xenolepisma monteithi*, 20. basal section of antennae of male with highly modified pedicel, *Metrinura taurus*, 21. mandible with incisor (**i**) and molar (**mr**) regions indicated, *Metrinura taurus*, 22. apex of maxilla showing the pectinate prostheca (**p**) and conule (**c**) of galea, *Pseudogastrotheus undarae*. All scale bars 0.1 mm.

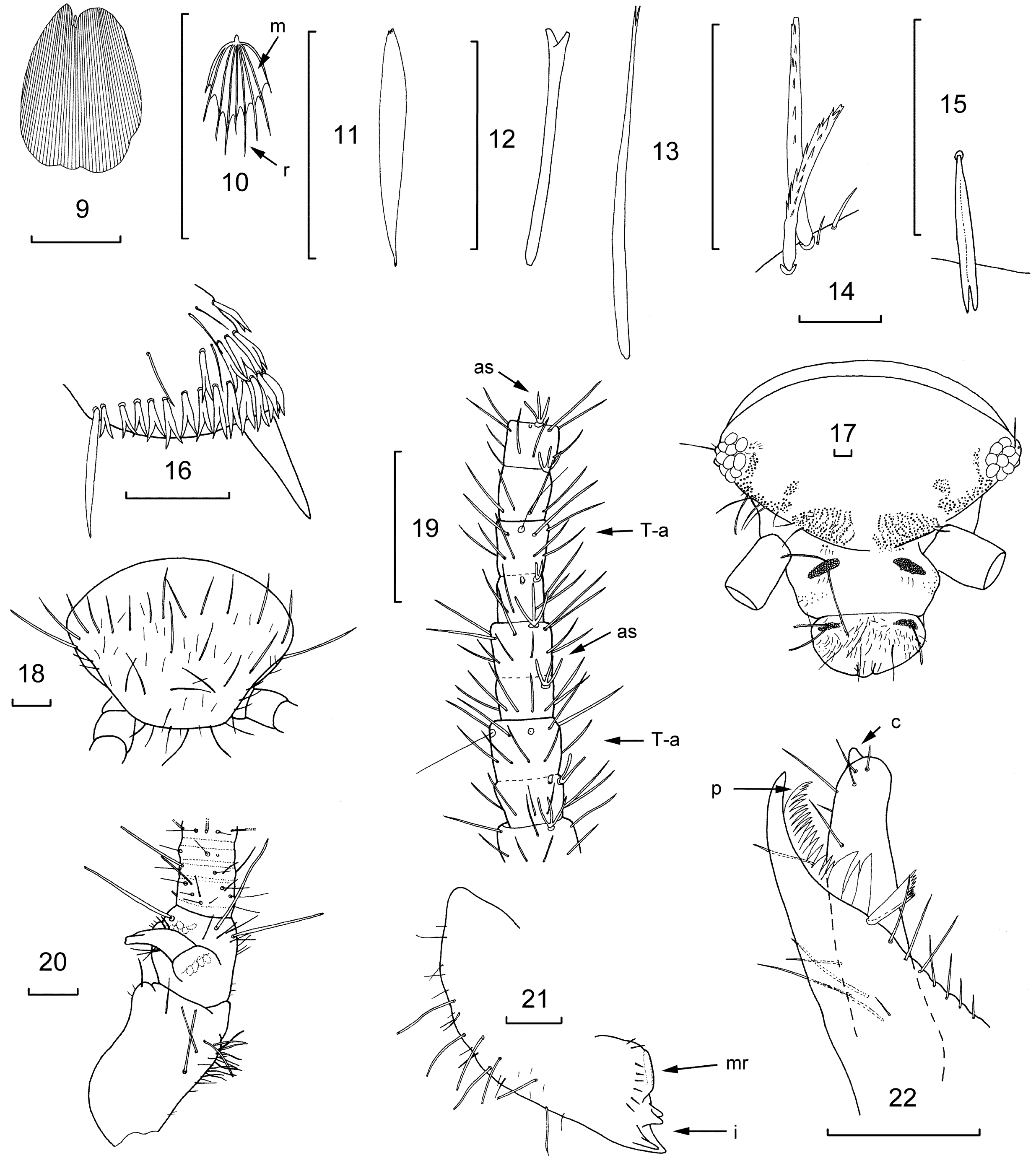


Table 1. Checklist of described Australian species

Type species is underlined, (number Australian of world total), * believed introduced

ZYGENTOMA

(2 of 5 extant families, 21 of 148 extant genera, and 70 of 624 extant species)

LEPISMATIDAE (Latreille, 1802)

(4 of 6 subfamilies, 10 of 41 genera, 34 of 310 extant species)

Acrotelsatinae Mendes, 1991

(2 of 6 genera, 5 of 16 species)

Acrotelsa Escherich, 1905 (1 of 1 species)
Acrotelsa collaris (Fabricius, 1793): 64.*

Anisolepisma Paclt, 1967 (4 of 4 species)
Anisolepisma aquilonaridum Smith, 2016c: 279.
Anisolepisma hartmeyeri (Silvestri, 1908b): 51.
Anisolepisma pigmentum Smith, 2016c: 295.
Anisolepisma subpectinum Smith, 2016c: 300.

Ctenolepismatinae Mendes, 1991

(5 of 17 genera, 16 of 174 extant species)

Acrotelsella Silvestri, 1935 (7 of 19 species)
Acrotelsella devriesiana (Silvestri, 1908b): 53.
  Acrotelsella devriesiana devriesiana (Silvestri, 1908b): 53.
  Acrotelsella devriesiana perspinata (Silvestri, 1908b): 54.
  Acrotelsella devriesiana westralis (Nicholls & Richardson, 1926): 137.
Acrotelsella erniei Smith, 2015d: 170.
Acrotelsella escherichi Womersley, 1939: 37.
Acrotelsella parlevar Smith, 2016a: 66.
Acrotelsella producta (Escherich, 1905): 111.
Acrotelsella silvestri Womersley, 1939: 37.
Acrotelsella splendens (Nicholls & Richardson, 1926): 134.

Ctenolepisma Escherich, 1905 (1 of 2 subgenera, 3 of 118 extant species)*

Ctenolepisma (Ct.) Escherich, 1905 (3 of 39 extant species)
Ctenolepisma (Ctenolepisma) lineata (Fabricius, 1775): 300.*
Ctenolepisma (Ctenolepisma) longicaudata Escherich, 1905: 83.*
Ctenolepisma (Ctenolepisma) rothschildi Silvestri, 1907: 514.*

Hemitelsella Smith, 2016 (2 of 2 species)
Hemitelsella clarksonorum Smith, 2016a: 73.
Hemitelsella transpectinata (Smith, 2015b): 115.

Qantelsella Smith, 2015 (3 of 3 species)
Qantelsella aurantia Smith, 2015b: 107.
Qantelsella louisae Smith, 2015a: 68.
Qantelsella maculosa Smith, 2015b: 99.

Thermobia Bergroth, 1890 (1 of 4 species)
Thermobia domestica (Packard, 1873): 48.*

Heterolepismatinae Mendes, 1991

(1 of 1 genus, 8 of 24 species)

Heterolepisma Escherich, 1905 (8 of 24 species)
Heterolepisma buntonorum Smith, 2016a: 58.
Heterolepisma highlandi Smith, 2014: 16.
Heterolepisma howensis Womersley, 1942: 116.
Heterolepisma kraepelini Silvestri, 1908b: 50.
Heterolepisma michaelseni Silvestri, 1908b: 49.
Heterolepisma parva Smith, 2013: 232.
Heterolepisma sclerophylla Smith, 2014: 9.
Heterolepisma stilivarians Silvestri, 1908b: 47.

Lepismatinae (Latreille, 1802)

(2 of 8 extant genera, 5 of 77 species)

Lepisma Linnaeus, 1758 (2 of 6 species)
Lepisma saccharina Linnaeus, 1758: 608.*
Lepisma umbra Smith, 2015c: 27.

Xenolepisma Mendes, 1981 (3 of 5 species)
Xenolepisma penangi Smith & Kuah, 2011: 27.
Xenolepisma perexiguum Smith, 2015b: 125.
Xenolepisma monteithi Smith, 2015a: 76.

Table 1. (continued).

NICOLETIIDAE (Lubbock, 1873)

(3 of 5 subfamilies, 13 of 100 genera, 36 of 301 species)

Atelurinae Remington, 1954

(1 of 5 tribes, 9 of 71 extant genera, 18 of 142 species)

Atopatelurini Mendes, 2012

(8 of 12 genera, 17 of 46 species)

Allatelura Silvestri, 1947 (2 of 2 species)

Allatelura hilli Silvestri, 1947: 78.
Allatelura amitermina Smith, 2016b: 28.

Ausallatelura Smith, 2007 (2 of 2 species)

Ausallatelura ordoarmata Smith, 2007: 20.
Ausallatelura pauciarmata Smith, 2016b: 33.

Australiatelura Mendes, 1995 (5 of 5 species)

Australiatelura eugenanae Smith, 2016a: 52.
Australiatelura hartmeyeri (Silvestri, 1908b): 60.
Australiatelura kraepelini (Silvestri, 1908b): 58.
Australiatelura michaelseni (Silvestri, 1908b): 57.
Australiatelura tasmanica (Silvestri, 1949): 35.

Australotheus Smith, 2016 (2 of 2 species)

Australotheus eberhardi Smith, 2016b: 40.
Australotheus similatus (Silvestri, 1908b): 55.

Dodecastyla Paclt, 1974 (2 of 3 species)

Dodecastyla crypta Smith & M^{c}Rae, 2014: 108.
Dodecastyla rima Smith & M^{c}Rae, 2014: 114.

Galenatelura Smith, 2009 (1 of 1 species)

Galenatelura deflexa Smith, 2009: 16.

Pseudogastrotheus Mendes, 2003 (2 of 24 species)

Pseudogastrotheus disjunctus (Silvestri, 1908b): 56.
Pseudogastrotheus undarae Smith, 2016b: 44.

Troglotheus Smith & M^{c}Rae, 2014 (1 of 1 species)

Troglotheus bifurcus Smith & M^{c}Rae, 2014: 120.

Unplaced Atelurinae

Wooroonatelura Smith, 2016

Wooroonatelura lenta Smith, 2016b: 52.

Coletiniinae Mendes, 1988

(1 of 6 genera, 1 of 60 species

Lepidospora Escherich, 1905 (1 of 34)

Lepidospora (Brinckina) Wygodzinsky, 1955 (1 of 6)

Lepidospora (Brinckina) relicta Smith & M^{c}Rae, 2016: 42.

Subnicoletiinae Mendes, 1988

(3 of 13 genera; 17 of 42 species)

Metrinura Mendes, 1994 (7 of 10)

Metrinura humusa Smith, 1998b: 164.
Metrinura pedicella Smith, 1998b: 169.
Metrinura queenslandica Smith, 1998b: 167.
Metrinura russendenensis (Smith & Shipp, 1977): 121.
Metrinura subtropica Smith, 2006: 164.
Metrinura taurus Smith & McRae, 2016: 49.
Metrinura tropica Smith, 2006: 166.

Subtrinemura Smith, 1998 (4 of 4)

Subtrinemura anemone (Smith, 1988): 47.
Subtrinemura excelsa (Silvestri, 1920): 216.
Subtrinemura norfolkensis (Smith, 1988): 52.
Subtrinemura spelaea Smith, 1998b: 177.

Trinemura Silvestri, 1908 (6 of 6)

Trinemura calcaripalpa Smith, 1998b: 153.
Trinemura callawae Smith *et al.*, 2012: 105.
Trinemura cundalinae Smith *et al.*, 2012: 109.
Trinemura novaehollandiae Silvestri, 1908b: 62.
Trinemura troglophila Smith, 1998b: 150.
Trinemura watsoni Smith, 1998b: 147

extract DNA from specimens stored for more than a couple of years in 70% ethanol so new, preferably topotypic, material would have to be collected to establish sequences on most currently described species. The little data that do exist suggest that cryptic speciation may be a common feature of some morphospecies. The author now currently places at least one leg from each collection event in 100% ethanol stored in a refrigerator at 4°C, to facilitate later molecular studies.

GENERAL MORPHOLOGY

Body shape: Dorsoventrally flattened although some inquiline forms can be quite arched, almost globular. Body elongate, sometimes parallel-sided or almost cylindrical (e.g. subterranean Nicoletiidae), others with thorax wider than abdomen, the latter tapering strongly posteriorly. Always with three terminal filaments, although in inquiline species these can be very short. Head sometimes partially or completely covered by prothorax.

Scales: Most species, except the Tricholepidiidae, Maindroniidae and many subterranean Nicoletiidae are covered by scales; which are sometimes also found on the appendages. Scales with or without pigment and sometimes arranged to give characteristic patterns. Scales of variable form; those of the Lepismatidae with subparallel ribs that rarely protrude beyond the membranes between the ribs (Figure 9). Ribs of nicoletiid scales converge basally, their distal ends often protruding well beyond the membranes between the ribs (Figure 10). Some scales are narrow without multiple ribs and are referred to as lanceolate scales (Figure 11).

Chaetotaxy: Macrochaetae generally smooth, their apices often apically bifurcate (Figures 12, 13). Many Lepismatidae however have strongly barbed macrochaetae (e.g. Figure 14), which may also be referred to as pectinate or feathered. These macrochaetae can be quite variable in shape including stout “carrot-shaped” forms or others with rounded tips. Macrochaetae in the Lepismatidae are often clustered together forming a single line referred to as a comb, or in a clump referred to as a bush. Mendes (1988c) reviewed the various types of lepismatid macrochaetae. Some Atelurinae have flattened abiesiform macrochaetae (Figure 15) and the tibia may be armed with strong lyriform macrochaetae (Figure 16).

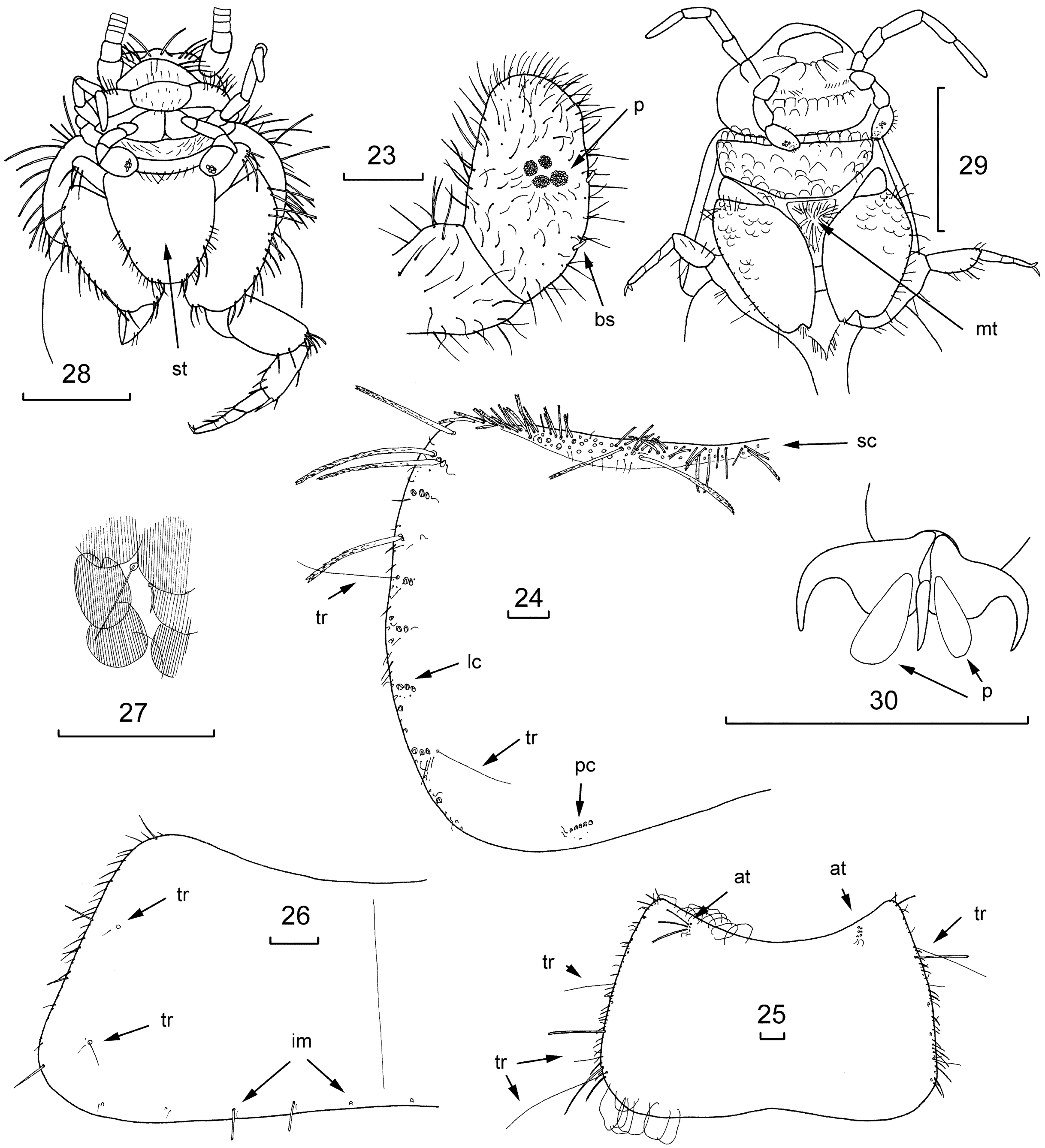
Head: With small eyes composed of about 12 ommatidia, located near the postero-lateral corners (Lepismatidae) (Figure 17) or without eyes (Nicoletiidae) (Figure 18). The arrangement of macrochaetae on the head is generally diagnostic at the level of genus. In some cases, the macrochaetae are restricted to the antero-lateral margins, in other cases they are grouped into very prominent bushes on the frons, clypeus and even the labrum (compare Figures 17 and 18).

Antennae: Long, filiform in most Lepismatidae and the subterranean Nicoletiidae; shorter in the inquiline Atelurinae. Flagellomeres or annuli grouped into repeated patterns distally, referred to as a chain or interval, the most distal annulus of each interval usually with one or two trichobothria. The type of sensillae and their arrangement is diagnostic in some Lepismatidae (Mendes, 1986a, Molero-Baltanás *et al*., 2000 and Adel, 1984) (Figure 19). Pedicel and sometimes the scape in the Nicoletiidae often quite modified in mature males (Figure 20). The apical article in the Atelurinae with a three-pronged sensillum.

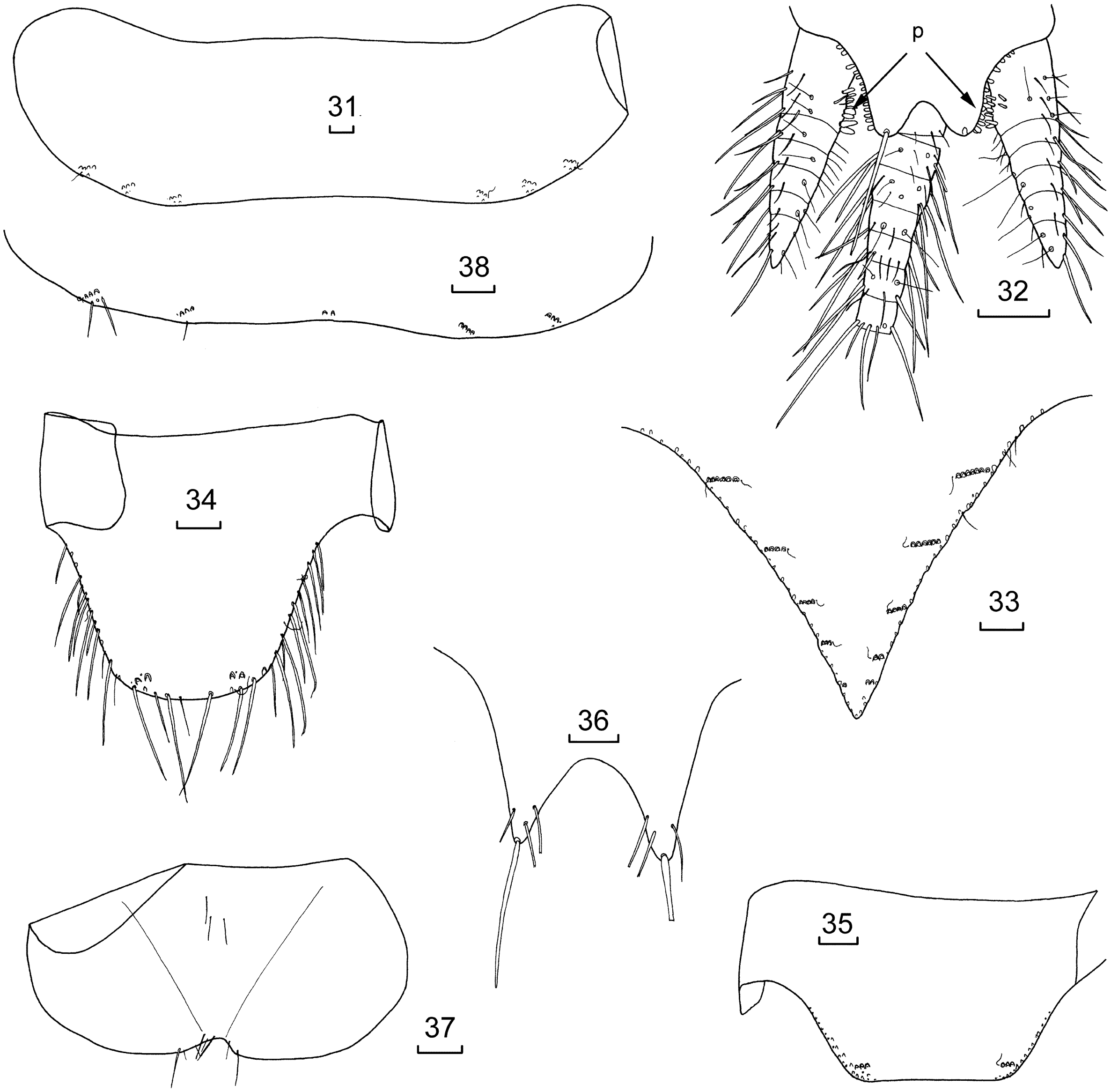
Mouthparts: Mandibles generally strong, usually with well-developed molar and incisor regions and macrochaetae on the outer face (Figure 21). In some Nicoletiidae, especially inquiline Atelurinae, the mandibles are reduced in size relative to the maxillae and the molar region lost. Maxillae (Figure 22) with sclerotised lacinia bearing one to three teeth and usually some lamellate processes at the base of the teeth; external lobe (galea) of similar length, often bearing one or two apical conules; lacinia in the Nicoletiidae also with subapical pectinate prostheca. Maxillary palp of five articles, the most distal often bearing papillae or sensillae of various types; articles occasionally modified in adult males. In one species only (*Thermobia domestica*) the last article of the maxillary palp is secondarily subdivided giving the appearance of six articles. Labium usually with rounded postmentum but sometimes the lateral corners are angled forward; labial palp of four articles, the most distal usually much widened into a flattened circle, oval or axe-shape. The type of papillae (whether compact or “aufgelöst” = dispersed) and their number and arrangement (e.g. in single row or in multiple rows) is taxonomically significant (Figure 23).

Thorax: Thoracic nota often well-developed, sometimes extending well over the sides of the body, thus protecting the legs. Anterior margin of pronotum often with a band of macrochaetae (setal collar) (Figure 24) or else mostly glabrous. In some Acrotelsatinae there are 1+1 tufts of macrochaetae isolated from the anterior margin by scales (Figure

Figures 23-30. Morphology 23. distal article of labial palp showing the four “aufgelöst” papillae (**p**) and basiconic sensillae (**bs**), *Anisolepisma aquilonaridum*, 24. pronotum (left half) showing setal collar (**sc**), trichobothria (**tr**), lateral comb (**lc**) and posterior comb (**pc**), *Acrotelsella erniei*, 25. pronotum showing anterior tufts (**at**) and trichobothria (**tr**), *Anisolepisma pigmentum*, 26. pronotum showing isolated posterior macrochaetae (**im**) and trichobothria (**tr**), *Xenolepisma monteithi*, 27. idem, detail of trichobothrial area showing surrounded by scales, 28. ventral view of head and prothoracic sternum showing free sternal plate (**st**) which partially covers the coxae, *Heterolepisma* sp., 29. ventral view of head and prothoracic sternum showing medial tuft (**mt**) of macrochaetae on raised sternum with the coxae covering most of the sternum, *Anisolepisma pigmentum*, 30. pretarsus showing lamellate pulvilli (**p**) between the two outer claws and the medial empodial claw, *Galenatelura deflexa*. All scale bars 0.1 mm.



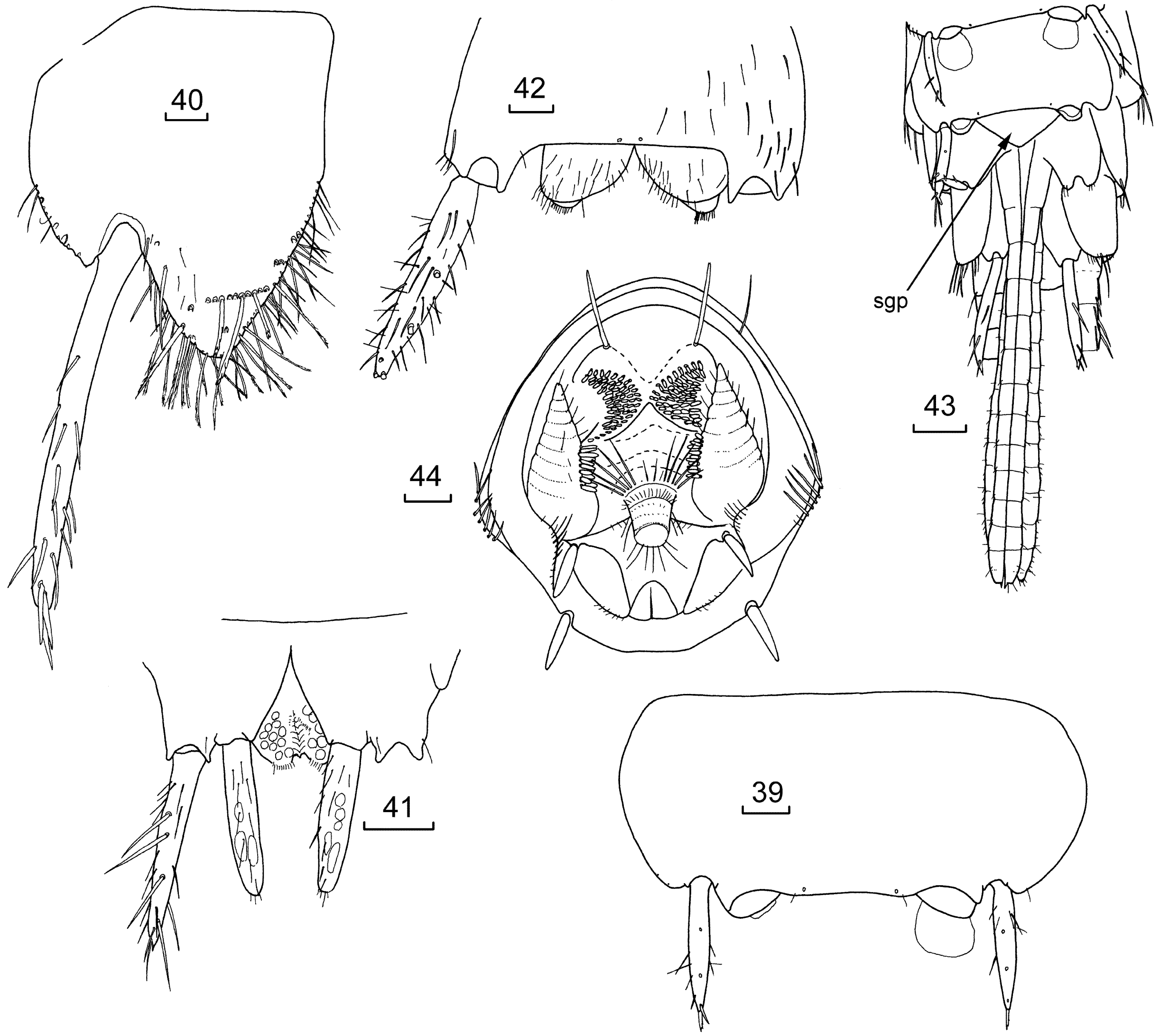
Figures 31-38. Morphology 31. typical urotergite with 3+3 combs, *Hemitelsella transpectinata*, 32. urotergite X and terminal filaments showing pegs (**p**), *Allatelura amitermina*, 33. triangular urotergite X, *Acrotelsella erniei*, 34. round urotergite X, *Anisolepisma hartmeyeri*, 35. trapezoidal urotergite X, *Ctenolepisma rothschildi*, 36. deeply incised urotergite X, *Australiatelura tasmanica*, 37. urosternite I showing division by sutures into median sternum and 1+1 lateral coxites, *Lepidospora (Brinckina) relicta*, 38. urosternite IV with 2+1+2 combs, *Anisolepisma hartmeyeri*. All scale bars 0.1 mm.



25). Lateral margins usually with strong marginal or submarginal macrochaetae, the latter often grouped together into combs in the Lepismatidae. These combs can be quite long (e.g. more than ten macrochaetae) or consist of only one or two macrochaetae. Margins of nota of most lepismatid genera also bearing long, thin trichobothrial hairs (Figure 24) usually limited to well-defined anterior and posterior areas devoid of scales. These trichobothrial areas may be in contact with the margins or isolated from the margins by scales (see Mendes 1986b) (Figures 26, 27). The posterior margins also usually carry strong bristles, often grouped together into 1+1 combs (Figure 24) or else with isolated macrochaetae or glabrous (Figure 26). In one species (*Anisolepisma pigmentum*) there are 1+1 trichobothria in this position.

In the Protrinemuridae, Lepidotrichidae and most Nicoletiidae the macrochaetae are generally restricted

Figures 39-44. Morphology 39. urosternite VI which is entire (not divided into separate sternum and lateral coxites) with styli and eversible vesicles, *Metrinura taurus*, 40. coxite IX and stylus with transverse comb on inner process, *Hemitelsella transpectinata*, 41. separate coxites IX, penis and parameres, *Pseudogastrotheus undarae*, 42. entire sternite IX of male (fused coxites) with stylus and parameres which are apically subdivided, *Trinemura cundalinae*, 43. ventral view of segments VII-IX and ovipositor of female showing subgenital plate (**sgp**), *Metrinura taurus*, 44. posterior view of male showing backwardly-directed fields of pegs on urotergite X and on base of cerci, *Galenatelura deflexa*. All scale bars 0.1 mm.



to the lateral and posterior margins, with smaller setae scattered over the disc. In the Atelurinae, the arrangement and type of macrochaetae is quite diverse with single or multiple transverse rows of simple or abiesiform macrochaetae.

The thoracic sterna in the Nicoletiidae are largely hidden beneath the legs, usually with 1+1 submedial setae. In most Lepismatidae the sternum of each thoracic segment is developed into a free plate, articulated anteriorly only, covering the inner margins of the coxae (Figure 28). The size and shape of these free sterna and their chaetotaxy is important for the taxonomy of some species. The arrangement of the sterna in the Acrotelsatinae is somewhat intermediate as the sterna of the meso- and metathoracic segments are raised to the level of the outer face of the coxa but joined with the body and not free; the coxae can rest against the sides of the raised sternum but are not covered by it. The sternum of the prothorax consists of a raised "bump" bearing a medial tuft of macrochaetae (Figure 29).

Legs: These are held in an almost horizontal plane. The abbreviations PI, PII and PIII used for the pro-, meso- and metathoracic legs respectively. The presence and type of scales on the coxae or tarsi etc can be taxonomically significant, as is the arrangement of bristles, although the latter has probably been under-utilised in systematics. There are usually four tarsal articles (Figure 28) but only three in the Lepismatinae and five in the Tricholepidiidae (not present in Australia); the suture between the last three articles can often be quite indistinct. The pretarsus generally consists of two outer claws and a medial empodial claw. In some non-Australian species the medial claw is not present and in some extremely modified African species there is only one claw. Many species of Atelurinae and just a single lepismatid (from Kenya) have lamellate pulvilli between the claws (Figure 30).

Abdomen: Roman numerals are used to identify the abdominal segments with I being the most anterior. All Zygentoma have ten dorsal tergites (urotergites), the last covering the base of the terminal filaments. The urotergites extend around the sides of the body overlapping the corresponding urosternite. In some nicoletiid species the sutures with the paratergites are visible in dissected material. The dorsal and posterior chaetotaxy generally resembles that of the nota. In the Lepismatidae some or all of the posterior macrochaetae are often grouped into combs (Figure 31), referred to as submedial, sublateral and lateral combs, the latter sometimes referred to as infralateral combs when they are located under the body mediad of the widest part of the body.

Urotergite X in the Nicoletiidae may carry complex modified chaetotaxy in mature males, including pegs on the ventral surface (Figure 32). In the Lepismatidae urotergite X can be quite variable in shape at the genus or subgenus level including acutely triangular, parabolic and trapezoidal, often also bearing combs (Figures 33-36).

There are nine urosternites. In the primitive Tricholepidiidae, these are clearly divided into a basal sternite and 1+1 lateral coxites which carry the vesicles and styli. In some Nicoletiidae, the sutures delineating the sternites and coxites are still visible, especially on urosternite I (Figure 37), but in most silverfish these are completely fused into a single sternite.

In the Lepismatidae most urosternites have posterior combs, usually in a 1+1 arrangement but sometimes with just a single medial comb or 1+1+1 combs or even 2+1+2 combs (Figure 38). The combs may be quite long or, as in many Heterolepismatinae each consist of only a single macrochaeta. Urosternites II-IX may have 1+1 styli (urostyli), although there are fewer pairs in many genera, especially those of the Lepismatidae and Atelurinae. In the Nicoletiidae functional eversible vesicles may be present on urosternites II-VI (Figure 39) or on urosternites II-VII in the Tricholepidiidae. Non-functional vesicles (pseudovesicles) may be present on VII in most Nicoletiidae or VIII in the Tricholepidiidae. Urosternites IV in some Cubacubaninae may bear long submedial processes in mature males. Coxites IX in *Hemitelsella* and some *Ctenolepisma* have transverse combs (Figure 40).

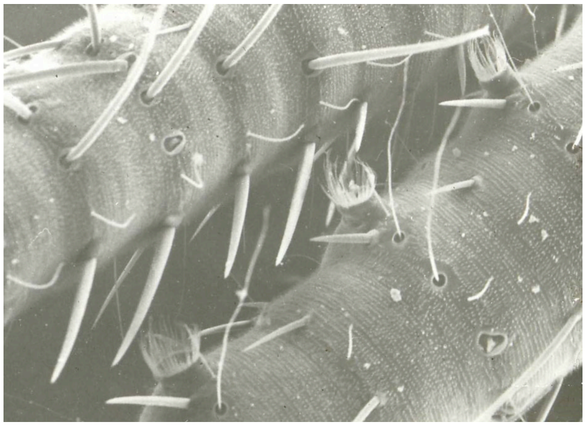
The two most posterior urosternites in the females (VIII, IX) are divided into separate free coxites. In males, urosternite VIII is always undivided and urosternite IX is divided into separated coxites (Figure 41) in the Lepismatidae, Maindroniidae, Protrinemuridae, Atelurinae and Coletiniinae but fused into a single urosternite in the remaining Nicoletiidae (Figure 42).

Genitalia: The penis is composed of two articles (three in the Tricholepidiidae) with a circular or longitudinal opening. The penis is flanked by parameres emerging from coxites IX except in some Lepismatidae. The parameres are apically subdivided in the Subnicoletiinae (Figure 42).

The female ovipositor is composed of four gonapophyses, the anterior two arise from the anterior margin of urosternite VIII and the posterior from urosternite IX. In the Nicoletiidae only, the base of the ovipositor is covered by a free subgenital plate articulating with the posterior margin of urosternite VII (Figure 43). The gonapophyses are pseudo-segmented with a few to as many as 40 divisions. In the Nicoletiidae there is a field of curved hooked setae on the posterior valve. The ovipositor is usually armed with fine simple setae but in some Lepismatidae the apical articles have strongly modified macrochaetae or cuticular spines.

Terminal filaments: These are generally long and slender but are very much reduced in length and more conical in shape in inquiline species of both the Lepismatinae and Atelurinae. Some species of Lepismatidae have scales on the terminal filaments. In mature males of many Nicoletiidae the basal divisions of the cerci, and sometimes the median filament, carry modified stout macrochaetae or pegs (Figure 44). In several Subnicoletiinae there are anemone-like structures (Figure 45).

Figure 45. Anemone-like structures on the cerci of *Subtrinemura anemone.*



GENERAL BIOLOGY

Apart from a few peridomestic, economically significant Lepismatidae, the biology of most Zygentoma genera is poorly known. Adams (1933, 1937), Sweetman (1938), Lindsay (1940) and Laibach (1952) examined the biology of *Thermobia domestica*, *Ctenolepisma longicaudata*, *Lepisma saccharina* and to a lesser extent *Ctenolepisma lineata*. Sturm (1956, 1987, 1997) examined the mating behaviour of *Lepisma saccharina*, *Thermobia domestica* and *Tricholepidion gertschi* Wygodzinsky respectively. Dougherty Picchi (1972) reared the nicoletiid *Nicoletia phytophila* Gervais through two generations. Janet (1896) held large numbers of the inquiline *Atelura formicaria* von Heyden in artificial nests for more two years. The following information is mostly extracted from these publications.

Eggs: The peridomestic Lepismatidae used their ovipositor to deposit soft, oval-shaped eggs, about 1 mm in length, into cracks. Eggs were laid singly or in lots of up to 25 over several days or weeks, some species only laid one or a few eggs at a time, others deposited a batch of eggs over several minutes. The eggs became darker and more opaque with time and deformed relative to the shape of the crack into which they were laid. In the absence of cracks, the eggs were laid into food or even deposited loosely on the surface. On average about 50 eggs were laid per female per year but there were large ranges among individuals. The lepismatid eggs hatched after two to seven weeks and appeared to be quite tolerant of wide ranges in temperature and humidity. Irish (1988a) reported eggs of *Stylifera galapagoensis* (Banks) from the Galapagos Islands in great masses in old beetle borings or cracks in dry wood or in dry cactus pads; all apparently mature and ready to hatch, suggesting a seasonal diapause.
Handschin (1940) reported the eggs of Atelurinae to be very large corresponding to the size of the ovipositor but did not disclose the source of this information.

Females of the nicoletiid *Nicoletia phytophila* each laid one or two pale to dark grey oval eggs per month. Eggs were laid free, unattached to the substrate and most hatched within 46-59 days.

Continuous moulting and life expectancy: The first instar lepismatid silverfish lacked scales and styli and had short appendages (e.g. only two tarsal articles) and probably did not feed, moulting again after just 1-3 days. The length of each instar gradually increased, lasting one to 10 weeks in mature individuals under optimum conditions. Scales appeared in the fourth instar, styli IX in the fourth or fifth, styli VIII in the seventh to ninth and (when present) styli VII in the tenth or even as late as the 21st instar (Sweetman, 1952). Sexual maturity was achieved by the 8th to 13th instar occurring in as little as 7-8 weeks in *Thermobia* but as long as 2.5-3 years in *Ctenolepisma longicaudata*. Silverfish continued to moult after attaining sexual maturity and females could double in size during their fertile life. Moulting was quite a hazardous procedure and most deaths in captive populations occurred during a moult.

The number of moults in a lifetime was not fixed but depended on the life span of the individual. Life expectancy was quite variable between species and individuals. In *Lepisma saccharina* females averaged 20 moults in 698 days but up to 36 moults in 1379 days. One *Ctenolepisma lineata* individual survived more than 66 moults living almost four years. For *Thermobia domestica*, some individuals survived 60 moults, attaining ages of 416 to 551 days; the longest living for almost three years. *Ctenolepisma longicaudata* could live for another four years after reaching sexual maturity so in total perhaps up to seven years. The large number of moults can complicate the interpretation of morphology. New species are usually described using the largest individual in a sample as the holotype.

Regeneration of appendages: Appendages (antennae, palps, legs and terminal filaments) and cuticular outgrowths (scales and macrochaetae) could be completely regenerated at each moult as long as injury did not occur just before the moult. Occasionally more than one moult was necessary before regenerated appendages appeared completely normal (e.g. Sweetman 1934, 1938). Scale covering was often quite damaged by the end of an instar giving the animals a white or blotchy appearance but complete scale patterns returned after a moult. This ability to regenerate lost appendages is probably extremely beneficial when it comes to avoiding predation.

Speed and agility: Silverfish have long legs that articulate in an almost horizontal plane. Movement can sometimes seem explosive when they are first disturbed making capture difficult. They tend to move quickly for short distances before stopping and then moving rapidly again. Manton (1972) described this gait as unstable but very rapid. In complete contrast, some silverfish employ thanatosis either after their initial escape burst or from the beginning. They are very difficult to see in leaf litter when immobile often only becoming obvious when rolled onto their backs revealing the light-coloured ventral surface.

Temperature tolerance: Optimum temperature for each species can vary. *Thermobia domestica* preferred exceedingly warm conditions with an optimum of 37°C. It could survive for a few days in temperatures of 47°C. The lowest temperature at which reproduction occurred was around 32°C. The optimum for *Lepisma saccharina* was around 25°C. *Ctenolepisma longicaudata* preferred a lower temperature range, but population survival depended on indoor temperatures above 16°C. Survival was only a few months at 29°C. *Nicoletia phytophila* was reared at 18-24°C.

Moisture control: With early observations that silverfish do not appear to drink, Beament *et al.* (1964) and Heeg (1967), among others, examined various possible cuticular mechanisms to explain their extraordinary ability to tolerate very hot dry conditions. Noble-Nesbitt (1970) eventually demonstrated that poorly hydrated *Thermobia domestica* could absorb moisture directly from the atmosphere via the anus when returned to 83% RH. Lindsay (1940) had earlier noted rows of papillae around the anus and that the faeces is nearly dry when excreted. Perhaps these papillae contribute to resorption from sub-saturated atmospheres. Edney (1971) later found that a Namibian desert-dwelling *Ctenolepisma* species could regain all lost moisture within a few days when placed into atmospheres of 45.7% or above. *Ctenolepisma longicaudata* tolerated humidity near zero for a couple of weeks and regained the lost moisture within four hours under higher humidity conditions. Moulting was clearly a moisture stress point for this species. Presumably desert species are able to find pockets of higher humidity at intervals frequent and long enough to replenish water lost during hot dry periods.

Nicoletiidae appeared to absorb moisture from damp surfaces using their eversible vesicles (Dougherty Picchi, 1972) as has been demonstrated for the Archaeognatha (Houlihan, 1976).

Diet: Most silverfish are polyphagous. Plant fragments were found in the crop of just about all field collected *Ct. longicaudata* as well as fungal spores and hyphae, pollen, sand grains, insect remains and animal hairs (in general similar to the dust collected from the same homes). In captivity *Ct. longicaudata* bred well on a diet of rolled oats alone, however when offered protein sources they readily ate it. *Thermobia domestica* was fed on whole grain flour plus dried meat. Silverfish ate their own exuviae and were also cannibalistic.

Silverfish could survive long periods without feeding. The last three of 20 test animals (*Ct. longicaudata*) died after 252, 276 and 307 days without food. When fed only filter paper the last three adult insects died after 449, 576 and 636 days. Nymphs however required a more complex diet to grow. Treves & Martin (1994) failed to eliminate cellulose digestion in *Thermobia domestica* with a range of antibiotics suggesting that their cellulase is of intrinsic origin.

Nicoletia phytophila was reared for two generations on a diet of lettuce leaves alone. They were seen to be cannibalistic and to eat some eggs. The absence of any shed skins suggested these too were eaten.

Mating & reproduction: Fertilisation in silverfish is external. In the three species examined, the male engaged the female in a complex "dance" with the aid of some silken threads, before depositing a spermatophore. With further encouragement from the male, the female placed the base of her ovipositor over the neck of the spermatophore for some minutes before then eating the spermatophore. Females must mate after every moult in order to lay fertile eggs. Successful mating appeared to require a degree of synchrony in the moulting cycle between the males and females.

Parthenogenesis has not been demonstrated in the Lepismatidae but the complete absence of males in most populations of *Namunukulina funambuli* suggests parthenogenetic reproduction may be involved. It appears to be much more common in the Nicoletiidae. Females of *Nicoletia phytophila* were reared through two generations proving parthenogenesis (Dougherty Picchi, 1972). Many subterranean and inquiline species are only known from populations of females.

Diurnal rhythms: Pitfall trap studies in dune systems in Somalia (Mendes, 1995b) and Namibia (Watson & Irish, 1988) found many species to be mostly active at night with the largest activity peak just on dawn. Some species were most active just after sunrise, others active throughout day and night.

Life as an inquiline: Most Atelurinae and several Lepismatidae live within the nests of ants or termites. They are generally considered to be "tolerated guests" rather than having a symbiotic relationship. Silverfish are too fast to be caught easily by their hosts. In artificial nests, and in the absence of ants, many *Atelura formicaria* were still alive after more than two years on a diet of honey, sugar, flour and egg yolk (Janet, 1896). In the presence of ants (*Lasius umbratus* Nylander) the silverfish were constantly in motion. The ants had great difficulty catching the agile silverfish but on occasions did succeed. Changing the design of the nest to give "ant-free" refuges increased survival times. Janet reported that the *Atelura* gained their food by stealing from the ants as they passed food from one to the other. This report, with Janet's attractive illustration, created a lot of excitement in the literature at the time, however his observations with this species have not be been seen by others in spite of attempts to do so. Mendes & Schmid (2010) did report individuals of *Allograssiella floridana* Mendes & Schmid contacting the mouth region of two host ants (*Pseudomyrmex gracilis*). It is thought that, at best, such theft is a rare occurrence. The silverfish probably scavenge food remnants from the floor of the nest. Molero-Baltanás *et al.* (2017) examined the relationships of Zygentoma (mostly Lepismatidae) to host ants in Spain finding some species to be obligate inquilines restricted to a single ant genus or a range of host genera, and others to be occasional nest dwellers. More than one species of silverfish could often be found within the same ant nest. Witte *et al.* (2009) found that atelurin silverfish *Malayatelura ponerophila* Mendes *et al.* acquired the cuticular hydrocarbon profile of their host ant *Leptogenys distinguenda* (Emery) by frequent contact with the bodies of their host.

In termite nests the relationship with the hosts would appear to be very different. The silverfish seem to be largely ignored by their hosts. Silvestri (1903) reported silverfish walking over the queen without a reaction from the termites. Video of the Malaysian inquiline species *Crypturelloides mindeni* Smith & Veera Singham in a laboratory colony of the termite *Globitermes sulphureus* Haviland shows the silverfish pushing worker termites out of the way to access the surface below them, with no aggressive response from the termites.

KEY TO THE GENERA OF SILVERFISH KNOWN TO OCCUR IN AUSTRALIA

The following key has been created for the genera known to occur in Australia and will not work outside Australia. Any specimen identified should be compared to the diagnosis of the genus to minimise the chance that the key has resulted in a false identification. The families Tricholepidiidae, Maindroniidae and Protrinemuridae, the subfamilies Mirolepismatinae, Silvestrellatinae, Cubacubaninae and Nicoletiinae (sensu Mendes) and the Atelurinae tribes Atelurini, Dinatelurini, Dionychellini and Grassiellini have not yet been reported from Australia. The genus *Wooroonatelura*, in the absence of knowledge of the males, remains unplaced within the Atelurinae.

1. -Eyes present . . . . Family LEPISMATIDAE . . 2
   -Eyes absent . . . . Family NICOLETIIDAE . . 11

2. -Thoracic sterna largely covered by coxae, prosternum visible as a raised mound bearing a radiating tuft of macrochaetae between prothoracic coxae, meso and meta sterna visible as heart-shaped areas between the meso- and metacoxae (Figure 29) . . . . Subfamily ACROTELSATINAE . . 3
   -Thoracic sterna developed into large plates attached at their anterior margin only, which largely cover the inner anterior margins of the coxae (Figure 28) of all legs 4

3. -Urotergite X acutely triangular, macrochaetae with small pectinations, peridomestic . . . . *Acrotelsa* Escherich, 1905
   -Urotergite X round (Figure 34), macrochaetae smooth (Figure 12) . . . . *Anisolepisma* Paclt, 1967

4. -Macrochaetae pectinate (Figure 14) . . . . Subfamily CTENOLEPISMATINAE . . 5
   -Macrochaetae smooth 9

5. -Urotergites II-V with 3+3 combs (lateral, sublateral and submedial) (Figure 31) 6
   -Urotergites II-V with 2+2 combs (lateral and submedial) 8

6. -Urotergite X acutely triangular (Figure 33) or triangular with rounded apex and with at least 2+2 combs 7

   -Urotergite X trapezoidal (Figure 35) or very obtuse triangular, with only 1+1 combs, usually peridomestic . . . . *Ctenolepisma* Escherich, 1905

7. -Coxites IX in both sexes with transverse combs (Figure 40), styli on coxites IX only . . . . *Hemitelsella* Smith, 2016

   -Coxites IX without transverse combs, styli on coxites VIII and IX . . . . *Acrotelsella* Silvestri, 1935

8. -Urosternites III-VI with medial bristlecomb, maxillary palp may appear to have six articles, peridomestic . . . . *Thermobia* Bergroth, 1873

   -Medial bristlecombs lacking from all urosternites; maxillary palp with usual five distinct articles . . . . *Qantelsella* Smith, 2015

9. -Setal collar present (Figure 24), urotergites II-VII with 3+3 short combs, urotergite X rounded . . . . Subfamily HETEROLEPISMATINAE . . . . *Heterolepisma* Escherich, 1905

   -Setal collar absent, urotergites glabrous or with 3+3, 5+5 or 6+6 isolated macrochaetae (Figure 26), urotergite X trapezoidal . . . . Subfamily LEPISMATINAE . . 10

10. -All trichobothrial areas isolated from margins of nota (Figure 26) . . . . *Xenolepisma* Mendes, 1981

    -Anterior trichobothrial areas in contact with the margin of the nota . . . . *Lepisma* Linnaeus, 1758

11. -Thorax and abdomen with scales, coxites IX in males divided into separate coxites (Figure 41) 12

    -Without scales, coxites IX in males fused into single urosternite (Figure 42) . . . . Subfamily SUBNICOLETIINAE . . 13

12. -Elongate (at least six times longer than wide), subparallel-sided silverfish with long antennae and terminal filaments (>⅓ head and body length), generally in soil or subterranean . . . . .Subfamily COLETINIINAE . . . . *Lepidospora (Brinckina)* Wygodzinsky, 1955

    -Elongate oval or tapering posteriorly (no more than four times longer than wide), terminal filaments short (<⅓ head and body length), generally with ants or termites, sometimes subterranean . . . . Subfamily ATELURINAE . . 15

13. -Eversible vesicles absent from urosternites II-VI . . . . *Trinemura* Silvestri, 1908

    -Eversible vesicles (Figure 39) present on urosternites II-VI or III-VI 14

14. -Eversible vesicles present on urosternites II-VI . . . . *Metrinura* Mendes, 1994

    -Eversible vesicles present on urosternites III-VI . . . . *Subtrinemura* Smith, 1998

15. -Vesicles on urosternite VI glabrous; scales with a few strong ribs that protrude for ⅓ or more of their length beyond the membranes between the ribs (Figure 10) . . . . *Wooroonatelura* Smith, 2016

    -Vesicles absent on urosternite VI or when present, large with prominent setae on the vesicle; scales with ribs that do not usually protrude much more than 10% of their length beyond the membranes . . . . .TRIBE ATOPATELURINI . . 16

16. -Tergites glabrous except for 1+1 macrochaetae in each postero-lateral corner, elongate, subterranean (Figure 83) . . . . . *Troglotheus* Smith & McRae, 2014

    -Tergites with transverse rows of macrochaetae, body shape oniscoid (oval) or ateluriform (tear-drop), usually inquiline but sometimes subterranean 17

17 -All tergites with only a single subposterior row of abiesiform macrochaetae (Figures 15, 71) as well as 1+1 postero-lateral macrochaetae 18

   -Nota with several rows of long simple macrochaetae, urotergites with single submarginal row of simple macrochaetae as well as 1+1 postero-lateral macrochaetae (Figure 69) 21

18. -Urosternite III with 1+1 medial styli, IV-IX with 1+1 lateral styli . . . . *Atopatelura* Silvestri, 1908

    -Urosternites without medial styli on III, 1+1 lateral styli present on IV-IX, V-IX or VI-IX 19

19. -Styli present on urosternites VI-IX . . . . *Pseudogastrotheus* Mendes, 2003

    -Styli more numerous 20

20. -Styli present on urosternites IV-IX . . . . *Dodecastyla* Paclt, 1974

    -Styli present on urosternites V-IX . . . . *Australotheus* Smith, 2016

21. -Eversible vesicles with prominent setae on urosternite VI . . . . *Ausallatelura* Smith, 2007

    -Vesicles absent from urosternite VI 22

22. -Almost no macrochaetae with bifurcated tips; males with deflexed urotergite X with large field of pegs, exposed so that fields of pegs point backwards . . . . *Galenatelura* Smith, 2009

    -Many macrochaetae with bifurcated tips; urotergite IX of males small, not deflexed with the fields of pegs pointing downwards or slightly laterally . . . . *Allatelura* Silvestri, 1947

SYSTEMATICS

Only characters common to all genera in a subfamily or tribe are included in the diagnosis of the subfamily or tribe, and similarly, only characters common to all subfamilies are included in the diagnosis of that family. Diagnoses of the three families not represented in Australia are given; but not those of the subfamilies and tribes not represented.

Zygentoma Börner, 1904

Thysanura Latreille, 1810: 113 *pro parte.*
Zygentoma Börner, 1904: 524.
Type family: Lepismatidae Latreille, 1802.

Family Tricholepidiidae Engel, 2006

Tricholepidiidae Engel, 2006: 237.
Nominotypical genus: *Tricholepidion* Wygodzinsky, 1961.

Diagnosis

Body elongate, dorso-ventrally flattened. Scales absent. Macrochaetae smooth, not grouped into combs. Antennae and terminal filaments long, filiform; pedicel of male without secondary sexual modifications. Head hypognathous with epistomal and postfrontal sulci, compound eyes well developed, ocelli present. Labrum distinctly separated from clypeus. Lacinia with three pectinate projections, galea with apical conules; ultimate article of labial palp with six papillae in two rows. Thoracic sterna weakly developed, largely covered by coxae, not consisting of free plates articulating along the anterior margin. Tarsi of five articles, pretarsus of two lateral claws and one medial empodial claw, without pulvilli. Abdominal sterna large, divided into distinct anterior sternum and postero-lateral coxites which bear functional eversible vesicles on II-VII and non-functional vesicles on VIII in male; eight pairs of styli; female gonapophyses laterally compressed, apically pointed and more sclerotised, without subgenital plate. Male with parameres (Wygodzinsky, 1961).

Distribution

Only a single species known, living under decaying bark of Douglas Fir (*Pseudotsuga menziesii* (Mirb.) Franco) in California. Not known from Australia.

Family Maindroniidae Escherich, 1905

Maindroniinae Escherich, 1905: 37.
Maindroniidae Paclt, 1963: 2.
Nominotypical genus: *Maindronia* Bouvier, 1897.

Diagnosis

Body elongate, campodeiform, lacking scales. Macrochaetae smooth and apically bifurcate, not grouped into combs. Antennae and terminal filaments long, filiform. Head prognathous, with two eyes. Ocelli absent. Lacinia without pectinate processes. Labial palp with the ultimate article dilated and flattened or annular. Tarsi of four articles, pretarsi always with two lateral and one medial claw, without pulvilli. Abdominal tergites without dorsal macrochaetae, abdominal sternites not divided into separate sternum and coxites; eversible vesicles absent. Female with one, seven or eight pairs of styli. Male usually with only one pair of styli. Parameres well developed. Females without subgenital plate.

Distribution

Three species in one genus (*Maindronia* Bouvier, 1897) known from Egypt, Saudi Arabia, Afghanistan and Chile. Not known from Australia.

Family Protrinemuridae Mendes, 1988

Protrinemurinae Mendes, 1988b: 766
Protrinemuridae Mendes, 2002: 206
Nominotypical genus: *Protrinemura* Silvestri, 1942

Diagnosis

Body elongate, subcylindrical. Eyes and ocelli absent. Scales absent. Macrochaetae smooth, simple, sometimes apically bifurcate, not grouped into combs. Antennae and terminal filaments long, filiform, similar in both sexes; pedicel of male lacking a process or glandular area. Galea with two apical conules; prostheca absent; distal article of the maxillae palp very rich in globular sensillae. Tarsi of four articles, pretarsus with two outer claws and a medial empodial claw. Urotergite X of male not transformed, lacking pegs on the ventral face. All tergites with macrochaetae. Urosternites I -VII entire, not divided into sternite plus coxites. Styli on abdominal segments II-IX or less numerous (VII-IX or only IX). Coxal vesicles absent. Coxites IX of male free. Penis rounded with a large subtriangular or ovoid opening. Parameres present, never divided apically, entire or with an apical region more developed than the proximal. Gonapophyses smooth, lacking an area of spinules. Cerci and terminal filament of male like those of the female, lacking specialised chaetotaxy. Subgenital plate of female absent.

Distribution

Disjunct distribution including Greece, Iran, Turkey, China, Japan, Thailand, Indonesia, Malaysia and Chile. Not known from Australia.

Family Lepismatidae (Latreille, 1802)

Lepismenae Latreille, 1802: 70 *pro parte*.
Lepismida Leach, 1815: 76.
Lepismaedes Billberg, 1820: 124 *pro parte*.
Lepismidae Wiegmann and Ruthe, 1832: 475 *pro parte*.
Lepismatidae Burmeister, 1838: 452 *pro parte*.
Lepismidae Grassi, 1888: 582.
Lepismatinae Escherich, 1905: 36.
Gymnothrichi + Ptilothrichi Escherich, 1905: 39.
Lepismatidae (Latreille).—Remington, 1954: 284.
Lepismatidae (Latreille).—Paclt, 1967: 3.
Nominotypical genus: *Lepisma* Linnaeus, 1758.

Diagnosis

Body elongate to short and stout. Eyes present. Ocelli absent. Scales multiradiate, usually round but sometimes of complex shape, ribs not surpassing the posterior margins (except *Neoasterolepisma foreli* Moniez, which is not found in Australia) and almost always subparallel or slightly diverging distally, never arising from a common basal medial origin; lanceolate scales sometimes present. Macrochaetae smooth or pectinate, often grouped together into bushes or combs. Antennae long or short, filiform. Lacinia without pectinate processes but with lamellate processes along the inner margin. Ultimate article of labial palp with two to fifteen papillae, either arranged in a single row or in a 2+2 or 3+2 arrangement (never 3+2+1). Pronotum with or without macrochaetae along the anterior margin (setal collar). Thoracic nota usually with lateral combs and trichobothria which are mostly arranged as an anterior and a posterior trichobothrium on each side of each notum (rarely more numerous or absent or obscured); posterior margin usually with isolated macrochaetae, 1+1 combs of macrochaetae or rarely glabrous. All thoracic sterna usually present as plate attached along its anterior margin, but free posteriorly and covering much of the coxae, except for the Acrotelsatinae where the free sternal plate is absent and the sterna are largely covered by the coxae. Tarsi of three or four articles; pretarsus usually with 1+1 lateral claws and a medial empodial claw although in extremely modified forms only one lateral claw is present; pulvillae absent (except in *Lepitrochisma lawrencei* (Mendes) which is not found in Australia). Urotergites usually with posterior combs or rows of macrochaetae. Urosternites I-VII (VIII in males) entire, without vesicles; usually with various arrangements of one to five posterior combs (absent in *Lepismina*, which is not known from Australia). One to eight pairs of abdominal styli present. Parameres present or absent. Subgenital plate of female absent.

Distribution

All zoogeographic regions but rarely in the colder zones. See discussion on the zoogeography of the genera and subfamilies.

Subfamily Acrotelsatinae Mendes, 1991

Acrotelsatinae Mendes, 1991: 11.
Nominotypical genus: *Acrotelsa* Escherich, 1905.

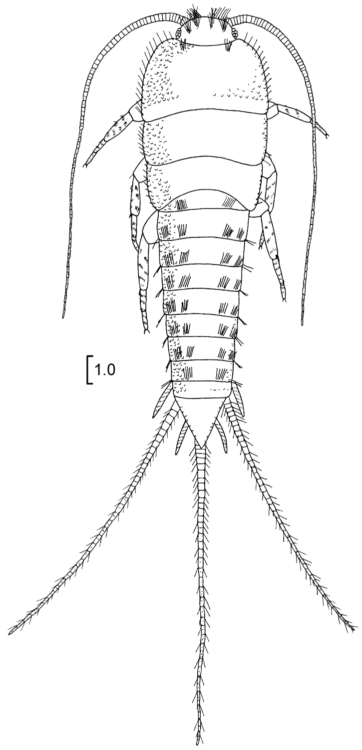
Diagnosis

Macrochaetae pectinate or smooth. Antennae with basiconic sensillae only. Clypeus of normal size (not reduced) and not fused with frons. Distal article of maxillary palp with neither the cylindrical apical sensillum nor branched papillae. Ultimate article of labial palp with 3+2 or 2+2 papillae or 5-6 papillae in a single row. Anterior border of pronotum largely devoid of setal collar but often with 1+1 isolated tufts of macrochaetae or with a small collar occupying about half of the front margin; posterior margin of some or all nota glabrous or with 1+1 macrochaetae or 1+1 trichobothria. All thoracic sterna not free, largely covered by coxae, visible as a raised area between the coxae, the prosternum usually bearing a medial tuft of macrochaetae, the meso- and metasterna cordiform. Tarsi with four articles. Pretarsi with two lateral claws and one medial empodial claw. Urosternites with 2+2 or 2+1+2 combs on at least some segments. Parameres tubuliform, long and thin, without glandular area, with numerous fine setae only. Gonapophyses of female with thin setae and sometimes apically provided with strong sclerotised cuticular teeth.

Acrotelsa Escherich, 1905

Acrotelsa Escherich, 1905: 105.
Type species: *Lepisma collaris* Fabricius, 1793 by subsequent designation, Silvestri, 1935: 307.

Figure 46. *Acrotelsa collaris* (Fabricius, 1793) modified from Escherich, 1905.



Diagnosis

Elongate. Macrochaetae with fine pectinations, grouped into four small bushes on each side of vertex;

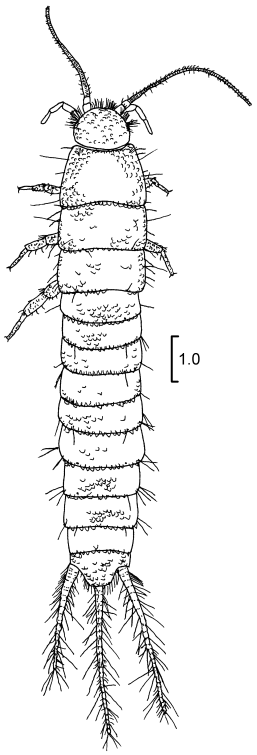
bushes present on large clypeus but only scattered setae on labrum. Antennae long. Papillae of ultimate article of labial palp in 3+2 arrangement. Pronotum with 1+1 isolated tufts of macrochaetae and no setal collar; all nota with small lateral combs. Medial region of prothoracic sternum with prominent tuft of macrochaetae. Urotergite I with 2+2 combs, urotergites II-VII with 3+3 combs and urotergite VIII with 2+2 combs. Urotergite X acutely triangular with series of combs along lateral margins. Urosternites I and II glabrous, urosternites III-VIII with 2+2 combs; coxites IX of female not greatly elongated. Styli present on VIII-IX in both sexes. Ovipositor with sclerotised cuticular teeth.

Habitat, distribution and abundance
Introduced, tropicopolitan anthropophilic species. Only Australian record from Darwin (Watson & Li, 1964). Known to occur in the wild in Afghanistan and Iran and also taken under bark in Hawaii.

Anisolepisma **Paclt, 1967**

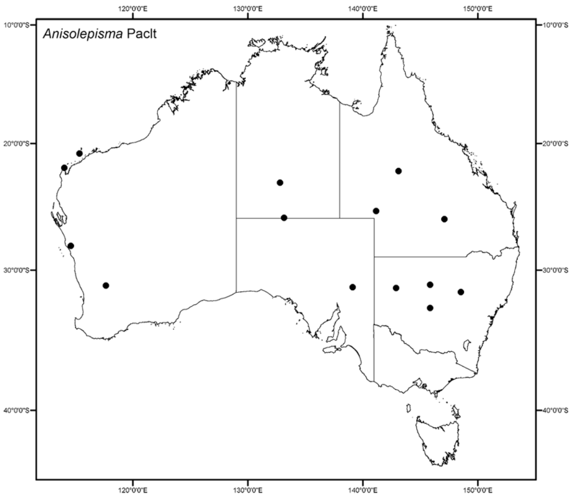
Anisolepisma Paclt, 1967: 27.
Anisolepisma Paclt.—Smith, 2016c: 271 [redefinition].
Type species: *Heterolepisma hartmeyeri* Silvestri, 1905 by original designation.

Figure 47. *Anisolepisma pigmentum* Smith, 2016.



Diagnosis
Elongate with short antennae and terminal filaments. Macrochaetae smooth with short apical bifurcations. Pedicel long with dark scales; distal intervals of antennae with basiconic sensillae and trichobothria. 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. Ultimate article of maxillary palp usually with a curved basiconic sensillum (type C of Adel, 1984)) and often some basiconic sensillae (type B of Adel, 1984). Ultimate article of labial palp with four papillae of the "aufgelöst" type in a diamond configuration. Pronotum with 1+1 isolated tufts, lateral margins with submarginal macrochaetae and four or five long trichobothria or trichobothria-like hairs on each side, posterior margin glabrous. Meso- and metanota also with submarginal macrochaetae and three or four long trichobothria-like hairs, posterior margins with 1+1 macrochaetae or 1+1 trichobothria-like setae. 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. One pair of styli present in both sexes. Ovipositor short, with fine setae only. Scales absent from terminal filaments.

Figure 48. Locality records of *Anisolepisma.*



Habitat, distribution and abundance
Endemic to Australia with four described species, two of which are known only from their type locality. With 16 collection events (Figure 48) this genus is reasonably uncommon but widespread, especially in drier regions. It has been collected in leaf litter, often in very hot exposed sites but has also been found

under or in logs or under stones and once in a pitfall trap.

Subfamily Ctenolepismatinae Mendes, 1991

Ctenolepismatinae Mendes, 1991: 11.
Nominotypical genus: *Ctenolepisma* Escherich, 1905.

Diagnosis

With or without specialised sensillae on the antennae; with pectinate or "false-smooth" (rounded tip) macrochaetae. Lanceolate scales sometimes present. Apical cylindrical sensillum and branched sensillae absent from distal article of maxillary palp. Clypeus of normal size, not reduced (except in some species of north African *Hyperlepisma*) and not fused with frons. Labial palp papillae always in a single row. Anterior margin of pronotum almost always with setal collar (except in the African genus *Monachina*). All nota with lateral combs as well as 1+1 posterior combs and two marginal trichobothrial areas on each side of all nota (trichobothrial areas lost or obscured by dense chaetotaxy in the African genera *Gopsilepisma* Irish, *Monachina* Silvestri, *Namibmormisma* Irish, *Sabulepisma* Irish and *Swalepisma* Irish). Thoracic sterna free and covering coxae (except in the African psammophilous genera *Hyperlepisma*, *Monachina*, *Mormisma* and *Namibmormisma* where the prothoracic sternum is free posteriorly but greatly reduced in size). Tarsi of four articles. Pretarsus with 1+1 lateral and a medial empodial claw. Urosternites never with more than 1+1+1 posterior combs. Parameres absent. Ovipositor variable with simple setae or strong spines formed from modified setae; without cuticular spines.

Acrotelsella Silvestri, 1935

Acrotelsella Silvestri, 1935: 307.
Stylifera (Acrotelsella) Paclt, 1967: 54.
Type species: *Acrotelsa producta* Escherich, 1905 by original designation.

Diagnosis

Elongate with long antennae and terminal filaments. Antennae with basiconic sensillae only. Macrochaetae on head extensive with bushes on frons, clypeus and labrum. Ultimate article of labial palp with 3-12 papillae. Urotergite I with 1+1 combs; urotergites II-VII with 3+3 combs; urotergite VIII with 2+2 combs, urotergite IX glabrous. Urotergite X sharply triangular with multiple combs on each lateral margin. Urosternites I-II glabrous (although one Australian species, *Acrotelsella erniei* Smith, has medial combs on II-VI), urosternites III-VIII with 1+1 combs of macrochaetae; coxites IX of female often greatly elongated. Ovipositor generally not extending far beyond the inner processes of coxite IX, apically variable (thin setae or with strong spines of modified setae). Styli present on urosternites VIII and IX only in both sexes. Scales often present on the terminal filaments.

Figure 49. *Acrotelsella* sp. Northwest Cape, WA.

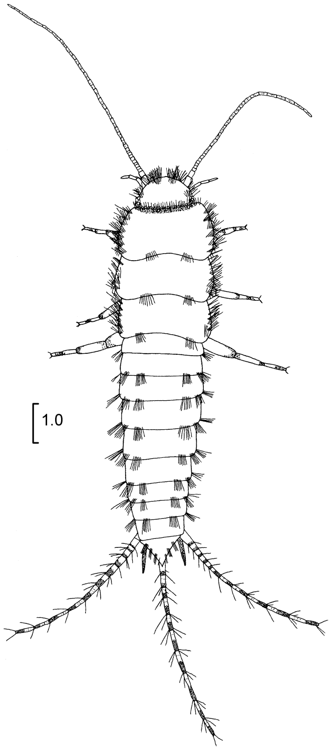
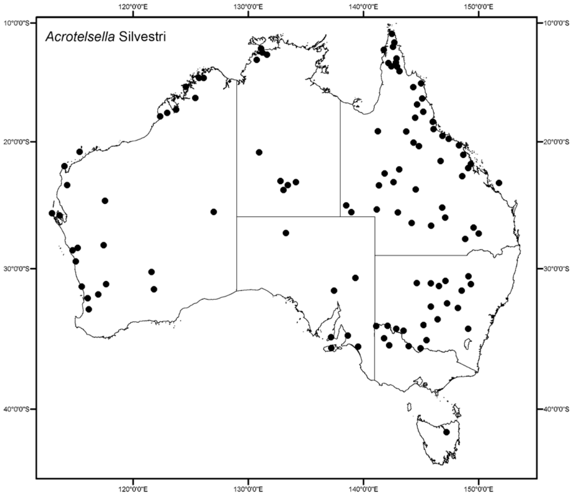


Figure 50. Australian locality records of *Acrotelsella*.



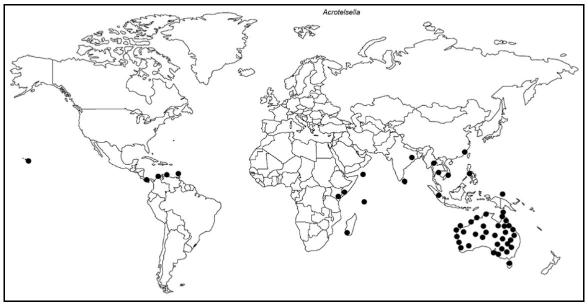
Habitat, distribution and abundance

This genus is one of the two most often encountered in Australia with 309 collection events (Figure 50). It is very common in hot dry regions but can also be found in vine forest or tropical rainforest with a long dry season. *Acrotelsella* is much less common in the temperate forests of south-eastern Australia although still occasionally collected. It is mainly found in leaf litter, under stones or logs, within or under the bark of trees (pyrethrum spray). Often taken in pitfall traps and occasionally within old termite nests or soil where termites are active but does not show typical inquiline morphologies. *Acrotelsella* has occasionally been collected with suction sampling of low vegetation and even taken in malaise traps, suggesting some species climb into bushes perhaps trying to find a dry refuge.

This genus is both large and poorly understood. Mendes (1989) redescribed the Australian species *Acrotelsella splendens* (Nicholls & Richardson) using material from Indonesia and Thailand. Given the large number of species that appear to be present in Australia and the inadequacy of earlier descriptions, the identity of the Asian material with *A. splendens* should be re-assessed.

Acrotelsella is widely distributed throughout the southern hemisphere (Figure 51) and can also be found on several isolated islands suggesting it has reasonable ability to cross oceans. Almost all Australian species appear to be endemic.

Figure 51. World locality records of *Acrotelsella.*



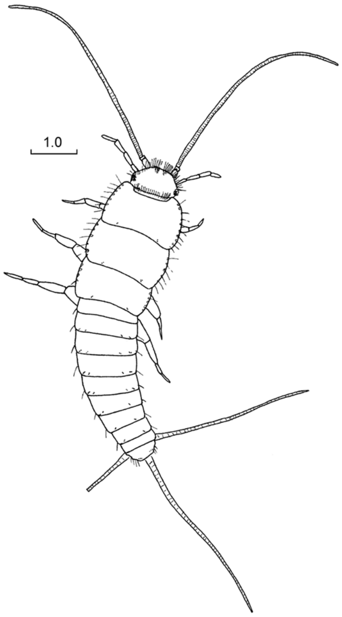
Ctenolepisma Escherich, 1905

Ctenolepisma Escherich, 1905: 75.
Ctenolepisma (Ctenolepisma) Escherich.—Irish, 1987: 149.
Type species: *Lepisma lineata* Fabricius, 1775 by subsequent designation of Paclt, 1967: 38 on grounds of priority.

Diagnosis (of species in Australia)

Elongate, with long antennae and terminal filaments. Lanceolate scales present in some species not found in Australia. Antennae with basiconic sensillae only. Macrochaetae on head extensive with bushes on frons, clypeus and sometimes on the labrum. Ultimate article of labial palp with 5-12 papillae. Urotergite I with 1+1 combs; urotergites II-V, II-VI or II-VII with 3+3 combs, corresponding urotergites VI-VIII, VII-VIII or VIII with 2+2 combs, urotergite IX glabrous. Urotergite X round, trapezoidal or broadly round obtuse triangular with 1+1 small combs. Urosternites I-II glabrous, urosternites III-VIII with 1+1 combs of macrochaetae (the subgenus *Sceletolepisma* Wygodzinsky, 1955, which has medial urosternal combs, has not been reported from Australia); coxites IX of female not greatly elongated, the ovipositor thin and extending well beyond the inner processes of coxite IX. Styli present on urosternites VII-IX, VIII-IX or IX only. Ovipositor long, thin without sclerotised apices or with modified chaetotaxy. Scales sometimes present on terminal filaments.

Figure 52. *Ctenolepisma rothschildi* Silvestri, 1907.



Habitat, distribution and abundance of Australian fauna

All three species found in Australia are anthropophilic and believed to be introduced, although *Ctenolepisma rothschildi* Silvestri has always been collected from outdoor situations, often in remote locations (Smith & Irish, 2013). Womersley (1939) reports *Ctenolepisma lineata* Fabricius, as well as the variety *pilifera* from warehouses in Melbourne. The variety *pilifera* has since been shown by Molero-Baltanás *et al.* (2012) to be a junior synonym of *Thermobia aegyptiaca* (Lucas, 1842). *Ctenolepisma longicaudata* Escherich is the common household species now found in much of the world, and probably occurs in most Australian homes. Lindsay (1940) studied its biology in great detail.

The genus *Ctenolepisma* is predominant in Africa and the Palaearctic, with limited records from the Americas.

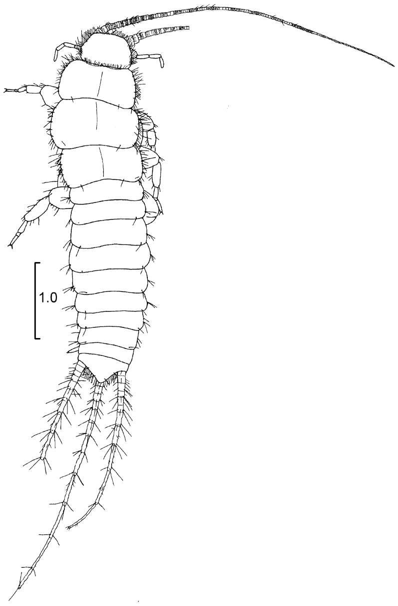
Qantelsella Smith, 2015

Qantelsella Smith, 2015a: 68
Type species: *Qantelsella louisae* Smith, 2015 by original designation.

Diagnosis

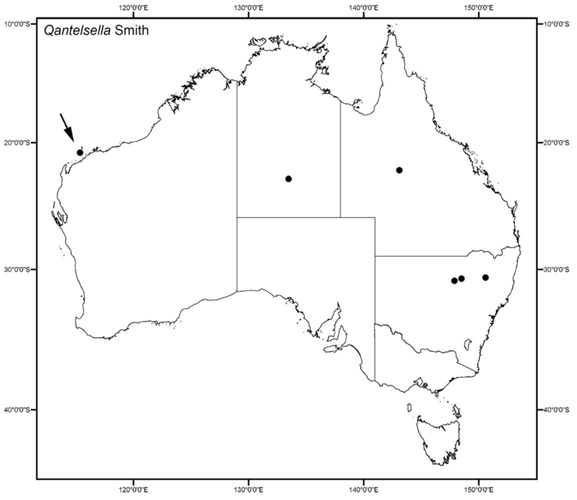
Elongate with long antennae and terminal filaments. Antennae with basiconic and poculiform sensillae. Chaetotaxy on head reduced to weak antero-lateral bushes, small weak bushes or combs on clypeus and labrum. Ultimate article of labial palp with 6-13 papillae. Pronotal collar often reduced in density of macrochaetae, especially in medial region. All nota with lateral combs reduced to only one or two macrochaetae and 1+1 posterior combs reduced to just a single macrochaeta. Thoracic sterna large. Urotergite I with 1+1 combs of only one or two macrochaetae; urotergites II-VIII with 2+2 short combs, the submedial consisting of only a single macrochaeta); urotergite IX glabrous. Urotergite X short, rounded triangular with strong marginal and submarginal setae not arranged in combs. Urosternites I-II glabrous, urosternites III-VIII with 1+1 combs of one to six macrochaetae; coxites IX of female sometimes elongated. Ovipositor extending slightly or well beyond the inner processes, apex with thin setae only. Styli present on urosternites VIII and IX or IX only. Scales absent from terminal filaments.

Figure 53. *Qantelsella louisae* Smith, 2015.



Habitat, distribution and abundance
Qantelsella is endemic to Australia. With 40 collection events (of which only five are not from Barrow Island), the genus appears to be relatively uncommon (Figure 54). All were collected from the drier regions. The two species on Barrow Island were mostly collected in pitfall traps but on a few occasions by suction sampling of low vegetation and using Winkler sack extractions of leaf litter. *Q. louisae* was hand collected in very dry leaf litter.

Figure 54. Locality records of *Qantelsella*



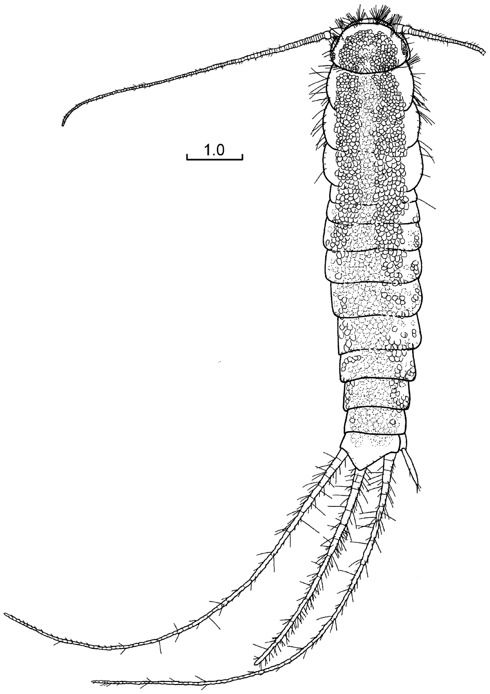
Hemitelsella Smith, 2016

Hemitelsella Smith, 2016a: 672.
Type species: *Acrotelsella transpectinata* Smith, 2015 by original designation.

Diagnosis

Elongate with long antennae and terminal filaments. Scales variable and also lanceolate. Antennae with basiconic and poculiform sensillae. Chaetotaxy on head reduced to weak antero-lateral bushes, small weak bushes or combs on clypeus and labrum. Ultimate article of labial palp with 8-12 papillae. All nota with lateral combs of one to three macrochaetae and 1+1 posterior combs of just one or two macrochaetae located quite laterad. Thoracic sterna large. Tarsi with strong round-tipped setae below. Urotergite I with 1+1 short combs of three to four macrochaetae; urotergites II-VII with 3+3 short combs, urotergite VIII with 2+2 combs; urotergite IX glabrous. Urotergite X triangular with a few short combs on either side. Urosternites I-II glabrous, urosternites III-VIII with 1+1 combs of three to eleven macrochaetae. Coxites IX in both sexes with short inner processes bearing long transverse combs.

Figure 55. *Hemitelsella transpectinata* (Smith, 2015), legs not illustrated.

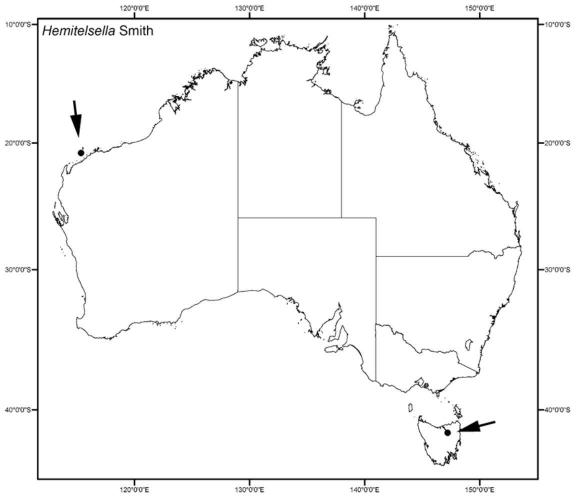


Ovipositor with apical setae modified as strong spines. Styli present on urosternite IX only in both sexes.

Habitat, distribution and abundance

Hemitelsella is endemic to Australia but known only from two areas (Figure 56). Ten collection events were from Barrow Island. Just a single specimen of the second species was collected in Tasmania. The two localities are very different from each other in terms of climate with Barrow Island being hot and dry while northern Tasmania is generally cool and damp, although the specimen was collected in a quite dry locality. All specimens were collected in pitfall traps suggesting a fairly mobile species, probably sheltering under rocks or in soil crevices.

Figure 56. Locality records of *Hemitelsella*.



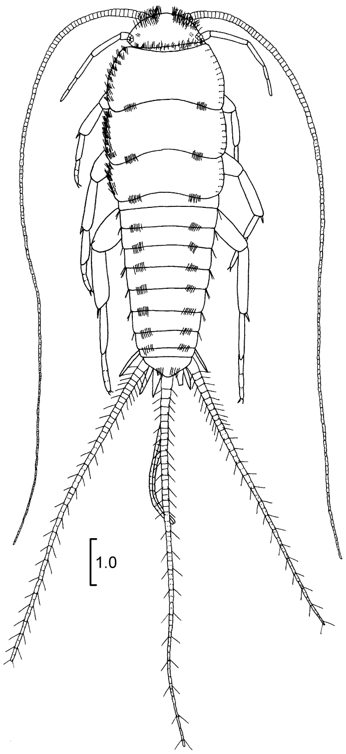
Thermobia Bergroth, 1890

Lepismodes Newman 1863: 13 [*nomen dubium*].
Lepisma (Termophila) Grassi, 1887: 58 [*lapsus calami*].
Lepisma (*Thermophila)* Grassi & Rovelli, 1889a: 3, 8 [*nomen praeoccupae*].
Lepisma (*Thermorphila*) Grassi & Rovelli, 1889b: 55 [*lapsus calami*].
Thermophila Rovelli.—Oudemans, 1889: 425.
Thermobia Bergroth, 1890: 233.
Type species: *Thermobia domestica* Packard, 1873 by monotypy.

Diagnosis (of species occuring in Australia)

Elongate with long antennae and terminal filaments. Antennae with basiconic and campaniform sensillae. Macrochaetae on head extensive with bushes on frons, clypeus and labrum. Maxillary palp may appear to have six articles. Ultimate article of labial palp with five papillae. Nota with numerous long lateral combs. Urotergite I with 1+1 combs; urotergites II-VIII with 2+2 combs, urotergite IX glabrous. Urotergite X rounded shallow triangular with 1+1 long combs.

Figure 57. *Thermobia domestica* (Packard), modified from Escherich, 1905.



Urosternites I-II glabrous, urosternite III with medial comb, urosternites IV-VI with 1+1+1 long combs, urosternites VII and VIII with 1+1 combs. Coxites IX of female elongated into acute triangular inner processes. Ovipositor long and thin, extending well beyond the inner processes of coxite IX, apex with thin setae only. Styli present on urosternites VII-IX.

Habitat, distribution and abundance in Australia
Thermobia domestica (Packard, 1873) is an anthropophilic species that prefers very hot locations such as near ovens in bakeries. It is free-living and probably native in Afghanistan, Iran, Iraq and Syria (Irish, 1988b). Silvestri (1908b) reported specimens from the remote, and now abandoned, WA mining town of Day Dawn. Womersley (1939) notes the species is rare in Australia and that he had only seen specimens from factories in Melbourne. Irish (unpublished) records a specimen in the California Academy of Sciences collection from Milly Milly (WA) collected in 1962 and there is another specimen in ANIC taken from a ship in Sydney in 1972. Womersley (1939) also noted the presence of *Ctenolepisma lineata* var. *pilifera*; a taxon recently confirmed as a synonym of *Thermobia aegyptiaca* (Lucas, 1842) (see Molero-Baltanás *et al.*, 2012). Irish (unpublished) confirms the presence of *Ctenolepisma lineata* var. *pilifera* in some of Womersley's material from Melbourne. It is therefore probable that a second species of *Thermobia* may be or has been present in Australia.

Subfamily Heterolepismatinae Mendes, 1991

Heterolepismatinae Mendes, 1991: 7.
Nominotypical genus: *Heterolepsma* Escherich, 1905.

The subfamily Heterolepismatinae contains only a single genus therefore the diagnosis of the subfamily is the same as for the genus. Mendes (pers. comm.) suggests the genus could be split into two based on the presence/absence of medial combs on urosternite I. Combs of more than one macrochaeta on the remaining abdominal sternites may also be important; both forms are represented in Australia.

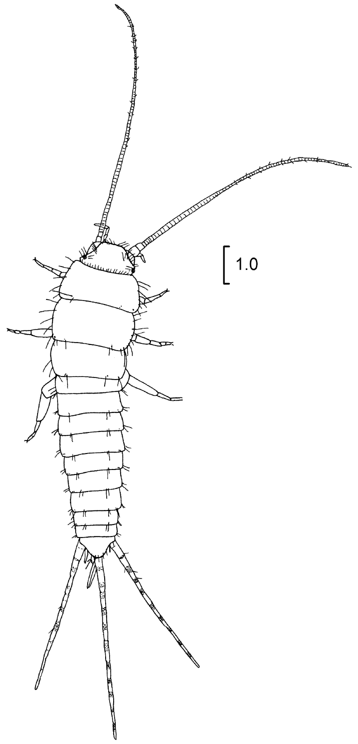
Heterolepisma Escherich, 1905

Heterolepisma Escherich, 1905: 63.
Isolepisma Escherich, 1905: 61.—Stach, 1933: 345.
Notolepisma Tillyard, 1924: 241.—Stach, 1933: 345.
Type species: *Lepisma pampeana* Silvestri, 1902 by subsequent designation of Paclt, 1967: 25.

Diagnosis

Elongate with long antennae and terminal filaments. Antennae with basiconic sensillae only. Macrochaetae smooth. Lanceolate scales sometimes present.

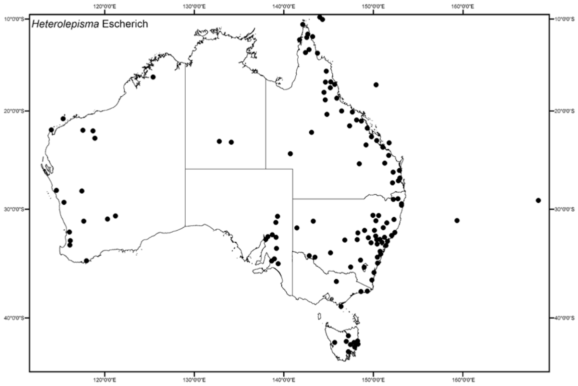
Figure 58. *Heterolepisma sclerophylla* Smith, 2014.



Macrochaetae on head largely restricted to the margins, without strong bushes; bushes absent from clypeus and labrum; clypeus of normal size. Ultimate article of maxillary palp, at least in the males, usually with three plumose sensillae. Ultimate article of the labial palp usually with 3+2 papillae although these can be arranged in an almost linear configuration in some undescribed Australian species. Pronotum with setal collar; all nota with small lateral combs and two trichobothria on each side plus 1+1 posterior combs. Thoracic sterna free. Tarsi of four articles. Pretarsus with two outer claws and a medial empodial claw. Urotergite I with 1+1, 2+2 or 3+3 combs; urotergites II-VII with 3+3 combs; urotergite VIII with 2+2 combs, urotergite IX usually with some infralateral setae. Urotergite X rounded posteriorly, without combs. Urosternite I with or without medial comb, urosternites II-VIII with 1+1 macrochaetae or 1+1 combs of several macrochaetae; coxites IX of female not greatly elongated. Ovipositor long and thin with thin simple setae only. Styli present on some or all of urosternites IV-IX, often one pair more in the female than in the male. Parameres present, usually small but elongate, lacking distinct glandular region. Scales absent from terminal filaments.

Habitat, distribution and abundance
This genus is one of the most often encountered in Australia, with 303 collection events (Figure 59). It is

Figure 59. Australian locality records of *Heterolepisma*.

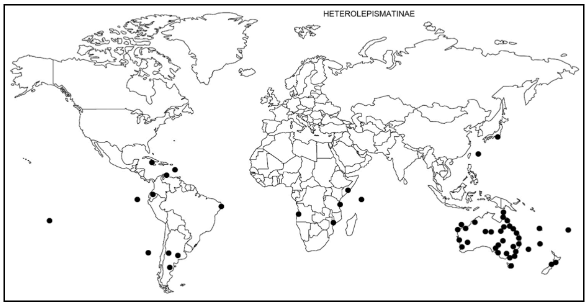


widely distributed from the extreme north to southern Tasmania and is found in most climate regions including wet rainforest fringes to extreme desert. While much less frequently encountered in sub-alpine regions, *H. buntonorum* has been taken at Steppes in Tasmania, an area where snow often occurs in winter. Species have been collected in vinescrub, temperate forests, open woodland and semi-desert. They are commonly collected using pyrethrum sprays to the bark of trees as well as in leaf litter accumulations sheltered from rainfall (e.g. under rock overhangs or fallen tree trunks or within tree hollows). *Heterolepisma* is also found in leaf litter accummulations that dry out quickly such as those caught between the fronds of *Macrozamia* sp. [Zamiaceae] or the dead leaves of grass trees (*Xanthorrhoea* spp.) [Asphodelaceae] and sometimes in leaves accumulating on ledges of exposed rock faces and in leaf or bark litter around the base of trees, occasionally under stones and within abandoned termite galleries. *H. parva* has been taken in pitfall traps in large numbers.

All described Australian species appear to be endemic. The genus however has a fairly wide Gondwanan distribution, including many oceanic islands (Figure 60), as far north as Japan and along the African east coast.

The morphology of the group is much more complex than currently suggested. In addition to the presence of medial combs already mentioned, some species have both round and lanceolate scales. One undescribed species lacks the branched papillae on the apical article of the maxillary palp. On other undescribed species the papillae on the labial palp approach a single line format of five papillae rather than the standard 3+2 arrangement considered as typical for this subfamily. The number of abdominal styli varies from only a single pair in both sexes to as many as six pairs. The number of combs on urotergite I can be 3+3, 2+2 or 1+1. Combs on urosternites II-VIII can consist of just a single macrochaeta on each side (most often in Australia) or longer (up to 11 in one undescribed Australian species).

Figure 60. World locality records of *Heterolepisma* Escherich.



This genus may well contain over 100 morphospecies in Australia alone. They can be sorted into preliminary species groups using the following combination of a number of characters (in order of this author's hypothesised phylogenetic significance): the presence of a medial comb on urosternite I, whether urosternal combs II-VII consist of a single macrochaeta only or combs of macrochaetae, the arrangement of combs on urotergite I (1+1, 2+2 or 3+3) and the number of pairs of abdominal styli (five in both sexes, four in both sexes, three in the female and two in male, two in female and one in male or one only in both sexes). The arrangement of vesicles on the ultimate article of the labial palp (classical 3+2 arrangement or tendency to forming a single line), the size and shape of the thoracic sterna and the shape of urotergite X may also be useful.

Recent, as yet unpublished, molecular studies (of Smith, Mitchell, Lee and Espinasa) suggest the cryptic speciation may be more common than realised. Large differences in base pairs of the mitochondrial genes COI and 16S rRNA and (to a lesser extent) with the nuclear gene 28S exist between various populations of very similar appearance. The number of species therefore may be much greater than indicated by currently used morphological characters.

Subfamily Lepismatinae Mendes, 1991

Lepismatinae Mendes, 1991: 7.
Nominotypical genus: *Lepisma* Linnaeus, 1758.

Diagnosis

Antennae often with specialised asteriform or campaniform sensillae. Macrochaetae smooth, apically bifid or trifid. Clypeus of normal size, reduced or fused with frons. Apex of last article of maxillary palp usually with a single cylindrical sensillum. Apical article of labial palp with 3+2 papillae. Anterior margin of pronotum without setal collar. Thoracic sterna large and free. PIII of male sometimes modified (not in species found in Australia). Tarsi of three articles. Pretarsus with two lateral claws and a medial empodial claw. Parameres primitively with single glandular area, secondarily pseudoarticulated or with strong tendency for reduction and loss of chaetotaxy or vesiculiform and reduced. Ovipositor with simple setae apically. Scales absent from terminal filaments.

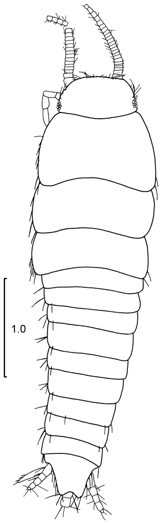
Lepisma Linnaeus, 1758

Lepisma Linnaeus, 1758: 602.
Type species: *Lepisma saccharina* Linnaeus, 1758 by subsequent designation of Latreille, 1810: 423, 113.

Diagnosis

Elongate with short or long antennae and terminal filaments. Antennae with basiconic and campaniform sensillae. Macrochaetae on head largely restricted to the margins, without strong bushes; clypeus and labrum with isolated setae only; clypeus of normal size. Pro- meso- and metanota with anterior trichobothrial areas trianguloid and open, posterior trichobothrial areas all subcircular and isolated from margins by scales; posterior margins glabrous. Thoracic sterna free, prosternum small, meso– and metasterna also somewhat reduced. Urotergite I with 1+1 small infralateral groups plus 1+1 lateral and 1+1 sublateral submarginal macrochaetae; urotergites II-VIII usually with 1+1 infralateral groups, 1+1 lateral, 1+1 sublateral and 1+1 submedian submarginal macrochaetae; urotergite IX with small infralateral groups. Urotergite X trapezoidal, its posterior edge more or less straight, or slightly concave. Urosternites I and II with one medial comb, III-VII (in female) or III-VIII (in male) with 1+1+1 combs. Coxites IX of female not elongated. Ovipositor long and thin with thin simple setae only. Styli present on coxites VIII and IX or on IX only. Parameres well developed, sacciform, exceeding or equalling the posterior limit of the internal process of coxite.

Figure 61. *Lepisma umbra* Smith, 2015, legs not illustrated.



Habitat, distribution and abundance

Lepisma saccharina is a cosmopolitan anthropophilic species. Smith (2015c) discusses the records of the species suggesting that it may no longer be found in Australia even though Womersley (1939) reported the species to be common in most "grain and similar stores in the Commonwealth". Even in Europe this species seems to be becoming less common than *Ctenolepisma longicaudata* in homes. *Lepisma umbra* on the other hand, seems to be an endemic species, found with native termites in QLD. It has only been collected on two occasions (Figure 62).

Figure 62. Locality records of autochthonous *Lepisma umbra*

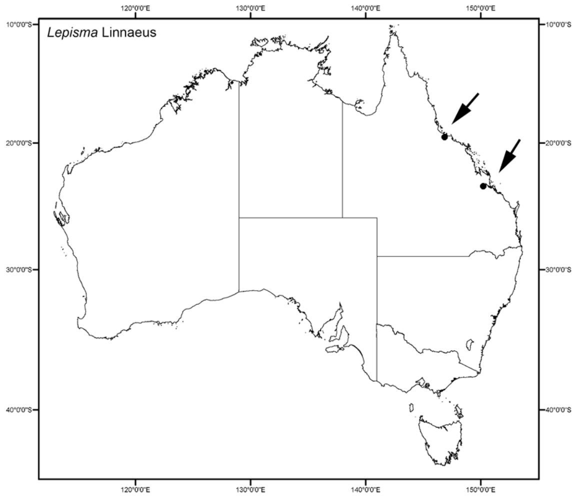


Figure 63. World locality records of *Lepisma* spp. excluding the peridomestic *L. saccharina*

The single Australian native species is the only non-anthropophilic species of the genus yet described outside the Mediterranean and Caucasian area (Figure 63). It is considered a relic of a much more widely distributed ancient genus.

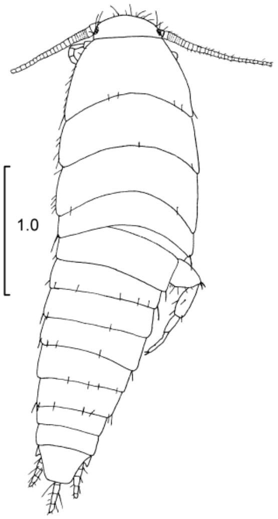
Xenolepisma Mendes, 1981

Asterolepisma (Xenolepisma) Mendes, 1981: 200.
Xenolepisma Mendes, 1988a: 12.
Xenolepisma Smith, 2015a: 74 [redefinition].
Type species: *Lepisma globosa* Escherich, 1905 by original designation.

Diagnosis

Compact with short antennae and very short terminal filaments. Antennae with basiconic and asteriform sensillae (Figure 19). Macrochaetae on head largely restricted to the anterior margin and around eyes, clypeus merged with frons; clypeus and labrum with isolated setae only. All trichobothrial areas of all nota closed (isolated from margins by scales); posterior margins glabrous (except for macrochaeta in posterolateral corner) or with isolated submarginal macrochaetae. Thoracic sterna free, prosternum smaller than also somewhat reduced meso- and metasterna. All urotergites with infralateral macrochaetae with remaining medial part of posterior margin of urotergites II-IX glabrous or with up to six submarginal macrochaetae on each side. Urotergite X trapezoidal, its posterior edge more or less concave. Urosternite I glabrous, II with a medium comb, III-VII (in female) on III-VIII (in male) with 1+1+1 combs. Coxites IX of female not elongated. Ovipositor not long, but thin with thin simple setae only. Styli present on coxites VIII and IX in both sexes. Parameres sacciform, reduced.

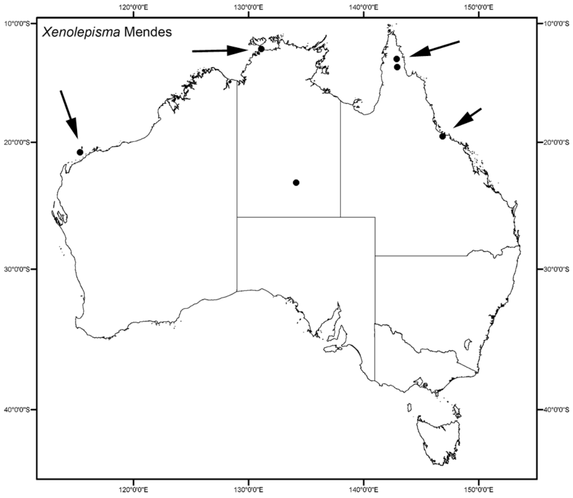
Figure 64. *Xenolepisma monteithi* Smith, 2015, most legs not illustrated.



Habitat, distribution and abundance

Xenolepisma species were collected on seven occasions (Figure 65), usually with ants. It has a body form typical of mymecophilic species (tapered form with short terminal filaments).

Figure 65. Australian locality records of *Xenolepisma* spp.



The genus is known from just a few widely scattered localities in Australia. It is also known from southern Africa, India and Malaysia (Figure 66). Two of the described Australian species appear to be endemic and one was originally described from Malaysia (Smith *et al.*, 2011).

Figure 66. World locality records of *Xenolepisma* spp.

Family Nicoletiidae (Lubbock, 1873)

Nicoletiadae Lubbock, 1873: 201.
Gymnodermata Joseph, 1882: 25.
Nicoletiinae Lubbock.—Escherich, 1905: 36.
Nicoletiidae Lubbock.—Remington, 1954: 284.
Nominotypical genus: *Nicoletia* Gervais, 1844.

Diagnosis

Body elongate to short and stout. Eyes and ocelli absent. Nearly always off-white or golden coloured. Scales, when present, multiradiate, the ribs usually originating from a single central base and often surpassing the posterior margins of each scale (with the exception of a single Portuguese species of Coletiniinae where the ribs are subparallel); scales sometimes quite modified. Macrochaetae never pectinate, always smooth and often with bifurcated apices, never grouped into closely packed bushes or combs; sometimes modified into flattened abiesiform or lyriform bristles. Antennae long filiform or shorter with fewer intervals (usually <20), the pedicel often modified in adult males. Lacinia with pectinate (prostheca) and lamellate processes along the inner margin; galea often with apical conules; apical article of maxillary palp usually with one to several branched papillae. Ultimate article of labial palp with six papillae arranged in a 3+2+1 arrangement. Pronotum with or without macrochaetae along the anterior margin. Thoracic nota usually with macrochaetae along the lateral and posterior margins and sometimes also on the face; trichobothria absent from nota. All thoracic sterna hidden below coxae of the legs, never developed into a free plate covering the coxae, nor raised into a medial process bearing a tuft of macrochaetae. Tarsi of four articles. Pretarsus usually with 1+1 lateral claws and a medial empodial claw (rarely absent); pulvillae sometimes present. Urotergites usually with macrochaetae along the lateral and posterior margins and sometimes over the face. Abdominal sternites often bearing vesicles and/or styli, sometimes divided by a visible suture into a medial sternum and postero-lateral coxites. Urosternite VII with 1+1 pseudovesicles. Coxites IX in males either as separated plates or fused into a single sclerite; coxites VIII and IX always separate in females. Parameres always present, sometimes apically divided. Base of ovipositor always covered by subgenital plate. Ovipositor never bearing apical spines. Gonapophyses IX in female with an internal subdistal area of spinules.

Subfamily Atelurinae Remington, 1954

Atelurinae Remington, 1954: 284.
Nominotypical genus: *Atelura* Heyden, 1855 by original designation.

Diagnosis

Body short and either oval (onisciform) or tear-drop shaped (ateluriform), dorsally convex with short terminal filaments. Scales always present, often giving a golden appearance; scales sometimes quite modified; scales present or absent from head. Head rounded, not emarginate at the level of the antennae. Antennae approaching moniliform; apical interval bearing a distinctive three-pronged sensillum. Pedicel of mature males with or without secondary sexual modifications. Mandibles sometimes reduced with molar region very small or absent. Galea often with apical conules. Pronotum mostly without macrochaetae along the anterior margin. Nota obviously wider and longer than abdominal tergites. Tibia of legs usually with apical lyriform macrochaetae. Pretarsus with or without pulvillae. Abdominal sternites never divided into a medial sternum and postero-lateral coxites; often bearing vesicles and/or styli. Coxites IX never fused into single plate. Urotergite X of mature males usually with pegs on the ventral surface as well as on the basal divisions of the cerci. Median dorsal appendage of mature males with or without pegs.

Tribe Atopatelurini Silvestri, 1908

Atopatelura Silvestri, 1908a: 369.
Atopatelurini Mendes, 2012: 22.
Nominotypical genus: *Atopatelura* Silvestri, 1908 by original designation.

Diagnosis

Head almost always exposed, setose, without scales. Body scales typical, rarely modified. Pedicel of mature males with fovea but without apophysis. Galea with or without a single apical conule. Legs with lyriform spines that are sometimes very abundant; pulvillae sometimes present. Urotergite X of males incised trapezoidal with 1+1 apical macrochaetae, often with pegs on the ventral surface. Cerci of mature males with pegs; rarely transformed. Abdominal vesicles VI present or lacking, when present always armed with setae. Parameres never apically divided. Male cerci with cylindrical pegs; male paracercus not modified.

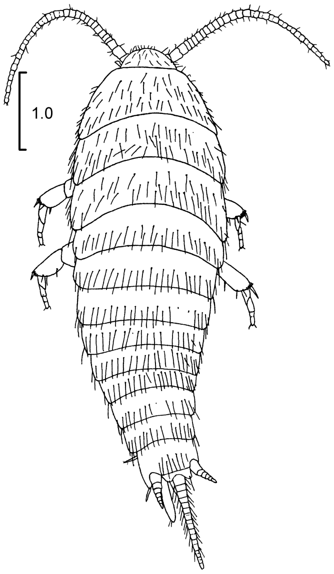
Allatelura Silvestri, 1947

Allatelura Silvestri, 1947: 74.
Allatelura Silvestri.—Smith, 2016b: 23 [redefinition].
Type species: *Allatelura hilli* Silvestri, 1947 by original designation.

Diagnosis

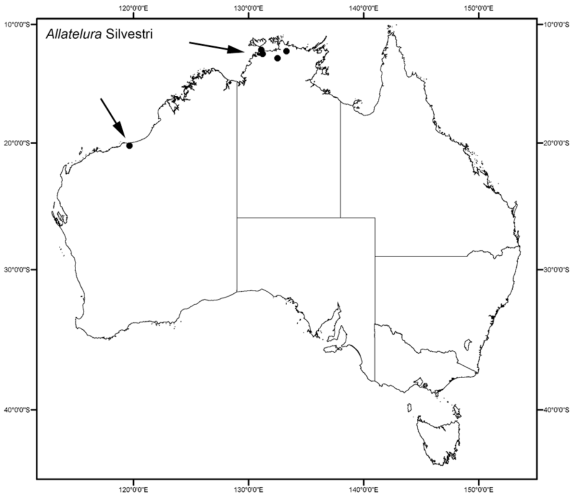
Ateluriform with short antennae. Scales round or pointed with ribs of both dorsal and ventral scales surpassing the margins by about 10% of their length. Macrochaetae with delicately bifurcate apices; abiesiform macrochaetae absent. Head only slightly covered by pronotum along posterior margin, with long, strong setae in irregular rows. Mandibles comparatively small with a reduced or absent molar region. Galea without apical conules. Maxillary palp of mature males with wart-like process on penultimate article. Labium with distinct forward directing process on each of the postero-lateral corners of postmentum. Last article of labial palp very elongate oval. Thoracic nota with multiple

Figure 67. *Allatelura hilli* Silvestri, 1947.



irregular rows of long macrochaetae on the face. Tibia with long rows of lyriform macrochaetae distally. Pretarsus with large membranous pulvillae. Urotergites each with a single irregular row of long macrochaetae as well as a marginal macrochaeta in each postero-lateral corner. Urotergite X small with rounded posterior corners; ventral face with 1+1 fields of pegs in mature males. Urosternites I-V without vesicles or styli; urosternite VI without vesicles; urosternite VIII in male with concave posterior margin. Urosternites VI-IX with short styli. Parameres deeply set in urosternites IX, long and wide with large numbers of minute glandular rods clustered into large fields on the inner surface. Cerci short, basal division in both sexes several times longer than remaining divisions, basal division in mature males with group of pegs. Median dorsal appendage curved downwards without pegs in both sexes.

Figure 68. Locality records of *Allatelura* spp.



Habitat, distribution and abundance

Endemic to Australia with just fourteen collection events, all in the north (Figure 68). Collected with termites of the genera *Mastotermes* [Mastotermitidae], *Amitermes* [Termitidae] and *Coptotermes* [Rhinotermitidae].

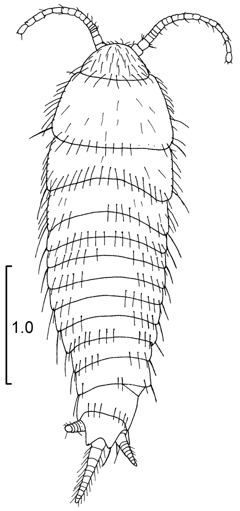
Ausallatelura Smith, 2007

Ausallatelura Smith, 2007: 19.
Ausallatelura Smith.—Smith, 2016b: 32 [redefinition].
Type species: *Ausallatelura ordoarmata* Smith, 2007 by original designation.

Diagnosis

Ateluriform, elongate with short antennae. Scales round or pointed with ribs on both dorsal and ventral scales surpassing the margins by about 10-15% of their length. Macrochaetae simple or with delicately bifurcate apices; abiesiform macrochaetae absent. Head not or only slightly covered by pronotum along posterior margin, with long, strong setae in irregular rows. Mandibles comparatively small with a reduced molar region. Galea without apical conule or with single low flat conule. Labium with rounded postero-lateral corners of postmentum. Ultimate article of labial palp very elongate, oval. Thoracic nota with single submarginal row of macrochaetae as well as one or more irregular rows of long, fine setae on the face. Tibia with either just two to three lyriform macrochaetae distally or else two to three rows of

Figure 69. *Ausallatelura pauciarmata* Smith, 2016, legs not illustrated.

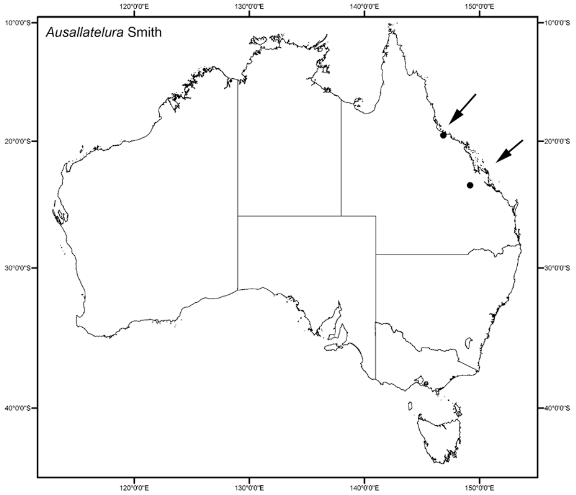


lyriform macrochaetae. Pretarsus simple, without pulvillae. Urotergites each with a single irregular row of long macrochaetae as well as a marginal macrochaeta in each postero-lateral corner. Urotergite X trapezoidal with deep or shallow medial notch. Urosternites I-V without vesicles, styli present on urosternites V-IX or VI-IX, urosternite VI with styli and large eversible vesicles bearing setae. Males unknown.

Habitat, distribution and abundance

Endemic to Australia with three collection events only, all in eastern QLD (Figure 70), all with termites of the genus *Amitermes* [Termitidae].

Figure 70. Locality records of *Ausallatelura* spp.



Australiatelura Mendes, 1995

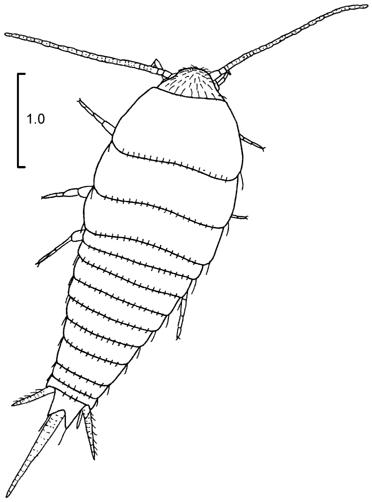
Australiatelura Mendes, 1995a: 98.

Type species: *Atopatelura kraepelini* Silvestri, 1908 by original designation.

Diagnosis

Ateluriform with short antennae. Scales round with ribs not or only slightly surpassing the margins of the scale dorsally but by about 10% on the ventral scales. Macrochaetae simple or apically bifurcate, abiesiform macrochaetae present on all nota and urotergites. Head not or only slightly covered by pronotum along posterior margin, with longer and shorter, strong setae in slightly irregular rows. Mandibles with well-developed incisor and molar regions. Galea with a single prominent apical conule. Labium with round postero-lateral corners. Ultimate article of labial palp oval. Thoracic nota with a submarginal row of abiesiform macrochaetae as well as a longer macrochaeta in each postero-lateral corner. Tibia with three lyriform macrochaetae distally. Pretarsus without obvious pulvillae. Abdominal tergites also with single row of abiesiform macrochaetae. Urotergite X trapezoidal with acute apices and deep notch between. Underside of urotergite X in mature males with 1+1 fields of pegs. Urosternites I-V without vesicles; urosternite VI with large vesicles bearing setae; urosternite VII with pseudovesicles. Styli on segments III-IX, those on III located medially. Urosternite VIII in male with convex posterior margin. Parameres long and sometimes wide. Cerci short, basal division not longer than other divisions, the basal divisions in mature males with group of pegs. Median dorsal appendage without pegs in both sexes.

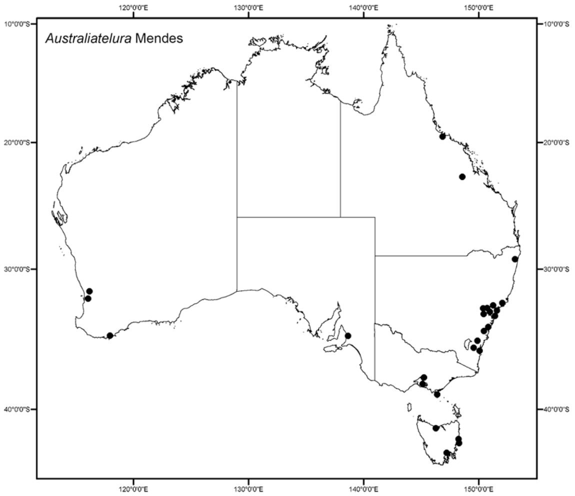
Figure 71. *Australiatelura tasmanica* Silvestri 1949.



Habitat, distribution and abundance

Endemic to Australia and fairly abundant (62 collection events), predominantly in the south, including Tasmania (Figure 72). Generally collected

Figure 72. Locality records of *Australiatelura* spp.



under stones with ants including species of *Amblyopone* Erichson, 1842, *Camponotus* Mayr, 1861, *Colobopsis* Mayr, 1861, *Iridomyrmex* Mayr, 1862, *Myrmecia* Fabricius, 1804, *Pheidole* Westwood, 1839, *Rhytidoponera* Mayr, 1862, but occasionally it is also found with termites (e.g. *Coptotermes* Wasmann, 1896). Limited molecular data (COI) of several morphologically very similar forms, collected along the east coast of Australia, suggest much work is required to clarify the systematics of the genus.

Australotheus Smith, 2016

Australotheus Smith, 2016b: 38.

Type species: *Australotheus eberhardi* Smith, 2016 by original designation.

Diagnosis

Ateluriform. Scales round with ribs not or only slightly surpassing the margins of the scales. Abiesiform macrochaetae present on all nota and urotergites. Head free, with numerous flattened macrochaetae in irregular rows. Mandibles with well-developed incisor and molar regions. Galea with single prominent apical conule. Labium with round postero-lateral corners. Ultimate article of labial palp oval. Nota with single submarginal row of abiesiform macrochaetae as well as a longer macrochaeta in each postero-lateral corner. Tibia with three lyriform macrochaetae distally. Pretarsus without obvious pulvillae. Urotergites with chaetotaxy similar to nota. Urotergite X trapezoidal with acute apices and deep notch between. Ventral face of urotergite X with 1+1 fields of pegs in mature males. Urosternites I-V without vesicles; urosternite VI with large vesicles bearing setae; urosternite VII with pseudovesicles. Styli on segments V-IX. Parameres long. Basal division of cerci not longer than other divisions, bearing pegs in mature males. Median dorsal appendage without pegs.

Figure 73. *Australotheus eberhardi* Smith, 2016, legs not illustrated.

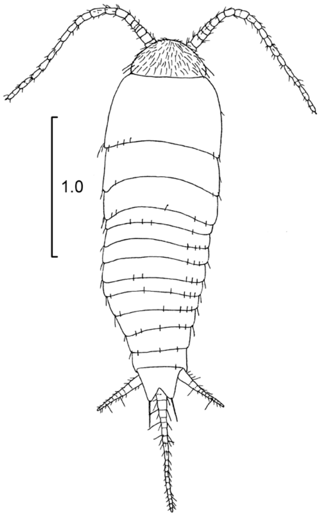
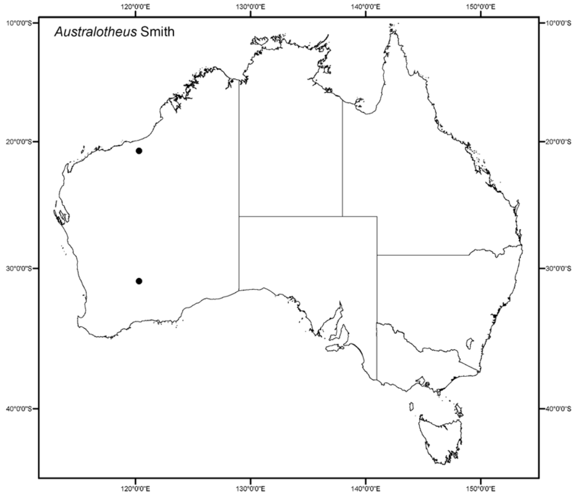


Figure 74. Locality records of *Australotheus* spp.



Habitat, distribution and abundance

Endemic to Australia with one species from deep subterranean habitat, the other of unknown WA habitat but probably not subterranean (Figure 74). It may be more common than these limited records suggest due to limited sampling in the west of Australia.

Dodecastyla Paclt, 1974

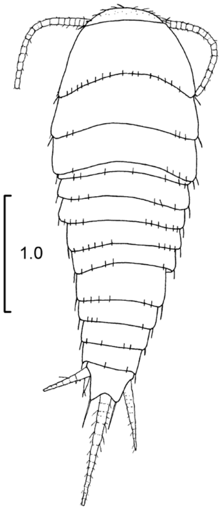
Dodecastyla Paclt, 1974: 545.

Type species: *Lepismina bifida* Schäffer, 1897 by original designation.

Diagnosis

Ateluriform. Scales round with ribs not or only slightly surpassing the margins of the scales. Abiesiform macrochaetae present on all nota and urotergites. Head more or less free, with numerous flattened macrochaetae in irregular rows. Mandibles with well-developed incisor and molar regions. Galea with a single prominent apical conule. Labium with round postero-lateral corners; last article of labial palp oval. Thoracic nota with submarginal row of abiesiform macrochaetae as well as longer macrochaetae in each postero-lateral corner. Tibia with three lyriform macrochaetae distally. Pretarsus without obvious pulvillae. Abdominal tergites with chaetotaxy similar to nota. Urotergite X trapezoidal with acute apices and deep notch between. Underside of urotergite X in mature males with 1+1 fields of pegs. Urosternites I-V without vesicles, urosternite VI

Figure 75. *Dodecastyla rima* Smith & McRae, 2015, legs not illustrated.



with large vesicles bearing setae, urosternite VII with pseudovesicles. Styli on segments IV-IX. Parameres long. Basal division of cerci not longer than other divisions, bearing pegs in mature males. Median dorsal appendage without pegs.

Habitat, distribution and abundance

With 36 collection events in Australia (Figure 76), all restricted to two very localised areas in the Pilbara, both described species appear to be locally common within very limited ranges. There does not appear to be any obvious host relationship although one species was occasionally collected with ants. The type species, *Dodecastyla bifida* Schäffer, 1897, was described from Chile. The two described Australian species are believed to be remnants of a more widespread Gondwanan genus which retreated into deep subterranean cavities as the continent dried out (Figure 77).

Figure 76. Australian locality records of *Dodecastyla*

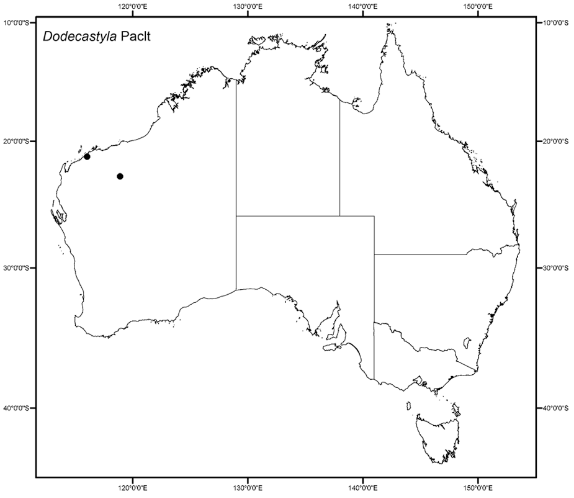


Figure 77. World locality records of *Dodecastyla*

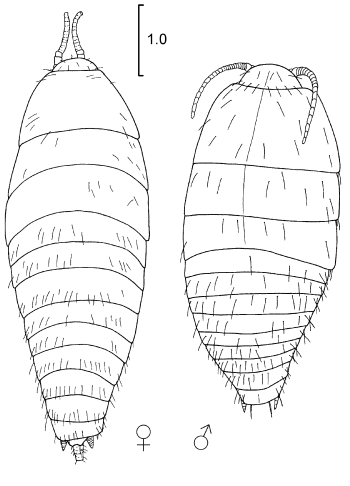
Galenatelura Smith, 2009

Galenatelura Smith, 2009: 15.
Type species: *Galenatelura deflexa* Smith, 2009 by original designation.

Diagnosis

Ateluriform. Scales subrectangular, the ribs extending by up to one third their length beyond the margin. Macrochaetae simple, thin, some a little apically bifurcate; abiesiform macrochaetae absent. Head partially covered by anterior edge of pronotum, with scattered long macrochaetae in irregular rows. Mandibles narrow with strong incisor but weak molar region. Galea without prominent apical conule. Labium with postero-lateral corners of postmentum angular. Ultimate article of labial palp elongate oval. Thoracic nota with multiple irregular rows of long thin macrochaetae about the same size and length as those on each postero-lateral corner. Tibia with apical row of several lyriform macrochaetae. Pretarsus with two lamellate pulvillae. Abdominal tergites also with long thin macrochaetae in one or more irregular rows.

Figure 78. *Galenatelura deflexa* Smith, 2007, legs not illustrated.

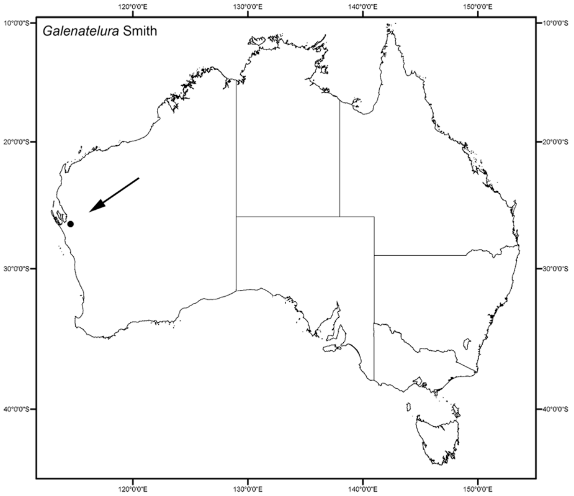


Sexually dimorphic. Urotergite X trapezoidal in female with acute apices and a shallow notch between; urotergite X strongly modified in mature males, largely hidden under urotergite IX with the lower surface pointing backwards exposing very large 1+1 fields of pegs. Urosternites I-VI without vesicles, urosternite VII with pseudovesicles. Styli on segments VI-IX. Posterior margin of urosternite VIII in male concave. Parameres large and rounded, curving around the large penis. Cerci in both sexes short and conical, those of mature male very widened internally, their basal divisions largely fused together, armed with numerous pegs and modified chaetotaxy. Median dorsal appendage in male deflected downwards between the cerci, without pegs.

Habitat, distribution and abundance

Endemic to Australia. It has been collected only once, from the nest of the termite *Coptotermes brunneus* (Gay, 1955) in WA (Figure 79). It appears to be closely related to *Allatelura* Silvestri, 1947 from northwestern Australia.

Figure 79. Locality records of *Galenatelura.*



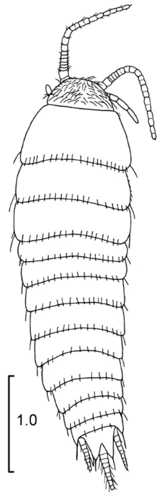
Pseudogastrotheus Mendes, 2003

Pseudogastrotheus Mendes, 2003: 344.
Type species: *Grassiella pallens* Escherich, 1903 by original designation.

Diagnosis

Ateluriform. Scales round with ribs only slightly surpassing the margins on dorsal scales and surpassing by about 10% of their length on ventral scales. Abiesiform macrochaetae present on all nota and urotergites. Head more or less free, with numerous wider macrochaetae in irregular rows. Mandibles with well-developed incisor and molar regions. Galea with a single prominent apical conule. Postmentum of labium with round postero-lateral corners. Ultimate article of labial palp round. Thoracic nota with a submarginal row of abiesiform macrochaetae as well as longer macrochaetae in each postero-lateral corner. Tibia with three lyriform macrochaetae distally. Pretarsus without obvious pulvillae. Abdominal tergites with chaetotaxy similar to nota. Urotergite X trapezoidal with acute apices and deep notch between. Underside of urotergite X in mature males with 1+1 fields of pegs. Urosternites I-V without vesicles, urosternite VI with large vesicles bearing setae, urosternite VII with pseudovesicles. Styli on segments VI-IX. Parameres long. Basal division of cerci not longer than other divisions, bearing pegs in mature males. Median dorsal appendage without pegs.

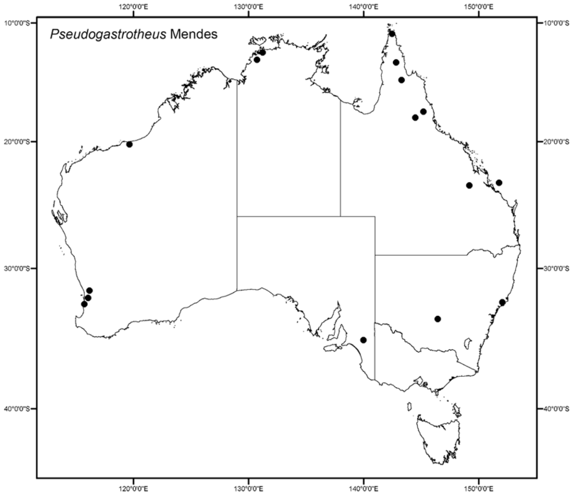
Figure 80. *Pseudogastrotheus undarae* Smith, 2016, legs not illustrated.



Habitat, distribution and abundance

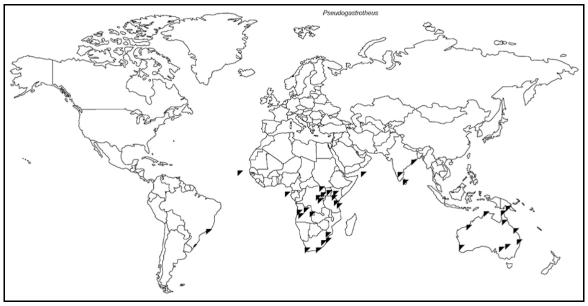
The genus *Pseudogastrotheus* is widespread with species described from the Afrotropical (Angola, Cape Verde Islands, Democratic Republic of Congo, Kenya, São Tomé, South Africa, Tanzania, Uganda, Yemen), Neotropical (Brazil), Indo-Malayan (India, Indonesia, Sri Lanka, Thailand) and Oceanic Regions (Papua New Guinea) (Figure 82). Twenty three collection events are recorded covering a wide area of Australia (Figure 81), mostly collected within termite nests, under stones and even within caves. The genus is likely to prove abundant given sufficient collection effort. The Australian fauna appears to form a clade distinct from the African fauna in that all(?) African species have two strong, deeply bifurcate macrochaetae mediad of the suture with the paratergites while the Australian species known so far have just one strong, and only slightly bifurcate macrochaeta plus a smaller seta in this position. The

Figure 81. Australian locality records of *Pseudogastrotheus* spp.



genera *Dodecastyla*, *Pseudogastrotheus* and *Australotheus* are very close to each other differing only in the number of pairs of styli, a character that can be variable in other genera. It may later prove to be an artificial construct but is useful at a practical morphological level.

Figure 82. World distribution of *Pseudogastrotheus* spp.



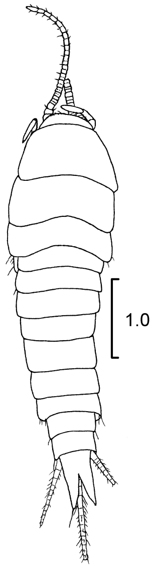
Troglotheus Smith & McRae, 2014

Troglotheus Smith & McRae, 2014: 119.
Type species: *Troglotheus bifurcus* Smith & McRae, 2014 by original designation.

Diagnosis

Very elongate ateluriform. Scales round with ribs only slightly surpassing the margins dorsally, extending slightly further on ventral scales. Macrochaetae mostly simple or apically bifurcate; abiesiform macrochaetae absent. Head more or less free, with numerous strong macrochaetae in irregular rows. Mandibles with well-developed incisor and molar regions. Galea with a single prominent apical conule. Postmentum of labium with round postero-lateral corners. Ultimate article of labial palp elongate oval. Thoracic nota glabrous except for a single strong macrochaeta in each postero-lateral corner.

Figure 83. *Troglotheus bifurcus* Smith & McRae, 2014, legs not illustrated.

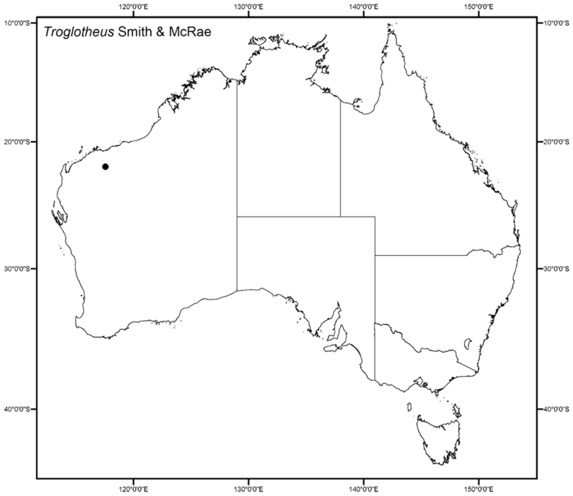


Tibia with three lyriform macrochaetae distally. Pretarsus without obvious pulvillae. Chaetotaxy of abdominal tergites similar to nota. Urotergite X trapezoidal with extremely long acute apices and a very deep notch between. Underside of urotergite X in mature males with 1+1 fields of pegs. Urosternites I-V without vesicles, urosternite VI with large vesicles bearing setae, urosternite VII with pseudovesicles. Styli on segments IV-IX. Parameres long. Cerci with basal division not longer than other divisions, bearing pegs in mature males. Median dorsal appendage without pegs.

Habitat, distribution and abundance

Endemic to Australia with only four collection events from deep subterranean habitat within a very

Figure 84. Locality records of *Troglotheus* Smith & McRae, 2014



restricted area (Figure 84). The species displays troglomorphic characters.

Unplaced

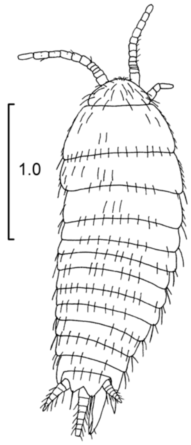
Wooroonatelura Smith, 2016

Wooroonatelura Smith, 2016b: 51.
Type species: *Wooroonatelura lenta* Smith, 2016 by original designation.

Diagnosis

Small, onisciform. Scales multiradiate, ribs on dorsal scales extending beyond margin by about half their length and by 10% on ventral scales. Macrochaetae long and thin with delicate apical bifurcations; abiesiform macrochaetae absent. Head exposed with scattered long macrochaetae. Mandibles with long incisor and shorter molar region. Galea without prominent apical conule. Ultimate article of labial palp elongate oval. Thoracic nota with multiple irregular rows of long thin macrochaetae about the same size and length as those in each postero-lateral corner. Tibia with two apical lyriform macrochaetae. Pretarsus without pulvilli, the outer claws with ventral keels, the medial empodial claw simple. Abdominal tergites each with a single row of long thin macrochaetae. Urotergite X trapezoidal with round apices and a deep notch between. Urosternites I-V without special features; urosternite IV with glabrous eversible vesicles, urosternite VII with pseudovesicles. Styli on segments VI-IX. Cerci and median appendage short, the basal divisions not elongated or fused. Males unknown.

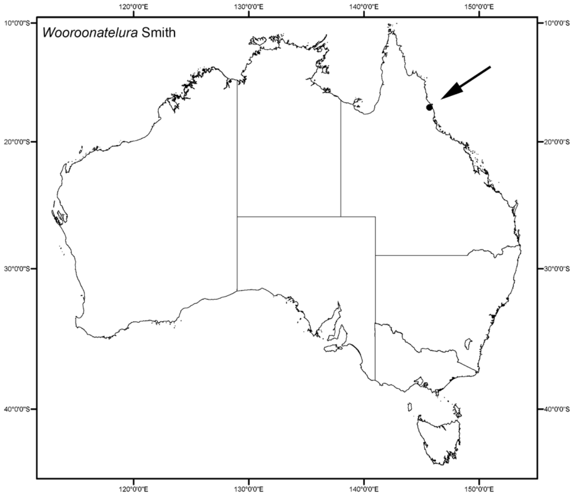
Figure 85. *Wooroonatelura lenta* Smith, 2016, legs not illustrated.



Habitat, distribution and abundance

Endemic, collected only once from a piece of rotting wood lying on the ground at the edge of rainforest with ants of the genus *Monomorium* Mayr, 1855 (Figure 86). In the absence of male specimens it is not currently possible to place the genus within any of the currently recognised tribes.

Figure 86. Locality records of *Wooroonatelura* Smith



Subfamily Coletiniinae Mendes, 1988

Coletiniinae Mendes, 1988b: 768.
Nominotypical genus: *Coletinia* Wygodzinsky, 1980.

Diagnosis

Body elongate, sub-cylindrical. Scales present or absent (only absent in some genera not yet reported from Australia), sometimes quite modified; ribs not significantly protruding beyond the margin. Antennae filiform, pedicel of mature males with distal apophyses which lack distinct glandular area. Head emarginate at level of antennae, with or without scales. Mandibles with well-developed incisor and molar regions. Galea apically with two large conules. Pronotum with isolated macrochaetae along the anterior margin. Nota not obviously wider than urotergites. Tibia of legs without apical lyriform macrochaetae. Pretarsus with two lateral claws and a medial empodial claw; pulvillae absent. Urosternite I divided by sutures into a medial sternum and postero-lateral coxites; urosternites II-VII (VIII) entire; coxites IX of male as two free sclerites, never fused into single plate. Styli present on II-X or III-IX. Eversible vesicles on II-VI or III-VI, pseudovesicles on VII. Parameres entire, not apically divided. Urotergite X of males with pegs on the ventral surface. Both cerci and median dorsal appendage of mature males usually with pegs but sometimes absent from both.

Lepidospora **Escherich, 1905**

Lepidospora Escherich, 1905: 179.
Type species: *Lepidospora braueri* Escherich, 1905 by subsequent designation Paclt, 1963: 44.

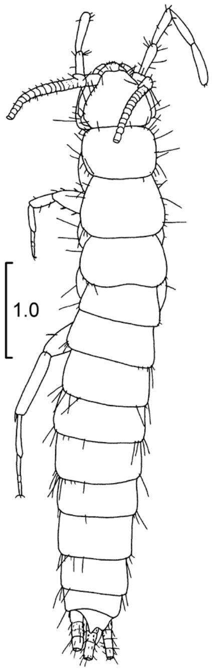
Lepidospora (Brinckina Wygodzinsky, 1955*)*

Lepidospora (*Brinckina* Wygodzinsky, 1955): 179.
Type species: *Lepidospora* (*Brinckina*) *makapaan* Wygodzinsky, 1955 by original designation.

Diagnosis

Scales round. Head without scales. Urotergite X of male extended into longer downward directed processes, always bearing a longitudinal row of pegs on the underside. Styli present on II-IX, eversible vesicles on II-VI. Both cerci and median dorsal appendage of mature males usually but not always, with pegs.

Figure 87. *Lepidospora (Brinckina) relicta* Smith & McRae**,** 2016.



Habitat, distribution and abundance

Lepidospora (Brinckina) is known from the Democratic Republic of Congo, Kenya, South Africa, China and Afghanistan, Australia and probably also Papua New Guinea (Smith, 1998b) (Figure 89). With just nine collection events in Australia (Figure 88), all from deep subterranean habitat in the Pilbara, little is known of its biology. Outside Australia, species of the subgenus have been collected from soil in forest, sometimes at higher altitudes (ca 2100m asl), under stones, in caves or even with termites of the genus *Odontotermes* Holmgren, 1912 i.e. all soil related habitats typical of the non-Atelurinae Nicoletiids. At least three morphospecies are representated in the material examined, all probably short-range endemics. It is likely that more species of this genus will be found.

Figure 88. Australian locality records of *Lepidospora (Brinckina)* spp.

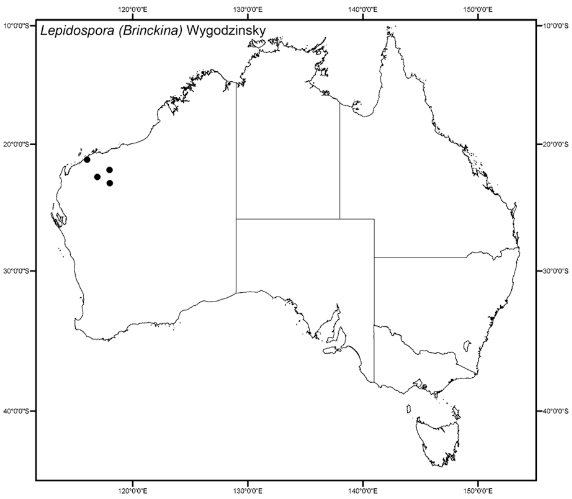
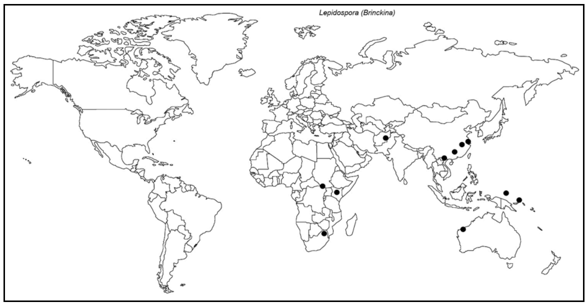


Figure 89. World locality records of *Lepidospora (Brinckina)* spp.



Subfamily Subnicoletiinae Mendes, 1988

Subnicoletiinae Mendes, 1988b: 769.
Nominotypical genus: *Subnicoletia* Silvestri, 1908.

Diagnosis

Body elongate, sub-cylindrical. Scales absent or quite modified (absent in all Australian species). Antennae filiform; pedicel of mature male with glandular area and no apophysis or with submedial inward directed process; scape of some species also with process. Head emarginate at level of antennae. Mandibles with well-developed incisor and molar regions. Galea apically with two large conules. Pronotum with or without isolated macrochaetae along the anterior margin. Nota not obviously wider than abdominal terga. Tibia of legs without apical lyriform macrochaetae. Pretarsus with two lateral claws and mostly with a medial empodial claw (absent in *Trinemurodes* from the Indo-Malayan region); pulvillae absent. Urosternites I-VII entire; coxites IX in males fused into single sclerite. Styli present on II-IX or less numerous. Eversible vesicles on II-VI or less numerous (even absent); pseudovesicles on VII. Parameres divided apically or, if entire, then with modified apical region. Urotergite X of males without pegs on the ventral surface. Cerci of mature males usually with modified chaetotaxy; sometimes also with anemone-like structures. Median dorsal appendage sometimes with modified chaetotaxy in mature males.

Comment: Mendes (1988b) noted this subfamily is more heterogeneous than other subfamilies. Mendes (1994) found that four of the genera (*Hematelura*, *Trichotriura*, *Trichotriuroides* and *Trichatelura*) had a close relationship to each other, lying close to the remaining Subnicoletiinae but on a separate branch. The three Australian genera and *Trinemurodes* however seem to be reasonably homogeneous.

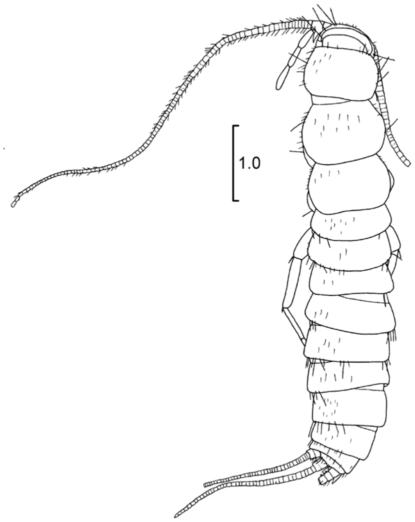
Metrinura **Mendes, 1994**

Metrinura Mendes, 1994: 99.
Metrinura Mendes.—Smith, 1998b: 162 [redefinition].
Type species: *Trinemura novaecaledoniae* Silvestri, 1915 by original designation.

Diagnosis

Male pedicel widened with glandular area and often an apophysis. Abdominal styli on segments III-IX. Eversible vesicles on II-VI. Cerci of mature male with modified spines and sometimes anemone-like structures. Median appendage rarely with modified chaetotaxy.

Figure 90. *Metrinura taurus* Smith & McRae, 2016, most legs not illustrated.



Habitat, distribution and abundance

The genus is known from the Indo-Malayan (Sulawesi), Neotropical (Colombia), Palaearctic (Afghanistan), Australian and Oceanian Regions (New Caledonia and probably Papua New Guinea) (Figure 92). The nine Australian collection events (Figure 91) are from caves, in soil, under logs or rocks.

Figure 91. Australian locality records of *Metrinura* spp.

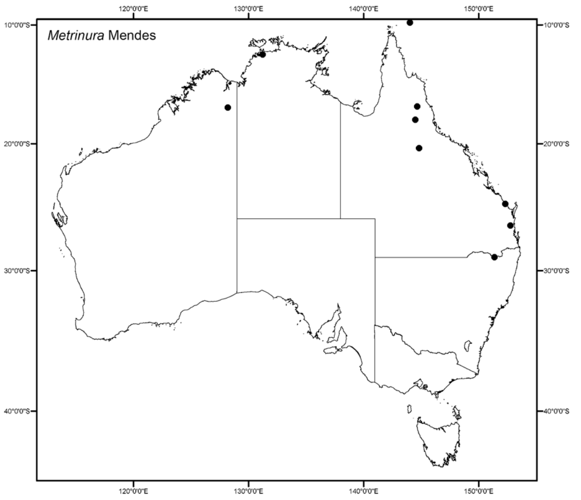


Figure 92. World locality records of *Metrinura* spp.

Subtrinemura **Smith, 1998**

Subtrinemura Smith, 1998b: 173.
Type species: *Trinemura excelsa* Silvestri, 1920 by original designation.

Diagnosis

Male pedicel widened with process, process sometimes also on scape. Pretarsus simple and with three claws. Abdominal styli on segments III-IX, eversible vesicles on III-VI. Cerci and terminal filament of male with sensory pegs; cerci of males sometimes also with basal anemone-like structures.

Habitat, distribution and abundance

Endemic to south-eastern Australia with seventeen collection events (Figure 94). Of the four described species, two are only known from caves and other two from under logs and stones on soil.

Figure 93. *Subtrinemura anemone* Smith, 1998

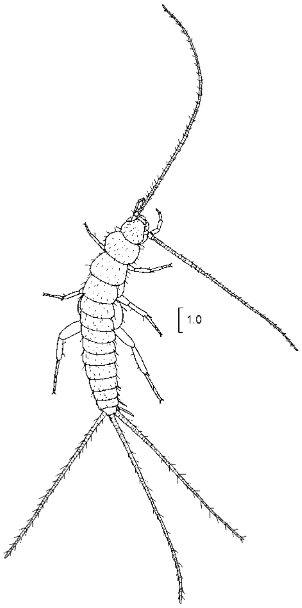
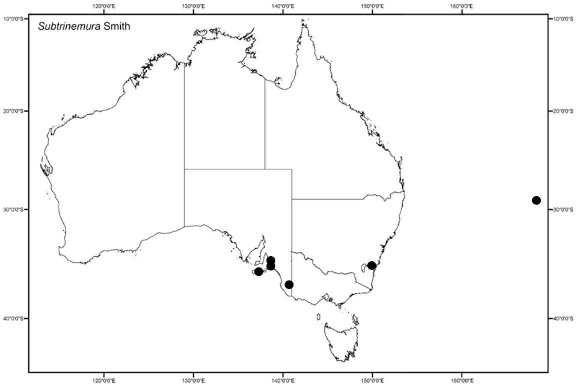


Figure 94. Locality records of *Subtrinemura* spp.



Trinemura Silvestri, 1908

Trinemura Silvestri, 1908b: 61.
Type species: *Trinemura novaehollandiae* Silvestri, 1908 by monotypy.

Diagnosis

Pedicel in mature male widened with glandular area and/or with medial processes. Scape of some males also with processes. Pretarsus with three claws. Abdominal styli on segments III-IX. Eversible vesicles absent. Cerci and terminal filament of mature males usually with sensory pegs and cerci sometimes with basal anemone-like structures.

Figure 95. *Trinemura callawae* Smith *et al.*, 2011, legs not illustrated.

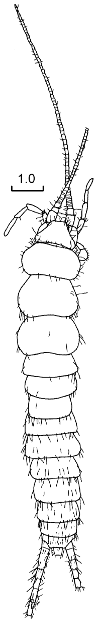
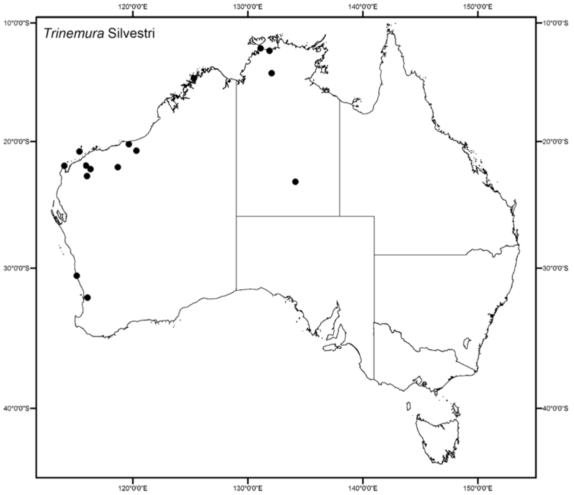


Figure 96. Locality records of *Trinemura* spp.



Habitat, distribution and abundance

Endemic to the western half of Australia with sixty-eight collection events, mostly from deep subterranean habitat in the Pilbara of WA (Figure 96), but also collected in caves and from under logs in forest, all typical soil related habitat. Many more undescribed species have been collected from deep subterranean habitats that appear to be short range endemic species.

EVOLUTION AND ZOOGEOGRAPHY

Dating and the fossil record

Zygentoma fossil evidence is rare, probably due to the poor preservation of these soft bodied animals.

The molecular clocks of Misof *et al.* (2014) suggest a radiation of the ectognathous hexapods in the Early Silurian (~441 Ma), with the Zygentoma diverging from the Archaeognatha at this time. They calculate *Tricholepidion* diverged from the other silverfish families in the late Triassic (~214 Ma), while the Nicoletiidae and Lepismatidae have existed as distinct families from the Jurassic (~160 Ma).

Mendes (in press) reviewed the limited fossil records of the silverfish-like orders (extinct Monura, Archaeognatha and Zygentoma). The earliest fossil attributed to Archaeognatha dates from the Devonian of Quebec (390-392 Ma) (Labandeira *et al.*, 1988). Mendes, however considers the position of this fossil as well as the Palaeozoic silverfish-like fossils of the genera *Bojophlebia*, *Carbotriplura* and *Ramsdelepidion* (all Kukalová-Peck, 1987) to be inconclusive. Bechly and Stockar (2011) described fossils of a Mid-Triassic Monuran *Dasyleptus* from limestone in Switzerland (225-242 Ma). Sturm (1998) described two specimens showing the typical habitus of the Lepismatidae from Lower Cretaceous sandstone of Araripe in Brazil (ca 110 Ma). Fossils considered as unambiguously zygentoman are more recent, mostly preserved in amber. Specimens described from 100-110 Ma Burmese amber, although assigned to *Allacrotelsa*, (Ross *et al.*, 2010) as well as four unidentified specimens (Grimaldi *et al.*, 2002), are considered doubtful by Mendes. However, Mendes & Poinar (2008) described *Burmalepisma* and Mendes & Wunderlich (2013) described *Cretalepisma* (both assigned with reasonable probability to the Lepismatinae) from the same Burmese amber deposits. Silvestri (1912b) redescribed a species of *Allacrotelsa* [Lepismatinae] (as *Lampropholis*) and a species of the extinct Lepidotrichidae from Eocene Baltic amber (38-50 Ma). Several species have been described from Dominican amber (20-30 Ma) including two species of Atelurinae assigned to the Grassiellini, a species of *Ctenolepisma* [Ctenolepismatinae], one of *Protolepisma* [Lepismatinae], two species of *Trinemurodes* and one belonging to *Hemitrinemura* [all Subnicoletiinae] (Mendes, 1997, 1998, Sturm and Mendes, 1998 and Mendes & Poinar, 2004). *Onycholepisma arizonae* and *Onychomachilis fischeri* were described from onyx marble of Arizona (12-50 Ma) (Pierce, 1951); the latter species is however considered by Mendes to belong, almost certainly, to the Nicoletiidae.

Zoogeography

The Zygentoma are clearly an ancient group and, judging from the fossil forms, morphologically conservative. They are an interesting model to correlate with the movement of the continents over geological time. Molecular clocks suggest they were present, probably in forms similar to those living today, since the Triassic and hence before the breakup of the supercontinent Pangea in the Jurassic (~175 Ma). The families Nicoletiidae and Lepismatidae are believed to have been established before Africa split apart from South America, Antarctica and Australia (~124 Ma) and hence well before Australia finally split from Antarctica and South America (30-50 Ma). Furthermore, the emergence of termites at the end of the Jurassic (~145 Ma) and the social ants in the Cretaceous (~100 Ma) opened up opportunities for the inquiline species.

Being primitively wingless and generally ground-dwelling their ability to cross oceans is presumably limited. Nevertheless, endemic species are known from many oceanic islands. The most likely means is by rafting on storm debris. Heatwole & Levins (1972) collected flotsam over three years in the vicinity of Puerto Rico and examined the fauna still alive, identifying 19 families of insects as well as pseudoscorpions, snails, spiders, mites, millipedes, isopods and worms. No Zygentoma were found but as silverfish are long-lived, able to survive many months without food and can absorb moisture from the atmosphere they would appear to be reasonably well adapted to survive such journeys. Furthermore, many species (especially *Heterolepisma* and to a lesser extent *Acrotelsella* spp.) shelter within or under the bark of trees and hence would be carried along with a tree washed into a river following storms. Indeed, it is these two genera, especially *Heterolepisma*, that are found on islands throughout the Pacific and Indian oceans. Furthermore Wheeler (1916) reported ants (*Pheidole peregrina* Wheeler) being found in a log washed up on an island at least 2 km off the coast of Brazil and termites were among the insect fauna collected on flotsam by Heatwole and Levins. If colonies of ants and termites can be transported, it would explain the presence of various Atelurinae such as *Lasiotheus nanus* on islands. Nevertheless, in spite of the possibility of transport over oceans, quite distinct patterns in the fauna are apparent and many species are known from very restricted distributions.

To avoid unnecessary confusion, it has been necessary to exclude widespread anthropophilic species from this zoogeographic analysis. Species excluded are the Lepismatidae *Lepisma saccharina* [Lepismatinae], *Ctenolepisma lineata, Ct. longicaudata*, *Ct. rothschildi* and *Thermobia domestica* [Ctenolepismatinae], *Acrotelsa collaris* [Acrotelsatinae] and the Nicoletiidae *Nicoletia phytophila* [Nicoletiinae] and *Lasiotheus nanus* [Atelurinae: Dionychellini]. Other unusual distributions suggested by various authors as accidental include *Acrotelsella impudica* (quarantine intercepted and found on a ship and now throughout the Caribbean), *Ct. targioniana* in the Americas, *Neoasterolepisma myrmecobia* in Peru (possibly introduced with its host ant *Pheidole megacephala*), *Namunukulina funambuli* (anthropophilic in South America) and *Bharatatelura malabarica* Mendes with ants in Fiji. In the absence of sufficient information and their low impact on the analysis, these records are here included in the distribution maps.

Any discussion of zoogeography is also constrained by the lack of research in many areas of the world. Asia and the Americas, in particular, have limited records and it is likely that a concerted effort in these regions would change the picture, just as this work in Australia has identified three subfamilies previously not considered to be present.

Heatwole (1987) and Austin *et al.* (2004) reviewed the zoogeography of the Australian region, recognising several zoogeographical elements of the fauna. These include a Pangean element, an old Gondwanan element, an element that evolved during the long isolation of Australia as it moved northward becoming drier, a modern element of arrivals from Asia as Australia drew closer, an element of highly mobile species found throughout a large part of the world and an element introduced by man. The subfamilies of Zygentoma and their Australian genera are discussed below for their conformity with this framework and the degree of endemism.

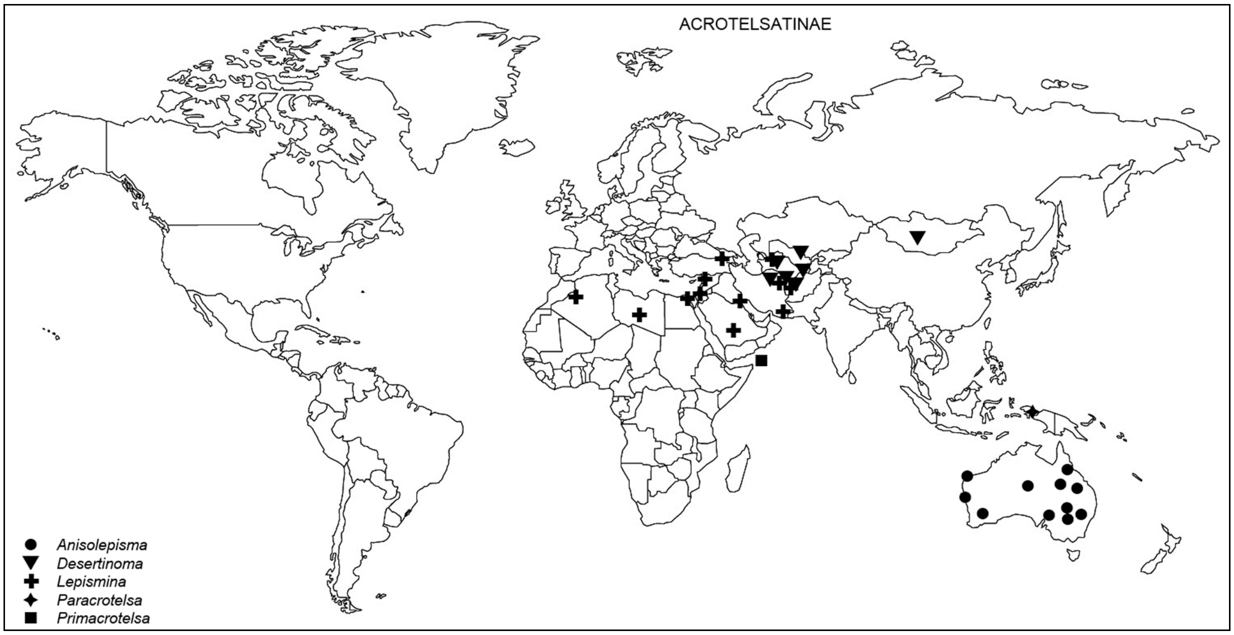
Molecular data would be of great value in elucidating the phylogeny and supporting discussions on the zoogeography of the Zygentoma but at present is very limited in extent. While some of the comments below are supported by recent molecular data with the 28S nuclear gene, this work is only at a preliminary stage and as yet unpublished.

LEPISMATIDAE

Acrotelsatinae

The subfamily Acrotelsatinae, apart from the cosmopolitan introduced *Acrotelsa collaris*, is not well known. Species occur in the Palaearctic, New Guinea and Australia but are not recorded from the Americas (Figure 97). This distribution suggests an ancient disjunct Pangean distribution for the earliest Acrotelsatinae with extinctions (or insufficient knowledge) in much of the world. However, no fossil evidence exists to support this. It is also possible that

Figure 97. Locality records of the Acrotelsatinae (excluding the peridomestic *Acrotelsa collaris*)



it is a modern element that has entered Australia from the north but given the difficulties of crossing water this seems unlikely. Known species of the Acrotelsatinae live in soil/litter in desert areas or are anthropophilic and have not been found in tree bark; little is known of the biology of the single New Guinea record, other than it was found within the home of a Papuan.

The genus *Anisolepisma* appears to be endemic to Australia and well adapted to the harsh dry conditions. Its ancestor was probably present in Australia before Gondwana split from Africa and has evolved as an independent line for more than 120 million years.

Ctenolepismatinae

The Ctenolepismatinae are very widespread (Figure 98) with species in all zoogeographic zones (except Antarctica) and hence possibly also Pangean in origin, although the only fossil evidence is quite recent 20-30 Ma. The presence of *Acrotelsella* species on many islands suggests however, that at least some members of the subfamily have survived long ocean crossings, so a more recent dispersal cannot be excluded. Some 13 genera have been described with *Ctenolepisma* by far the largest, containing 118 described species, mostly from Africa and the Palaearctic. *Acrotelsella* dominates in Australia but is also found in parts of eastern Africa, the Indo-Malay region and the Caribbean as well as on several Pacific and Indian Ocean islands. The distribution of the subfamily could also be explained by an African origin, prior to the split from Gondwana, with *Acrotelsella* being isolated in Australia but later dispersing more widely, either through Gondwana or by ocean crossings. Meanwhile, *Ctenolepisma* radiated in Africa, later dispersing into the Palaearctic, perhaps reaching the Americas more recently by oceanic means as the limited number of species in the America do not differ greatly from the African species in their morphology, at least not to the extent displayed by *Acrotelsella*.

The small genera *Hemitelsella* and *Qantelsella* would appear to be endemic to Australia probably evolving from a common ancestor with *Acrotelsella* and hence comparatively recent. The reduction in the number of abdominal bristlecombs seems to parallel the examples of *Thermobia* Bergroth and *Ornatilepisma* Irish in Africa, which are presumed to have evolved from *Ctenolepisma*-like ancestors.

Heterolepismatinae

The subfamily Heterolepismatinae currently contains a single genus, although preliminary molecular work suggests that there are several distinct groups. It is very well represented and found in all Australian states. The genus *Heterolepisma* is distributed almost entirely in the southern hemisphere (including on many oceanic islands), but with some records as far north as the islands of Japan and the Caribbean

Figure 98. Locality records of the Ctenolepismatinae (excluding the peridomestic species).

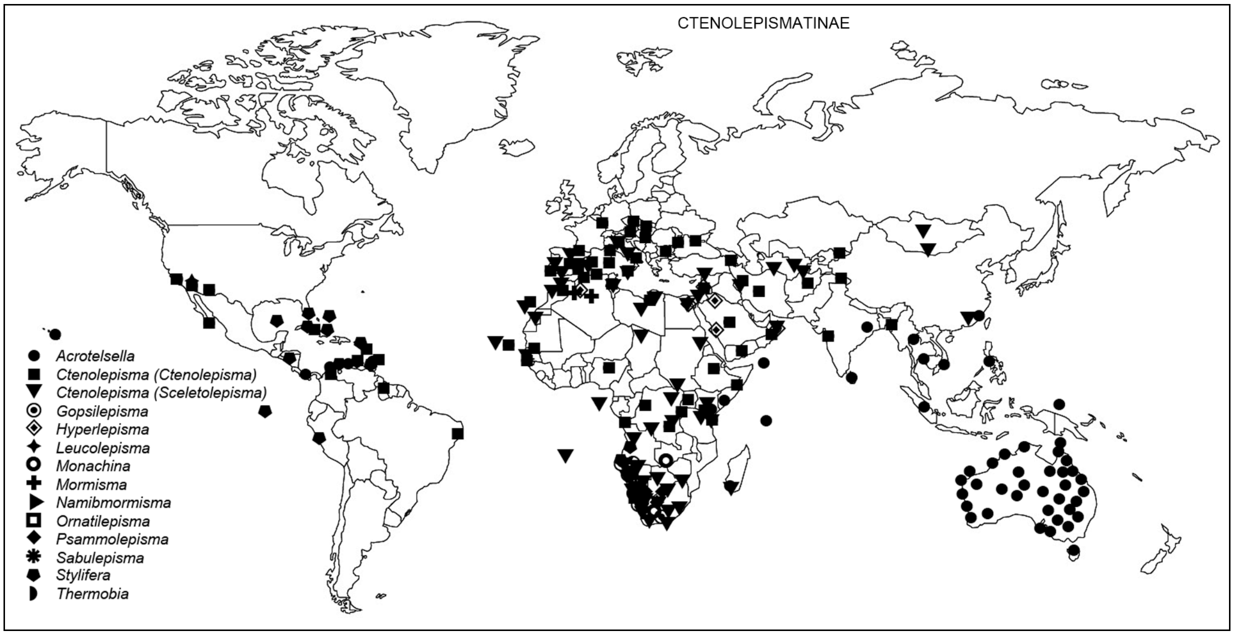
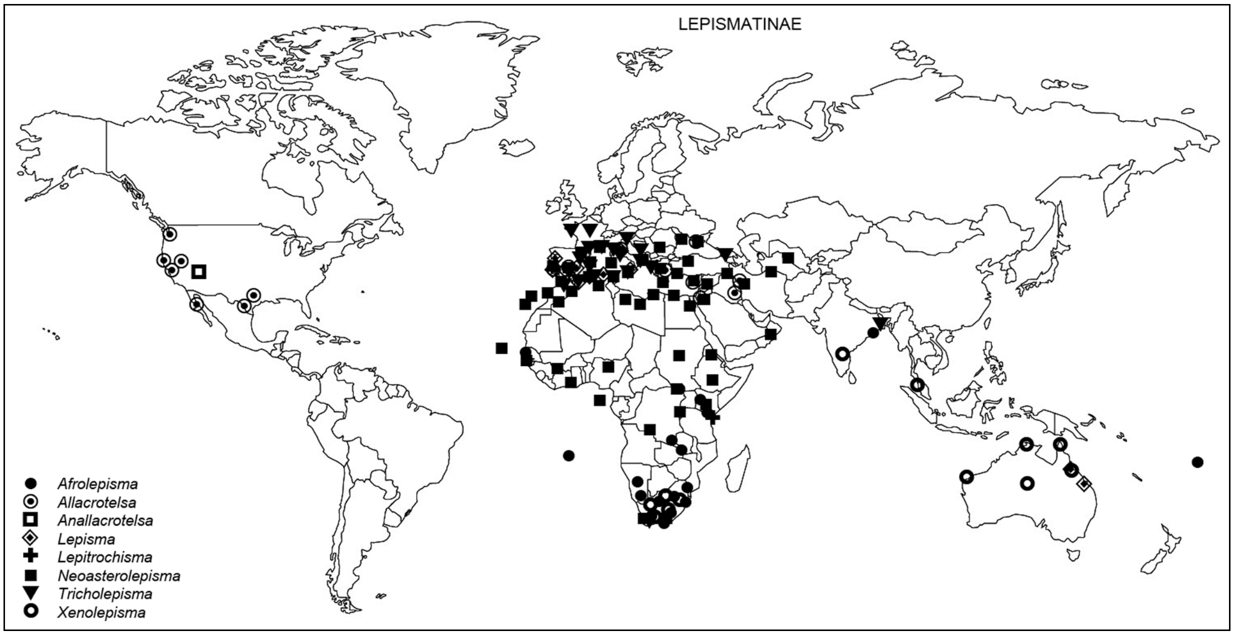


Figure 99. Locality records of the Lepismatinae (excluding the peridomestic *Lepisma saccharina*).



(Figure 60). The number of species and apparent diversity is by far highest in Australia suggesting that this may be its centre of origin. Its presence in Africa seems to be restricted to coastal locations. The subfamily is possibly of early Gondwanan origin but given the richness and abundance of the Australian fauna compared to Africa and South America, and the clear ability of the genus to cross oceans, it could also be of more recent origin, either late Gondwanan or even later, radiating within Australia as it drifted north, and at times being transported over oceans to islands and the coast of continents.

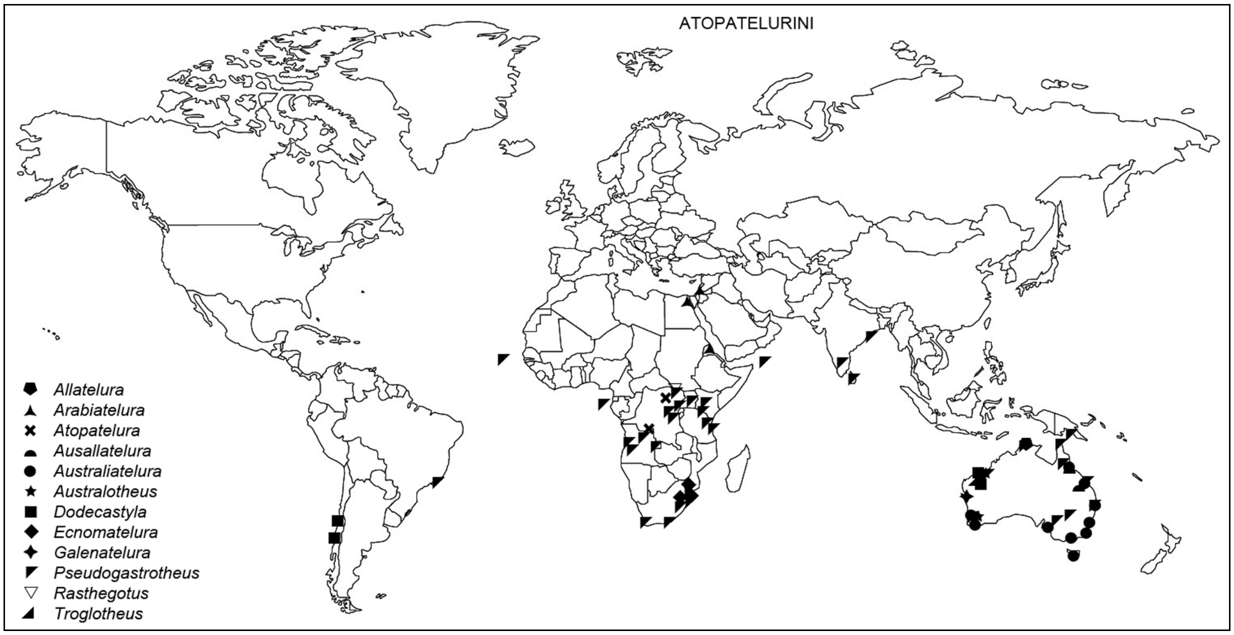
Mendes (1991: 7), Wygodzinsky (1967: 515) and Irish (1990: 145, 307) consider the Heterolepismatinae to exhibit numerous plesiomorphies and suggest it may represent the most primitive of the lepismatid subfamilies. The current author is unconvinced due to the more or less Gondwanan distribution of the genus and the comparatively homogeneous morphology of the species. It is possible that the simplified chaetotaxy and absence of specialised antennal sensillae are losses rather than representing the plesiomorphic state.

Counter to this argument is the unpublished evidence emerging from on-going molecular studies with the nuclear gene 28S which is finding very large differences between some clades of *Heterolepisma*, the differences being of similar magnitude to those between the subfamilies Heterolepismatinae, Ctenolepismatinae and Acrotelsatinae.

Lepismatinae

The Lepismatinae is the subfamily most represented in the fossil record with specimens as old as 110-100 Ma, from Baltic, Burmese and Dominican amber and therefore probably Pangean in origin. Its distribution (Figure 99) appears to be more restricted today with no native species described from South America, but this could reflect the lack of study. The extant fauna is dominated by the large genera *Neoasterolepisma* (41 species in Africa and the southwest Palaearctic) and *Afrolepisma* (16 species in Africa as well as one in India and most probably another on the Pacific Island of Niue). The subfamily was not recognised as native to Australia until one species of *Lepisma*, living with native termites, and three species of *Xenolepisma*, living with ants, were recently described (Smith, 2015a, 2015b, 2015c). *Xenolepisma penangi* is known from Australia and Malaysia and could represent a recent arrival in Australia or a recent dispersal. The fact that it has been found living with the tramp ant species *Monomorium pharaonis* (L.) in Malaysia, could also imply human involvement in its distribution. Apart from the introduced peridomestic species, the genus *Lepisma* had until then been thought restricted to the Mediterranean region and *Xenolepisma* to southern Africa, India and Malaysia. Recently Kaplin (2016) has described two additional species of *Lepisma* from the Caucases so the distribution of the subfamily may prove broader with more effort in under-surveyed parts of the world. The disjunct distribution of the

Figure 100. Locality records of the Atopatelurini.



extant species is consistent with that expected for an ancient Pangean subfamily.

Mirolepismatinae and Silvestrellatinae

Neither subfamily is known from Australia. The former is restricted to the western USA plus a few records from western Africa. The Silvestrellatinae are predominantly African with a few records from Sri Lanka and South America both of which may represent accidental introductions.

NICOLETIIDAE

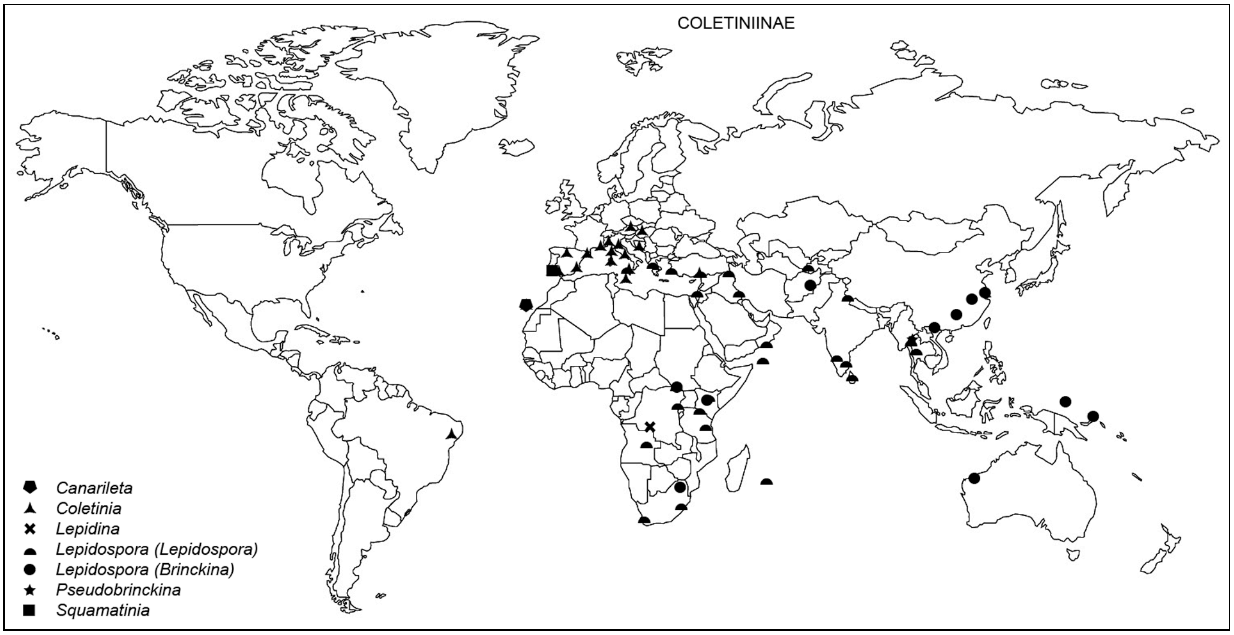
Atelurinae

The Atelurinae are morphologically diverse with many monotypic genera, found in all zoogeographic regions (except Antarctica). Mendes (2012) divided the subfamily into five tribes with all Australian species (except *Wooroonatelura lenta* Smith), being placed in the Atopatelurini. Of the other tribes, the Atelurini predominate in the Indo-Malay and Oriental Regions but also around the Mediterranean; the Dinatelurini are restricted to southern Africa, the Dionychellini are found through central Africa as well as in Brazil and Central America and the Grassiellini which predominate in the Americas also extend into Africa, predominantly along the western coast. The only known fossils from Dominican amber belong within the Grassiellini. Given estimates (Misof *et al.,* 2014) that termites and ants emerged about 146 and 100 Ma respectively, it is reasonable to assume that the radiation of the Atelurinae follows that of their hosts, probably arising from an ancestor in common with the soil-dwelling Coletiniinae, the only other nicoletiid subfamily to have separated coxites IX.

The Atopatelurini show an early Gondwanan distribution with nine of its 13 genera being found in Australia. Of these nine, only *Pseudogastrotheus* and *Dodecastyla* are not endemic, sharing congeners with Africa and India or South America respectively. Some of the Australian endemic genera show a considerable divergence from the more generalised morphology, with loss of dorsal chaetotaxy and tendency to troglomorphism in *Troglotheus* and the strong modifications of the chaetotaxy and genitalia of the males in termitophilic species such as *Galenatelura*. *Wooroonatelura*, is the only Australian species which cannot reliably be placed within the Atopatelurini. It has scales and modifications to the pretarsi which resemble some of the Dionychellini (Afrotropical and Neotropical), however mature male specimens are required to resolve its position.

It would appear that the Atopatelurini had their origins in the early Gondwanan construct which included Africa, and which have since radiated extensively within Australia, with only one genus (*Dodecastyla*) representing a late Gondwanan element shared with South America.

Figure 101. Locality records of the Coletiniinae.



The South East Asian fauna is dominated by the Atelurini, a tribe that has not been reported from Australia, suggesting that there is no recent Asian element to the Australian atelurin fauna.

Coletiniinae

The presence of this subfamily in Australia has only recently been confirmed with the description of *Lepidospora* (*Brinckina*) *relicta* Smith & McRae, 2016, although some poorly preserved specimens had earlier suggested it was present in New Guinea (Smith, 1998b). The subfamily has a widespread distribution (Figure 101) throughout Africa, the Palaearctic and into the Oriental region with a single troglobitic species reported from South America, suggesting it too belongs to the Pangean element.

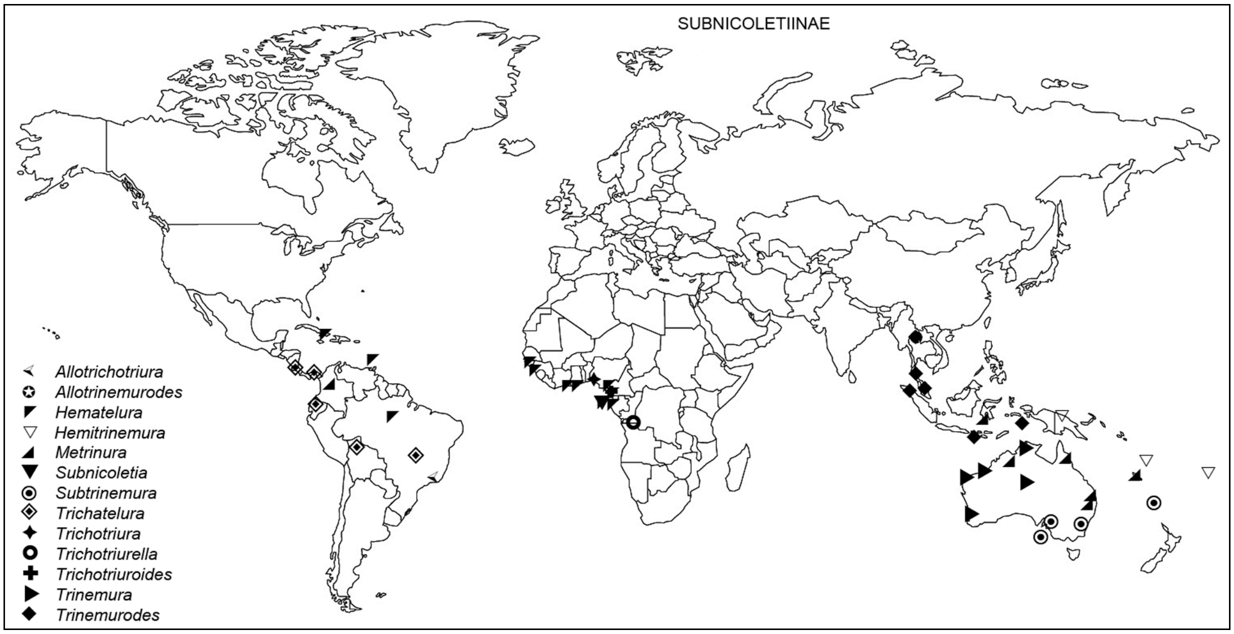
Lepidospora species are found in sub-Saharan Africa, in the Near and Middle East, through Asia to China and Vietnam and on some New Guinea islands and now in Australia. The nominotypical subgenus is more common in the west of this range and the subgenus *Brinckina* is more common in the East. *Coletinia* and some smaller genera are found in Europe. As they are soil-dwelling insects it is hard to imagine how this distribution could be explained other than as of ancient Pangean origin, however its presence on islands such as the Seychelles and Canary Islands demonstrates successful ocean crossings by unknown means.

Subnicoletiinae

This is the only subfamily of the Nicoletiidae with some fossil evidence, but it is of relatively recent origin (30-20 Ma). Extant species have been described from western Afrotropical, northern Neotropical, Indo-Malaya and Australian regions, suggesting an early Gondwanan origin with incursions into South East Asia from Australia. The Asian genera seem most closely related to the Australian endemic genera *Trinemura* and *Subtrinemura* than to the African clade. The distribution of each genus (Figure 102) seems to be quite limited with the exception of *Metrinura*, which has been found in Australia, Indonesia and Colombia. Some species are found on remote islands such as Western Samoa, confirming its ability to cross large ocean distances.

In summary, the zoogeography of the Australian silverfish fauna, contains elements best considered as Pangean. These include the lepismatid genera *Lepisma* and *Xenolepisma* with representatives also in Africa and the Palaearctic, *Anisolepisma* which is endemic but related to various Palaearctic genera, and the soil-dwelling Coletiniinae. Various other genera could be considered as old Gondwanan elements. The genus *Acrotelsella* would appear to have an origin shared with the African *Ctenolepisma* and has radiated rapidly within Australia once the continents separated and has now spread from Australia to South

Figure 102. Locality records of the Subnicoletiinae.



America and various islands or coastal regions of the Indian and Pacific Oceans. The Subnicoletiinae are similarly old with African, Australian and South American elements, each radiating within their continents since separation. The Australian elements appear to have spread into South East Asia.

The Heterolepismatinae are more difficult to understand. They are most common and diverse in Australia and show a late Gondwanan distribution with isolated species appearing on islands in the Indian and Pacific Oceans as well as in coastal locations around these oceans. There is no evidence of its presence in Laurasia. Yet the morphology of this group is considered by many authors to be the most plesiomorphic. It is here considered as a Gondwanan element with Australia being the centre of diversification.

Australia's inquiline Atelurinae are also probably derived from an old Gondwanan element with close relatives in Africa and South America. The group has radiated within Australia with several endemic genera.

There is very little support for Asian elements in the fauna, but perhaps some support for the radiation of some Australian Subnicoletiinae into Asia.

Finally, there is a small, very recently introduced element of cosmopolitan anthropophilc species dominated by *Ctenolepisma longicaudata*. There is no element that could be considered as representing highly mobile global species, other than those transported by human activity.

ENDEMISM

The Australian silverfish fauna displays a high degree of endemism with 88% of the described species and 52% of the genera known only from Australia. Almost 10% of the recorded species are introduced anthropophilic species (13.6% of the genera) while just under 3% of the species (just two species) and one third of the genera are considered native to Australia as well as elsewhere. This high level of endemism supports the hypothesis that transoceanic distribution is a limited event and that there has been a high degree of radiation in isolation within island Australia, with the genera *Heterolepisma* and *Acrotelsella* being particularly successful with some of their species possibly being dispersed over water to islands and continental margins of the Indian and Pacific Oceans.

CONSERVATION

Silverfish have survived for hundreds of millions of years and are likely to survive long into the future. The ability of many species to thrive in hot dry environments suggests they may cope well with global warming however this cannot be said for all species. One species (*Acrotelsella erniei* Smith) is only known from near the summit of Mt Sonder in central Australia. It was postulated (Smith, 2015d) that it may require the cooler conditions on the top of this mountain for survival and, given current rates of global warming, may only have another 70 years before it cannot move any higher up the mountain. An undescribed *Heterolepisma* species, collected on the isolated Herald Keys off the Queensland coast lives only a metre or so above sea level and is likely to disappear as ocean levels rise. One cave dwelling species, *Metrinura russendenensis* Smith & Shipp, is probably already extinct. It was known only from caves in south-eastern Queensland before these were flooded by the rising waters of Glenlyon Dam in the 1970's; it has not been collected since.

Competition from introduced pests may be a threat. Surveying typical silverfish habitat in south-eastern SA only resulted in finding large numbers of millipedes, presumably the introduced *Ommatoiulus moreletii*, in the niches generally occupied by silverfish of the usually common genus *Heterolepisma*.

The author's collection efforts have always been more fruitful in less disturbed habitats. It is rare to collect autochthonous species in pasture or suburbia. The greatest threat to silverfish is therefore that typical for most species, habitat reduction and degradation. Habitat destruction is particularly a risk for the numerous short range endemic subterranean species threatened by mining activities and changes to drainage patterns.

Conservation efforts to protect habitat in general, even if the focus is on larger, more iconic plant or animal species, is likely to be of the greatest benefit to silverfish conservation.

FUTURE

Many species of undescribed silverfish have already been collected and await description. Large parts of the country appear not to have been adequately surveyed, including habitats such as dune and gibber deserts. Similar deserts in south western Africa have yielded highly apomorphic xerophilic genera. Other under-sampled potential habitats include the nests of animals and birds, termite and ant nests and deep soil. It is likely that the number of genera in Australia will increase and the species will number in the hundreds should sufficient effort be directed at their discovery and description. The introduction of molecular techniques will be of great benefit in determining species definitions and allowing identification of taxa by non-experts. However, much work is still required if we are to link molecular data to the current morphology-based knowledge. Given the lack of interest in this order worldwide, and the great decline in support for taxonomy in general, silverfish will probably continue to be seen as a minor group rather than as a diverse and well represented order which has survived and thrived over hundreds of millions of years.

CONCLUSION

The Australian silverfish fauna is surprisingly rich, with over 10% of the total described world species and 14% of the genera. A large percentage of the fauna consists of endemic species. The fauna contains ancient Pangean elements and both early and late Gondwanan elements with the genera *Acrotelsella* and *Heterolepisma*. being particularly successful. The number of genera and species is likely to increase should more attention be paid to the group, especially in the survey of different habitats and using new methods, including molecular techniques.

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