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.

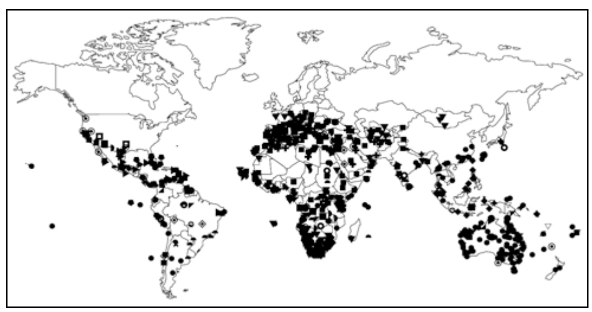
Keywords: Thysanura, key, Lepismatidae, Nicoletiidae, zoogeography

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.

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).

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



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).

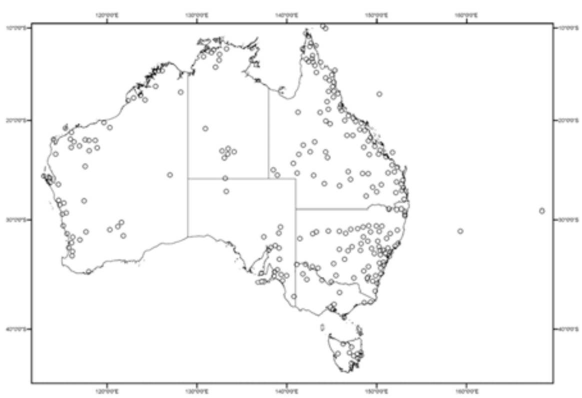
Since the last published review of the Australian fauna (Smith, 1998a), the number of species described has doubled to 72, with the number of genera increasing from 12 to 23 (Table 1). Four of these genera belong to subfamilies not previously recognised as part of the native Australian fauna. The fauna 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.

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

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.

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.

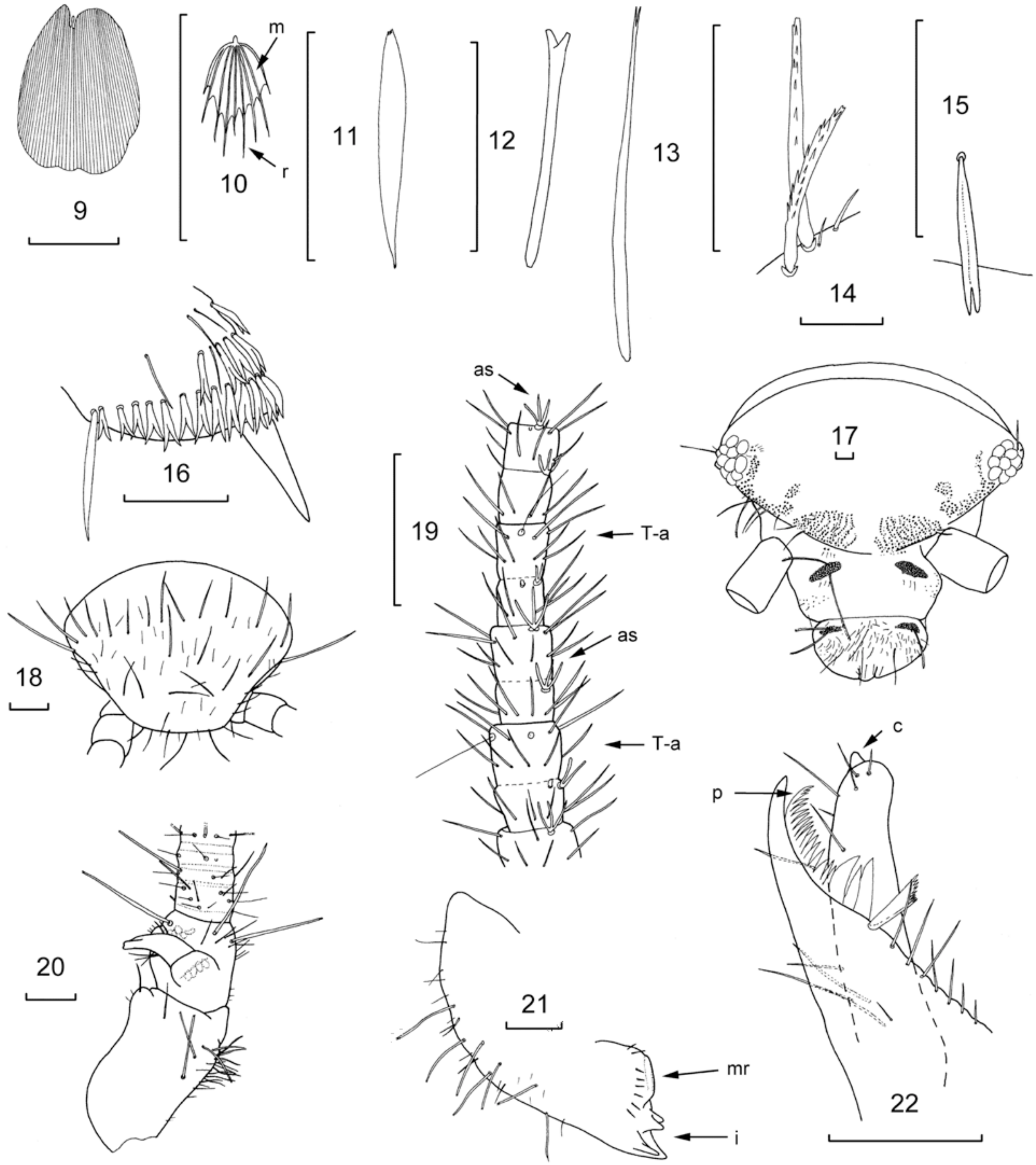


Table 1. Checklist of described Australian species

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).

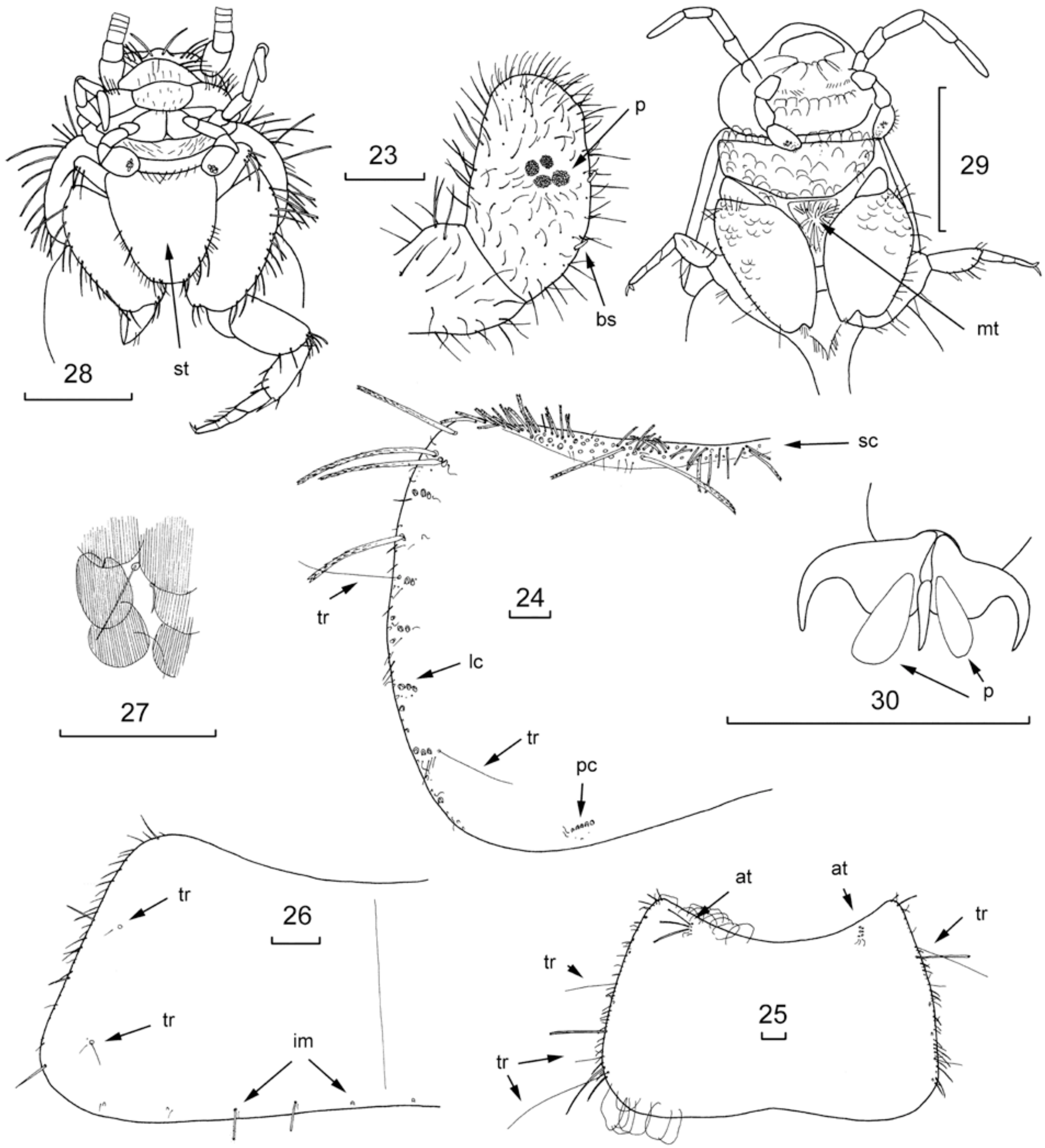
Head: With small eyes composed of about 12 ommatidia, located near the postero-lateral corners (Lepismatidae) (Figure 17) or without eyes (Nicoletiidae) (Figure 18). The arrangement of macrochaetae on the head is generally diagnostic at the level of genus. In some cases, the macrochaetae are restricted 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.

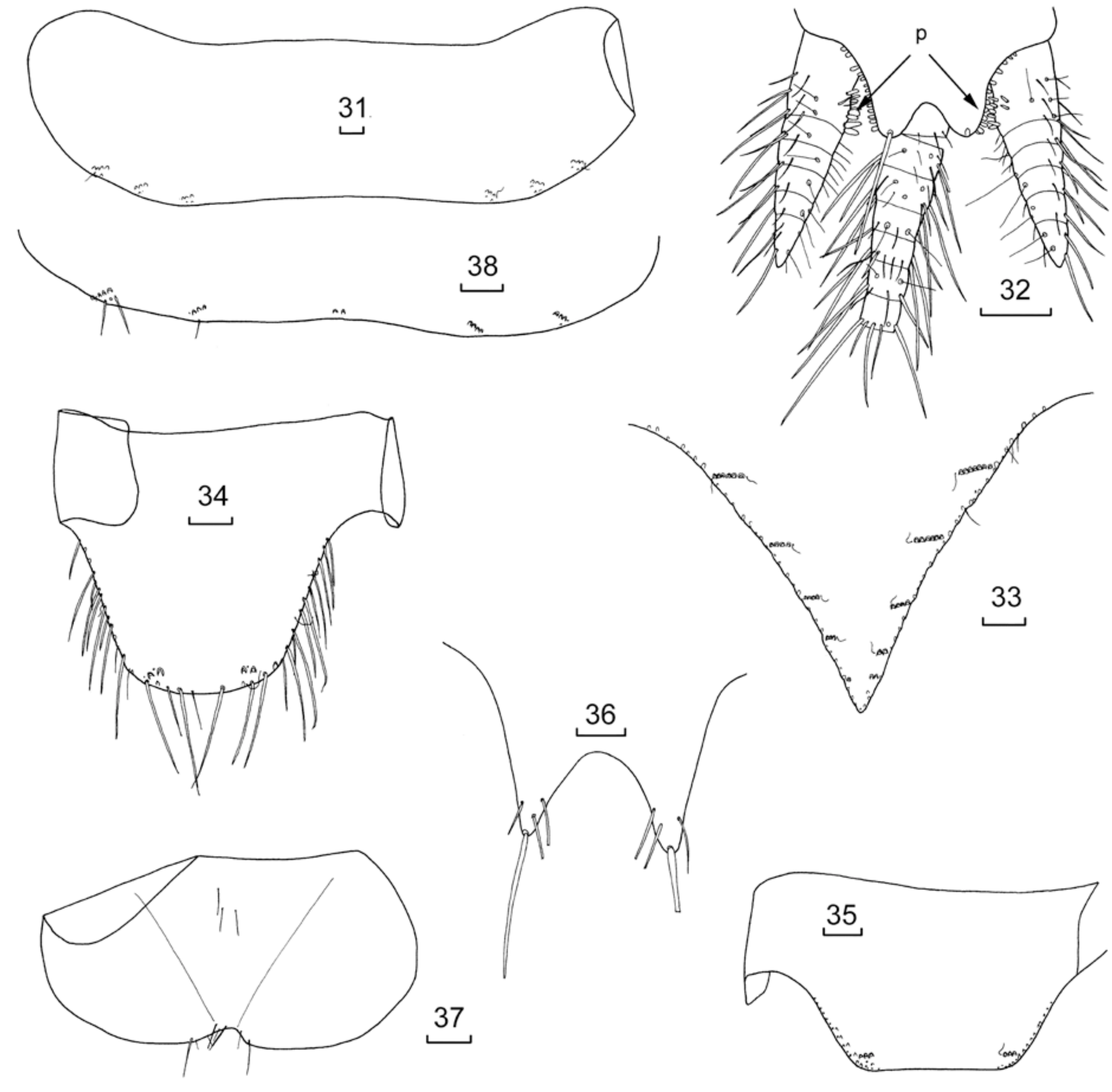
Mouthparts: Mandibles generally strong, usually with well-developed molar and incisor regions and macrochaetae on the outer face (Figure 21). In some Nicoletiidae, especially inquiline Atelurinae, the mandibles are reduced in size relative to the maxillae and the molar region lost. Maxillae (Figure 22) 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.



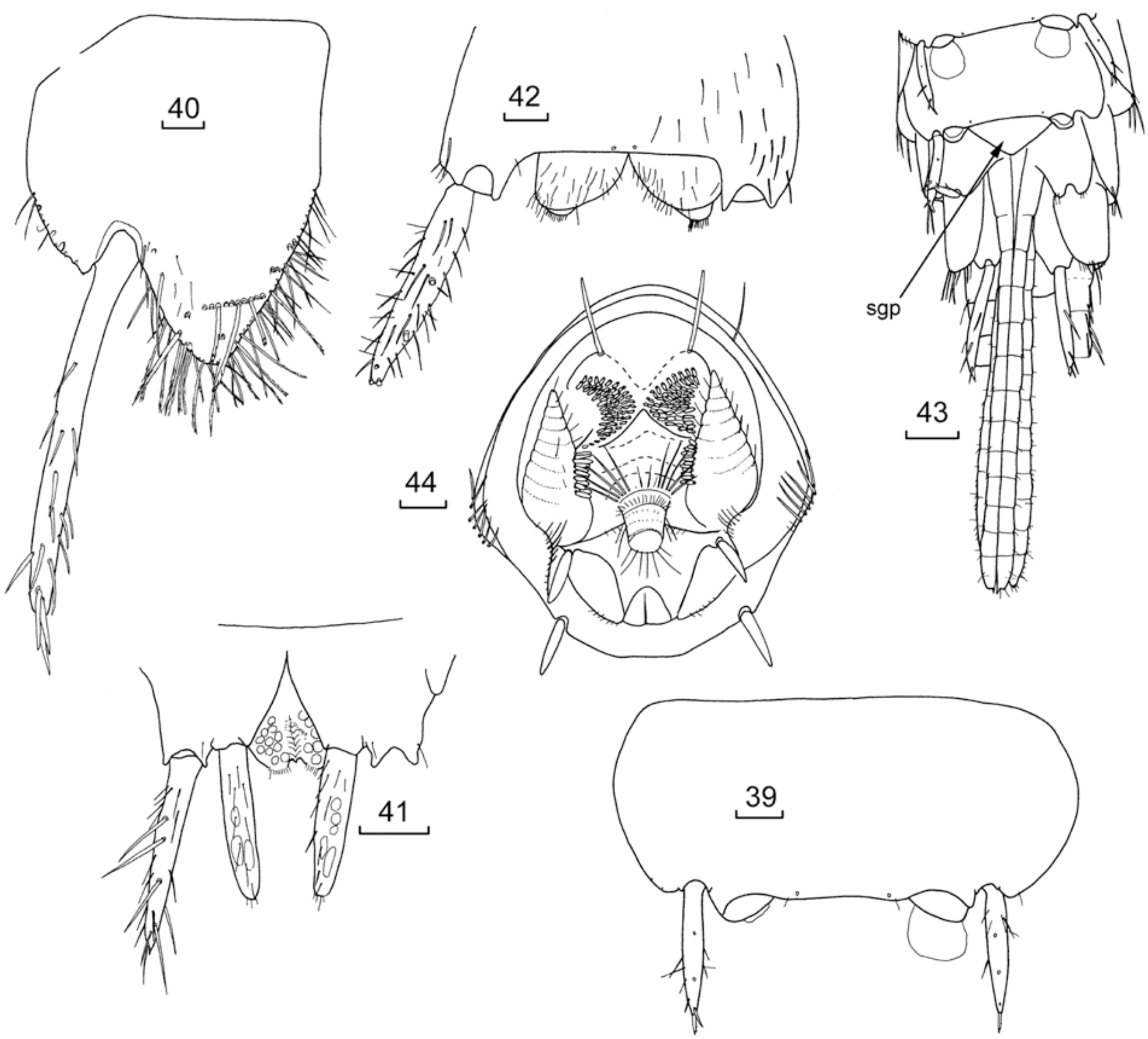
Figures 31-38. Morphology 31. typical urotergite with 3+3 combs, *Hemitelsella transpectinata*, 32. urotergite X and terminal filaments showing pegs (**p**), *Allatelura amitermina*, 33. triangular urotergite X, *Acrotelsella erniei*, 34. round urotergite X, *Anisolepisma hartmeyeri*, 35. trapezoidal 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