

**School of Science and Engineering  
Department of Environmental and Aquatic Sciences**

**The Systematics of the Monoscutidae (Arachnida: Opiliones)**

**Christopher Kenneth Taylor**

**This thesis is presented for the degree of  
Doctor of Philosophy  
of  
Curtin University of Technology**

**February 2010**

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgement has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

Signed

Christopher Taylor

Date

## Contents

Abstract .....	1
Introduction .....	3
Materials and Methods .....	8
Dorsal appearance of the enantiobunine prosoma .....	12
Phylogenetic Analysis .....	14
Characters used in analysis .....	16
Results and Discussion.....	37
Key to Genera of Enantiobuninae .....	47
Taxonomic Descriptions .....	50
<i>Acihasta</i> Forster 1948a.....	51
<i>Australiscutum</i> new genus .....	52
<i>Forsteropsalis</i> new genus .....	66
<i>Hypomegalopsalis</i> new genus .....	67
<i>Intutoportula</i> new genus .....	70
<i>Megalopsalis</i> Roewer 1923.....	83
<i>Monoscutum</i> Forster 1948a.....	103
<i>Neopantopsalis</i> new genus.....	104
<i>Scissorestis</i> new genus .....	124
<i>Spinibunus</i> new genus .....	125
<i>Spinicrurellum</i> new genus.....	129
<i>Spinicruroides</i> new genus .....	134
<i>Spinicrus</i> Forster, 1949a .....	138
<i>Templar</i> new genus .....	145
<i>Tercentenarium</i> new genus .....	147
<i>Thrasychiroides</i> Soares & Soares 1947 .....	153
<i>Thrasychirus</i> Simon 1884.....	154
Appendix I: <u>Revision of the Australian Gagrellinae (Arachnida: Opiliones: Sclerosomatidae), with a description of a new species</u> .....	155
Abstract .....	155
Introduction .....	155
Methods.....	157
Taxonomic Description.....	158
Acknowledgements .....	165
References .....	166

## Tables

1. Character state matrix for phylogenetic analysis.....	32–36
--	-------

## Figures

1. Dorsal view of Enantiobuninae exemplars, showing division of propeltidium into three areas.....	13
2–7. Genitalia of Enantiobuninae and Dyspnoi, SEM.....	18
8–11. Close-up images of enantiobunine glans to show differing pore morphologies.....	19
12–15. Spiracles of outgroup taxa.....	21
16–19. Neopilionid spiracles.....	22
20–23. Spiracles of <i>Thrasychirus</i> and <i>Pantopsalis</i> .....	23
24–27. Spiracles of <i>Spinicrus</i> species.....	24
28–31. Spiracles of <i>Neopantopsalis</i> and New Zealand <i>Megalopsalis</i> .....	25
32–35. Spiracles of Western Australian enantiobunines.....	26
36–39. Spiracles of <i>Megalopsalis</i> species.....	26
40–41. Modified distitarsi in <i>Megalopsalis</i> species.....	30
42. Strict consensus tree from parsimony analysis.....	38
43. Strict consensus, with mapped synapomorphies.....	39
44. Strict consensus of eight most parsimonious trees resulting from analysis constrained for monophyly of Monoscutidae.....	40
45. Distribution map for <i>Australiscutum</i> species.....	53
46–49. <i>Australiscutum hunti</i> new species .....	56
50. Male chelicerae of <i>Australiscutum</i> species.....	59
51–57. Genitalia of <i>Australiscutum</i> species.....	61
58–63. <i>Hypomegalopsalis tanisphyros</i> new species, male.....	68
64. Locality map for <i>Intutoportula</i> species in southern Western Australia.....	71
65–68. Spiracles of <i>Intutoportula</i> species.....	73
69–74. <i>Intutoportula minima</i> , major male.....	74
75–79. <i>Intutoportula porongorupensis</i> , male.....	76
80–83. <i>Intutoportula suffugiens</i> new species, male.....	78
84–86. <i>Intutoportula walpolensis</i> new species, male.....	81
87. Distribution map for <i>Megalopsalis</i> and <i>Hypomegalopsalis</i> .....	83
88–94. <i>Megalopsalis serritarsus</i> , male.....	86
95–100. <i>Megalopsalis epizephyros</i> new species, male.....	89
101–107. <i>Megalopsalis eremiotis</i> new species.....	93
108–116. <i>Megalopsalis hoggi</i> , male.....	96
117–122. <i>Megalopsalis leptekes</i> new species, male.....	99
123–128. <i>Megalopsalis pilliga</i> new species, male.....	102
129. Localities of <i>Neopantopsalis</i> in north-eastern Australia.....	104
130–137. <i>Neopantopsalis quasimodo</i> new species, male.....	109
138–139. <i>Neopantopsalis quasimodo</i> new species, male.....	110
140–143. <i>Neopantopsalis camelus</i> .....	112
144–150. <i>Neopantopsalis pentheter</i> new species.....	116
151–156. <i>Neopantopsalis psile</i> new species, male.....	119
157–158. <i>Neopantopsalis psile</i> new species, major male, SEM images.....	120
159. <i>Neopantopsalis psile</i> new species, body of female, dorsal view.....	121
160–163. <i>Neopantopsalis thaumatopoius</i> new species, male.....	123

164.	Locality map for <i>Spinicrus</i> and other Enantiobuninae in eastern Australia...	126
165–169.	<i>Spinibunus atrocidiana</i> new species.....	127
170–173.	<i>Spinibunus atrocidiana</i> new species and <i>Spinicrurellum coronatum</i> new species, SEM images.....	128
174–178.	<i>Spinicrurellum coronatum</i> new species, male.....	131
179–182.	Spiracles of <i>Spinicrurellum</i> species.....	132
183–186.	<i>Spinicrurellum puerile</i> new species, male.....	133
187–192.	<i>Spinicruroides caeruleomontium</i> new species.....	136
193–194.	<i>Spinicruroides caeruleomontium</i> new species, spiracle.....	138
195–197.	<i>Spinicrus stewarti</i> , male genitalia.....	141
198–200.	Spiracles of <i>Spinicrus</i> species.....	142
201–204.	<i>Spinicrus sublucens</i> new species, male.....	143
205–212.	<i>Templar incongruens</i> new species.....	146
213–219.	<i>Tercentenarium linnaei</i> new species.....	149
220–221.	<i>Tercentenarium linnaei</i> new species, right male pedipalp.....	150
222–224.	<i>Tercentenarium linnaei</i> new species, genitalia.....	151
225–226.	<i>Tercentenarium linnaei</i> new species, penis.....	152
227–231.	<i>Gagrella cauricrepa</i> new species.....	160



## Abstract

The taxonomy of the Australian species of the family Monoscutidae is reviewed, and a phylogenetic parsimony analysis is conducted of Monoscutidae and related taxa. As a result of this analysis, Monoscutidae (including subfamilies Monoscutinae and Megalopsalidinae) is synonymised with the subfamily Enantiobuninae of the family Neopilionidae. All Australian species of Phalangioidea now belong to Neopilionidae with the exception of *Gagrella cauricrepa* new species (Sclerosomatidae) which is described from Cape York Peninsula, Queensland. Ten new genera and twenty-one new species of Enantiobuninae are described, including *Scissorestis nigricans* (Hickman 1957) new genus and combination, *Templar incongruens* new genus and species (New Zealand), *Tercentenarium linnaei* new genus and species, *Hypomegalopsalis tanisphyros* new genus and species, *Megalopsalis epizephyros* new species, *Megalopsalis eremiotis* new species, *Megalopsalis leptekes* new species, *Megalopsalis pilliga* new species, *Spinicrurellum coronatum* new genus and species, *Spinicrurellum puerile* new species, *Intutoportula minima* (Kauri 1954) new genus and combination, *Intutoportula suffugiens* new species, *Intutoportula walpolensis* new species, *Spinicruroides caeruleomontium* new genus and species, *Neopantopsalis quasimodo* new genus and species, *Neopantopsalis pentheter* new species, *Neopantopsalis psile* new species, *Neopantopsalis thaumatopios* new species, *Spinibunus atrocidiana* new genus and species, *Spinicrus sublucens* new species, *Australiscutum huntii* new genus and species, *Australiscutum graciliforceps* new species and *Australiscutum triplodaemon* new species. New combinations are also proposed for *Intutoportula porongorupensis* (Kauri 1954), *Neopantopsalis camelus* (Forster 1949a) and *Neopantopsalis continentalis* (Roewer 1923). Genitalia are described for *Spinicrus stewarti* Forster 1949a. The presence of male dimorphism is established in *Intutoportula minima*, *Neopantopsalis quasimodo*, *N. pentheter* and *N. psile*. Asymmetrical chelae, the first record of such for Opiliones, are described for *Australiscutum triplodaemon*.

## Note on Publication and Formatting

Certain parts of this thesis have already appeared as separate publications; details are given below. Taxa described as new over the course of thesis preparation have still been indicated as “new genus/species”, but publication details have been given as for other previously published taxa. Publications arising from this thesis and the taxa affected are:

Taylor, C.K. (2008a) A new species of Monoscutidae (Arachnida, Opiliones) from the wheatbelt of Western Australia. *Records of the Western Australian Museum*, 24(4), 375-380 (*Tercentenarium linnaei*, published as *Megalopsalis linnaei*).

Taylor, C.K. (2008b) A new species of Monoscutinae (Arachnida, Opiliones, Monoscutidae) from New Zealand, with a redescription of *Monoscutum titirangiense*. *Journal of Arachnology*, 36, 176-179 (*Templar incongruens*).

Taylor, C.K. (2009a) Revision of the Australian Gagrellinae (Arachnida: Opiliones: Sclerosomatidae), with a description of a new species. *Australian Journal of Entomology*, 48, 217-222 (*Gagrella cauricrepa*).

Taylor, C.K. (2009b) *Australiscutum*, a new genus of Monoscutidae (Arachnida: Opiliones) from eastern Australia, with the first record of asymmetrical chelicerae in Opiliones. *Insect Systematics and Evolution*, 40, 319-332 (*Australiscutum* and included species).

Taylor, C.K. & Hunt, G.S. (2009) New genus of Megalopsalidinae (Arachnida: Opiliones: Monoscutidae) from north-eastern Australia. *Zootaxa*, 2130, 41-59 (*Neopantopsalis* and included species). Glenn Hunt [deceased] was named as an honorary author as the publication was based on material he had left unpublished; however, the article as published was primarily composed by C. K. Taylor.

## Introduction

Long-legged harvestmen of the family Monoscutidae are widespread in Australia and New Zealand, found in all parts of both countries except for the northwest part of Australia. In New Zealand, they are the only indigenous family of long-legged harvestmen (Eupnoi) except for the Caddidae represented by a single species, *Acropsopilio neozelandiae* (Forster 1948b) whereas the Australian fauna also includes representatives of Caddidae (Forster 1955; Hickman 1957) and Neopilionidae (subfamily Ballarrinae; Hunt & Cokendolpher 1991), with the family Sclerosomatidae marginally represented by a single species restricted to the northeasternmost tip of the continent (see appendix; Taylor 2009a). Three species of the families Phalangiidae and Sclerosomatidae have been recorded in Australia and New Zealand as introduced exotics (Hickman 1957; Gruber & Hunt 1973).

About forty species of Monoscutidae have been described to date (Taylor 2004, 2008a, b), but these species cover a notable disparity of morphologies, from short-legged, heavily sclerotised species (Forster 1948) to large, extremely long-legged and less sclerotised taxa (Forster 1944, 1949a; Hickman 1957). In the past, these extremes have been distinguished as the subfamilies “Monoscutinae” and “Megalopsalidinae” (Crawford 1992; Cokendolpher & Taylor 2007) but, as explained below, recently described species (Taylor 2008a, b) have put the distinction between the two subfamilies in doubt. To date, taxonomic studies of Monoscutidae have been conducted solely on a descriptive basis, a situation that is not unusual for Opiliones, and the current paper includes the first major attempt to classify the Monoscutidae phylogenetically. Sexual dimorphism is common in the family, with the males of many species possessing enlarged chelicerae relative to the females (Forster 1964; Taylor 2004).

A review of phylogenetic studies of Opiliones has been published by Giribet & Kury (2007). The phylogeny of the order as a whole has been investigated by Shultz (1998), Giribet *et al.* (1999, 2002, 2009), Giribet & Wheeler (1999) and Shultz & Regier (2001), using a variety of morphological (Shultz 1998; Giribet *et al.* 1999, 2002) and molecular (Giribet *et al.* 1999, 2002, 2009; Giribet & Wheeler 1999; Shultz & Regier 2001) methods. Each of these order-level analyses supported a monophyletic clade Eupnoi, including the superfamilies Caddoidea and

Phalangioidea. All analyses have also agreed in placing *Caddo* (the only representative of Caddoidea analysed to date) outside Phalangioidea, but not all phalangoid families have been represented.

The only other cladistic analysis to date to examine the Phalangioidea has been the morphological analysis by Hunt & Cokendolpher (1991). Hunt & Cokendolpher's (1991) analysis focused on Neopilionidae and Monoscutidae ('Phalangiidae' and 'Gagrellidae' [regarded by Crawford 1992 and Tourinho 2007 as part of Sclerosomatidae] were included as compound terminal taxa), assumed phalangoid monophyly, and was rooted by *a priori* polarisation of characters rather than use of an outgroup (unless otherwise indicated, family names used in the introduction and phylogenetic analysis refer to the classification used by Crawford 1992 and Cokendolpher *et al.* 2007). Selected rather than consensus results were presented, and several distinct hypotheses of phalangoid relationships were presented after analysis. Hunt & Cokendolpher (1991) proposed the existence of a clade uniting species of Phalangioidea in which the spiracle was closed by an occluding entapophysis (originally described by Šilhavý 1970). This clade was also implicitly supported by Martens (1976, 1978, 1986) who recognised its members as a single family Phalangiidae (including Sclerosomatidae) on the basis of genital morphology. Phalangioidea was represented in the analysis of Giribet *et al.* (2002) by species of Phalangiidae, Sclerosomatidae and the *incertae sedis* genus *Dalquestia* (placed by Crawford 1992 in the '*Metopilio* assemblage'), with support for monophyly of each family as well as their forming a monophyletic clade. However, members of the families Monoscutidae, Neopilionidae and Protolophidae were not analysed. Giribet *et al.* (2009) also included *Protolophus*, *Eurybunus* (another member of the '*Metopilio* assemblage'—Crawford 1992) and two New Zealand representatives of Monoscutidae but not Neopilionidae. Monophyly was supported for Phalangiidae and Sclerosomatidae (with *Protolophus* included in Sclerosomatidae) but the entapophyseate clade was not supported; instead, Monoscutidae was placed as the sister taxon to Sclerosomatidae. However, except for the monophyly of the families themselves, support for family relationships within the Phalangioidea was low.

*Macropsalis serritarsus* Sørensen 1886 was the first species of long-legged harvestman to be described from Australia, and the second from Australasia after the New Zealand *Phalangium listeri* White 1849. Both are now regarded as members of

the Monoscutidae, but were originally classified in the Phalangiidae (equivalent at the time to the current Phalangioidea). Simon (1879) established the genus *Pantopsalis* Simon 1879 for *Phalangium listeri*, and the history of that genus has been summarised by Taylor (2004). Sørensen (1886) distinguished *Megalopsalis* (then named *Macropsalis*) from the New Zealand genus *Pantopsalis* Simon 1876 by the presence in the former of spines on the ocularium, opisthosoma longer than prosoma, tibia II without pseudoarticulations, pedipalp tibia 1.5 times longer than patella (versus both segments subequal in *Pantopsalis*) and by an apophysis on the pedipalp patella. The first three characters are of doubtful generic significance (Taylor 2004) and in practice only the presence or absence of a pedipalp patellar apophysis was subsequently used to distinguish the genera (Roewer 1923; Forster 1944). *Macropsalis* Sørensen 1886 was enlarged by the description of *M. hoggi* Pocock 1903a from Australia and *M. chiltoni* Hogg 1910 from New Zealand. Roewer (1923) proposed the name *Megalopsalis* Roewer 1923 to replace *Macropsalis* Sørensen, which was preoccupied by *Macropsalis* Sclater 1866, and included both *Megalopsalis* and *Pantopsalis* in the subfamily Phalangiinae. Further species assigned to *Megalopsalis* all came from New Zealand—*Macropsalis fabulosa* Phillipps & Grimmett 1932, *Megalopsalis turneri* Marples 1944 and five species and one subspecies described by Forster (1944).

The harvestman subfamily Monoscutinae was originally described from the northern part of New Zealand by Forster (1948) to include two species of heavily armoured and relatively short-legged Eupnoi, *Monoscutum titirangiense* Forster 1948 and *Acihasta salebroso* Forster 1948. Seemingly using the classificatory system for Opiliones established by Roewer (1923), Forster (1948) included the Monoscutinae within the family Phalangiidae Latreille 1802 (then the only recognised family of Eupnoi), and suggested that it might be related to the Northern Hemisphere Oligolophinae Banks 1893.

*Megalopsalis* and *Pantopsalis* were included in the Holarctic and African subfamily Phalangiinae by Roewer (1911, 1923) despite the clear illustration by Roewer (1911) of a pectinate pedipalp claw in *Megalopsalis*, which character should have placed *Megalopsalis* in Leiobuninae according to the highly artificial classification of Roewer. Roewer (1911, 1923) made no comment on this inconsistency but Forster (1949a) established the subfamily Megalopsalinae [*sic*] on the basis of this very character. Forster (1949a) also identified a toothed pedipalp

claw in Australian *Pantopsalis* but not in New Zealand *Pantopsalis*. He therefore established the megalopsalidine genus *Spinicrus* Forster 1949a for the Australian species, with *S. tasmanicum* (Hogg 1909) as the type species, as well as describing the species *S. camelus* Forster 1949a and *S. stewarti* Forster 1949a. Despite including only four species, *Spinicrus* was a disparate genus right from its initial publication, containing very distinct species united only by the absence of the pedipalp patellar apophysis found in *Megalopsalis*. Lacking the diagnostic feature, *Pantopsalis* was implicitly excluded from Forster's (1949a) Megalopsalinae, but its taxonomic position was not explained (presumably it remained in Phalangiinae). Forster (1949a) also made no comment on the New Zealand species assigned to *Megalopsalis*, which too lack a tooth-row. The presence or absence of a pectinate pedipalp claw is now regarded as being of less taxonomic significance (Suzuki 1973, Crawford 1992), but *Spinicrus* is still distinguishable from *Pantopsalis* on the basis of the absence of a pedipalp patellar apophysis in females (present in female *Pantopsalis*), different shape of the male genitalia (Hickman 1957, Forster 1964, Taylor 2004), and differences in the spination of the spiracle (Hunt 1990b). Further species of *Spinicrus* were described from south-western Australia and Tasmania by Kauri (1954) and Hickman (1957), respectively. A third genus assigned by Forster (1949a) to Megalopsalinae, *Nodala* Forster 1949a, has been re-identified by Gruber & Hunt (1973) as a junior synonym of *Nelima* Roewer 1910 (Sclerosomatidae) based on specimens of the introduced species *Nelima doriae* (Canestrini 1871) (native to Europe), and is not closely related to *Megalopsalis*.

Šilhavý (1970) included both *Pantopsalis* and *Monoscutum* in the Megalopsalinae (no mention was made of *Acihasta*), and transferred this subfamily to the Neopilionidae, which had been established as a separate family from Phalangiidae by Kauri (1961). Šilhavý (1970) regarded Neopilionidae as a separate family from Phalangiidae on the basis of the lack in the former of a spiracular entapophysis, but, as described above, an entapophysis is probably apomorphic for a single clade within Phalangioidea, and hence its absence cannot be regarded as a uniting feature for the other species in that superfamily. Martens (1976) established Megalopsalididae (with corrected spelling) as its own separate family, presumably on the basis of the distinctive form of the male genitalia with paired bristle groups at the junction of shaft and glans (though this was not explicitly stated).

Hunt & Cokendolpher (1991) recognised Monoscutinae as a separate subfamily within Megalopsalididae. This family was represented in their analysis of Southern Hemisphere Phalangioida by ‘some *Pantopsalis*’, ‘new genus (?Monoscutinae)’ (probably *Australiscutum*, described below), ‘*Megalopsalis*’ (probably Australian species only) and *Spinicrus nigricans* Hickman 1957. Hunt & Cokendolpher’s (1991) analysis divided Megalopsalididae into two clades, *Pantopsalis* and *Australiscutum* in one clade and *Megalopsalis* and *Spinicrus nigricans* in the other, but this was based on only two characters. The association of *Pantopsalis* and *Australiscutum* was particularly suspect as their single supposed uniting character, the presence of four seminal receptacles (as opposed to only two in *Megalopsalis* and *Spinicrus nigricans*), was otherwise regarded as Hunt & Cokendolpher (1991) as a plesiomorphy for Phalangioida as a whole. Megalopsalididae itself was supported as monophyletic by a single character, the bristle groups on the penis.

Crawford (1992) maintained the separation of Monoscutinae (*Monoscutum* and *Acihasta*) and Megalopsalidinae (*Megalopsalis*, *Pantopsalis* and *Spinicrus*), but pointed out the one-year priority of the former, correcting the name of the family to Monoscutidae. The distinguishing features of the subfamilies were reviewed by Cokendolpher & Taylor (2007), with Monoscutinae containing short-legged, heavily sclerotised and sexually monomorphic taxa whereas Megalopsalidinae were long-legged, non-sclerotised and strongly sexually dimorphic. The significance of this distinction was questioned by Taylor (2008a, b) with the descriptions of the sexually dimorphic ‘monoscutine’ *Templar incongruens* Taylor 2008a, and the sexually near-monomorphic ‘megalopsalidine’ *Megalopsalis linnaei* Taylor 2008b. Taylor (2004) questioned the monophyly of Monoscutidae as a whole, suggesting that the presence of bristle groups on the penis might be a plesiomorphy for Phalangioida. Also notable in recent years is the publication of the new genus *Neopantopsalis* Taylor & Hunt 2009.

## Materials and Methods

Specimens came from the collections of the Auckland Museum (AMNZ), Australian Museum, Sydney (AMS), British Museum of Natural History, London (BMNH), California Academy of Sciences, San Francisco (CAS), Canterbury Museum, Christchurch (CMNZ), Museum Victoria, Melbourne (MV), Queensland Museum, Brisbane (QM), Te Papa Tongarewa, Wellington (MONZ), Western Australian Museum, Perth (WAM) and Zoologisches Museum Hamburg (ZMH). Specimens were examined under 70% ethanol using a Leica MZ6 stereo microscope and drawn with the aid of a camera lucida. Colours are described in alcohol. Genitalia were examined under an Olympus BH-2 compound microscope using KY<sup>®</sup> Brand jelly as a mountant as described in Cokendolpher & Sissom (2000). Genitalia and pedipalp specimens were examined using SEM microscopy after drying in sequential washes of increasing concentrations of ethanol to 100%, followed by washing in hexamethyl-disilazane (HMDS) and air-drying as described by Nation (1983). The specimens were then mounted and sputter-coated with gold to a depth of 20–30 nm and examined with a Philips XL30 SEM.

Measurements were taken using a reticle and are given below as means in millimetres with standard deviations in parentheses. The number of specimens measured is indicated at the beginning of the description. For those species in which not all available specimens were measured, the individuals measured are indicated as such in the specimen listings. Prosoma and total body lengths were both taken down the midline and width was measured at the widest part of the prosoma between the second and third legs. Leg measurements are given from leg I to IV.

Phylogenetic parsimony analysis was conducted using the programme TNT (Goloboff *et al.* 2008). Heuristic (“traditional”) searches were conducted using a Wagner-tree random seed, 10 replicates (default setting; runs using 100 replicates did not give different results and occasionally exceeded tree-buffer capacity) holding 10 trees per replication and constructing trees using a tree bisection-reconnection (TBR) swapping algorithm. Changes from an unambiguous character state to a polymorphic character are counted by TNT as a step, even if the ancestral character state is included in the polymorphism. Details of specimens of Monoscutidae examined are

listed in the descriptive section below. Specimens examined for remaining species are:

***Ischyropsalis kollari* Koch 1839 (Dyspnoi: Ischyropsalididae)**—1 male, Ennstaler Alps, Gesäuse National Park, Styria, Austria, 47°32'N 14°42'E, 1800 m, 10 August 2004, G. Komposch (WAM T94993); 1 female, ditto, 47°33'N 14°40'E, 1560 m, 9 August 2004, G. Komposch (WAM T94996).

***Taracus* Simon 1879 (Dyspnoi: Sabaconidae)**—1 male, 1 female, 5.6 miles E of Anthony Lakes Ski Area, Wallowa Whitman National Forest, Baker County, Oregon, United States of America, 5200 ft, 14 August 1972, T. Briggs, R. Lem, fir forest, underside of wood (CAS).

***Nipponopsalis yezoensis* (Suzuki 1958) (Dyspnoi: Nipponopsalididae)**—2 males, 2 females, Kraternaya Bay, peninsula base, Ushishir Island, Kuril Islands, 47.508°N, 152.819°E, 50 m, 14-20 August 1995, V. D. Roth, pitfalls (CAS, US-95-VR-026A).

***Nemastoma triste* (Koch 1835) (Dyspnoi: Nemastomatidae)**—1 male, Luna, Austria, 18 May 1971, Ressler (CAS).

***Caddo agilis* Banks 1891 (Eupnoi: Caddidae)**—2 females, Maruyama, Sapporo City, Hokkaido, Japan, 4 July 1980, N. Tsurusaki (WAM).

***Ballarra longipalpus* Hunt & Cokendolpher 1991 (Eupnoi: Ballarrinae)**—2 males, 1 female, Mt Cooke, Western Australia, 32°25'S 116°18'E, 31 July 1991, M. S. Harvey, J. M. Waldock, hand collected (WAM T72862).

***Thrasychirus* Simon 1884 (Eupnoi: Neopilioninae)**—1 female, 20 km E of Puyehue, Osorno Province, Chile, 26 January 1951, Ross & Michelbacher (CAS).

***Nelima doriae* (Canestrini 1871) (Eupnoi: Sclerosomatidae)**—1 male, 2 females, Geelong, Victoria, Australia, R. Easton, 23 May 1978 (WAM 87/1298-9); 1 female, Wagga Wagga, Koorringal, New South Wales, Australia, 35°07'S 147°22'E, March 1993, C. A. Car, in garden (WAM T72931).

*Phalangium opilio* Linnaeus 1758 (Eupnoi: Phalangiidae)—1 male, Latimer County, Boyd Lake, NE of Loveland, Colorado, United States of America, 1512 m, 2 August 1973, P. H. Arnaud, Jr (CAS).

*Opilio parietinus* (De Geer 1778) (Eupnoi: Phalangiidae)—1 male, Cluan Tier Mountains, Tasmania, 18 January 1998 (AMS KS66360).

*Monoscutum titirangiense* Forster 1948a (Eupnoi: Enantiobuninae)—1 male, 1 female, Titirangi, Auckland, New Zealand, 36°56'S, 174°39'E, 12 December 1945, R. Forster (MONZ AH.000076; syntypes); 2 males, Atuanui, Mt Auckland, New Zealand, 36°27'S, 174°28'E, February 2002, A. Warren (AMNZ 60921, 61795); 6 males, 2 females, ditto, January 2002, A. Warren (AMNZ 61121); 1 male, 3 females, ditto, April 2002, A. Warren (AMNZ 61796, 61805, 61997); 2 females, Mataitai Forest, Auckland, New Zealand, 39°59'S, 175°08'E, February 2002, A. Warren (AMNZ 61458, 61459); 1 male, 2 females, ditto, March 2002, A. Warren (AMNZ 61960, 61968).

*Forsteropsalis chiltoni* (Forster 1944) (Eupnoi: Enantiobuninae)—(MONZ, unless otherwise specified) 1 male, 1<sup>st</sup> bay north of Whale Passage, Port Pegasus, southern Stewart Island, New Zealand, 21 February 1972, F. M. Climo; 1 female, Freshwater Flats, Stewart Island, 46°51'S, 167°54'E, 16 May 1995; 1 male, Mason's Bay, Stewart Island, 46°54'S, 167°48'E, 15 May 1995; 1 male, 1 female, 3 juveniles, Bravo, Stewart Island, 23 November 1946, under logs; 2 females, Halfmoon Bay, 22 November 1946; 8, Maori Bay, Stewart Island, 25 November 1946, ex foliage; 1 male, Port Pegasus Camp, southern Stewart Island, 23 February 1972, ex foliage; 1 male, 1<sup>st</sup> bay north of Whale Passage, southern Stewart Island, 21 Feb 1972, Port Pegasus; 1 male, southern Stewart Island, Twilight Bay littoral, Port Pegasus, 29 Feb 1972; 2 females, Stewart Island [pre-1924] (BMNH).

*Forsteropsalis fabulosa* (Phillipps & Grimmett, 1932) (Eupnoi: Enantiobuninae)—(MONZ) 1 male, Rimutaka Hill, Wellington, New Zealand, 41°06.2'S 175°12.7'E, 14 July 2004, A Tennyson, on tree trunk at night (proposed neotype); 1 male, Karori Hills, 22 Jan 1947, on foliage.

*Forsteropsalis grimmetti* (Forster 1944) (Eupnoi: Enantiobuninae)—(MONZ) 1 female, Waiho Gorge, West Coast District, New Zealand, 12 February 1927, R. E. R. Grimmett (MONZ 2/12; holotype); 1 female, Anita Bay, Milford Sound, 16 Dec 1944, off ferns; 2 males, 2 females, Milford Sound, 19 Dec 1943; 4 females, Milford Sound I, 30 Jan 1946, beaten from ferns.

*Forsteropsalis inconstans* (Forster 1944) (Eupnoi: Enantiobuninae)—(MONZ) 1 female, Akatarawa, Wellington, New Zealand, 1 January 1943, R. Forster (MONZ 2/22; holotype); 2 females, ditto; 1 male, ditto, 21 Jan 1945; 1 female, Johnson's Hill, Karori, Wellington, New Zealand, 21 Dec 1946, under logs; 3 males, Karori, 16 Nov 1941; 1 male, ditto, 26 Feb 1942, beaten from "niggerhead" [probably *Carex secta*]; 1 male, ditto, 1 February 1942, R. Forster (MONZ 2/24, neotype of *Macropsalis fabulosa* as designated by Forster 1944); 2 males, ditto, under log [identified as *M. fabulosa* on label]; 1 male, Silverstream, 15 Feb 1920; 1 juvenile male, ditto, 18 Jul 1920.

*Pantopsalis albipalpis* Pocock 1903a (Eupnoi: Enantiobuninae)—2 males, 1 female, Opoho Bush, Dunedin, New Zealand, January 1946, T Smith (MONZ AH.00096).

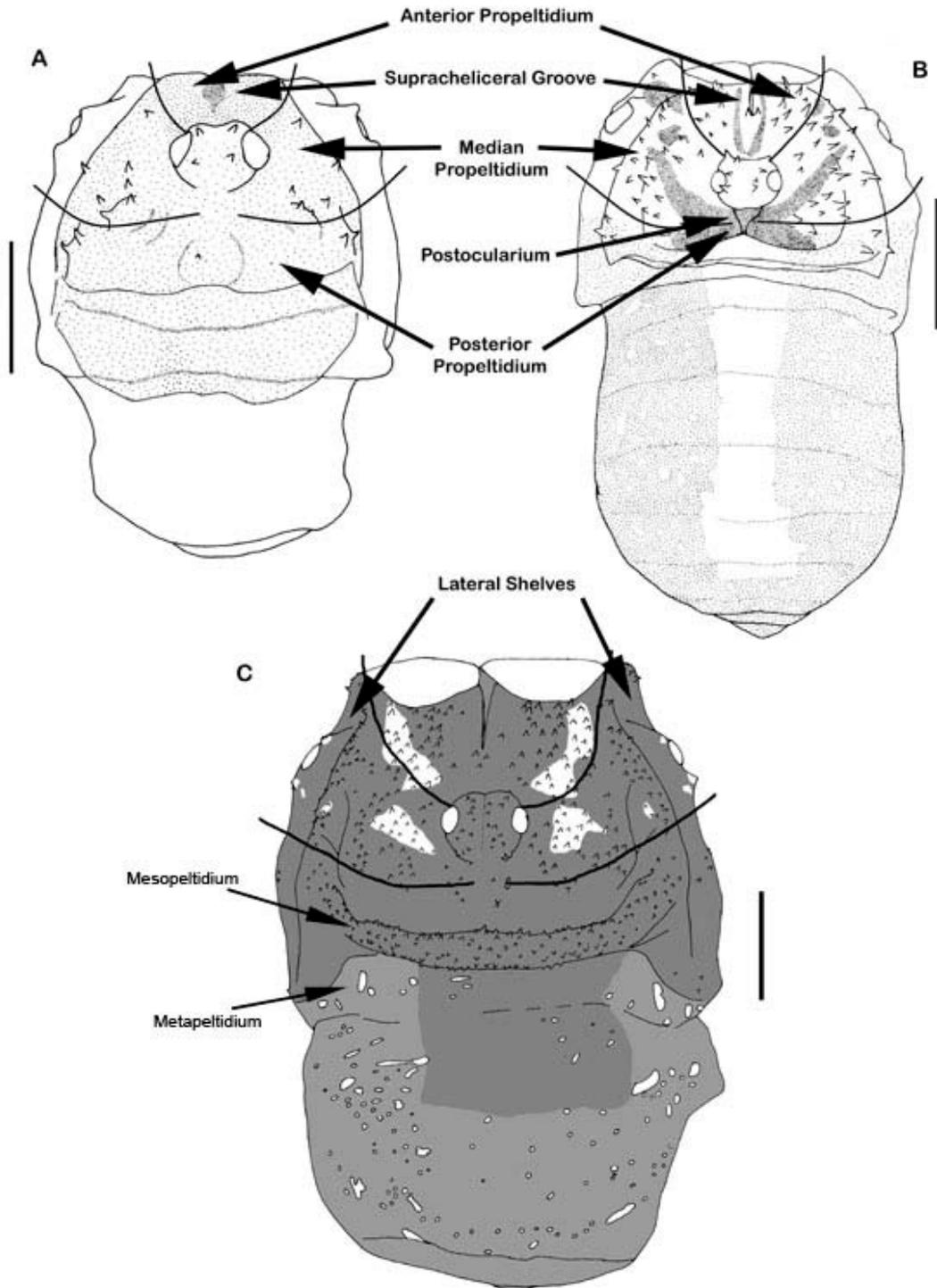
*Pantopsalis luna* (Forster 1944) (Eupnoi: Enantiobuninae)—3 males, Waiho Gorge, South Westland, New Zealand, 21 July 1927, A. Castle (MONZ AH.00090); 2 females, Waiho [misspelt as 'Waino'] Gorge, 12 July 1943, A. Castle (MONZ AH.00089).

*Spinicrus tasmanicum* (Hogg 1910) (Eupnoi: Enantiobuninae)—1 female, 3 km E of Bothwell, Tasmania, 42°23'17"S 147°2'37"E, 3 September 2005, M. S. Harvey, open eucalypt grove on road-side (WAM T70786); 1 male, Hillyer Gorge, Tasmania, 5 January 1965, R. Cockerill (AMS KS24237); 1 male, Trevallyn, Tasmania, 18 August 1928, V. V. Hickman (AMS KS23744).

## Dorsal appearance of the enantiobunine prosoma

The prosoma of Enantiobuninae has a distinct propeltidium, mesopeltidium and metapeltidium except in the genera *Monoscutum*, *Acihasta*, *Templar* and *Australiscutum*. The metapeltidium is separated by a suture from the propeltidium. The mesopeltidium is fused to the propeltidium but remains distinguishable as either a raised ridge, or by a crease separating it from the propeltidium. The anterior margin of the mesopeltidium is often bent anteriorly to form a triangular area directly behind the ocularium. The median part of the fused propeltidium and mesopeltidium is raised to form a dorsal prosomal plate whereas the outer edges form a lateral shelf. The dorsal prosomal plate in most male Megalopsalidinae is sclerotised whereas the metapeltidium and lateral shelves are not (though *Neopantopsalis quasimodo* here provides an exception). The colouration of the dorsal prosomal plate often differs from the remainder of the prosoma.

Species of Megalopsalidinae vary considerably in the pattern of armature or pigmentation on the prosoma, but there is generally an underlying arrangement that may be used as a basis for descriptions of the megalopsalidine propeltidium. The propeltidium may be divided into three major areas radiating from around the ocularium, here referred to as the anterior, median and posterior propeltidial areas (fig. 1). The boundary between the anterior and median areas runs from the ocularium to the anterior corners of the dorsal prosomal plate, with the anterior area lying within and anterior to this boundary. An indentation at the midpoint of the anterior margin of the dorsal prosomal plate between the chelicerae leads to a short groove (the supracheliceral groove) running posteriorly towards the ocularium. Two raised bands of darker pigmentation are often present on either side of the supracheliceral groove and often run further posteriorly than the groove. The median propeltidial area is retrolateral to the promedian area, and covers the area anterior to a line between the ocularium and the posterior corner of the lobe behind the ozopore. The remainder of the propeltidium comprises the posterior propeltidial area. Directly behind the ocularium there is often a recognisable pair of creases running from the ocularium to the anterior projection of the mesopeltidium, with the area between the creases (the postocularium) often distinguishable in appearance from the remainder



**FIGURE 1.** Dorsal view of male Enantiobuninae exemplars, showing division of propeltidium into three areas. A. *Neopantopsalis quasimodo* (QM S2481). B. *Megalopsalis hoggi* (WAM T72936). C. *Forsteropsalis inconstans* (QM S74252). Scale bars = 1 mm.

of the dorsal prosomal plate. In most cases, the postocularium is insignificant, but in *Neopantopsalis* it is often expanded as a large posterior hump.

It is tempting to compare the division of the propeltidium into areas of armature/pigmentation to the fused segments believed to comprise the propeltidium (Shultz & Pinto-da-Rocha 2007), but without any investigation into the embryology of Enantiobuninae such a comparison would be premature at best.

## Phylogenetic Analysis

All species of Monoscutidae described to date from Australia have been included in the analysis with the exception of *Neopantopsalis continentalis* (Roewer 1923), the identity of which remains uncertain, and *Spinicrus thrypticum* Hickman 1957 for which specimens were not available. *Spinicrus thrypticum* is very similar to *S. stewarti* Forster 1949a, and a close relationship between the two seems likely. New Zealand Monoscutidae are represented by *Monoscutum titirangiense* Forster 1948a, *Templar incongruens* Taylor 2008, *Pantopsalis albipalpis* Pocock 1903a, *P. luna* (Forster 1944), *Megalopsalis grimmetti* Forster 1944, *M. fabulosa* (Phillipps & Grimmett 1932), *M. chiltoni* (Hogg 1910) and *M. inconstans* Forster 1944. All genera recognised to date in Monoscutidae are represented in the analysis with the exception of the monotypic *Acihasta salebrosa* Forster 1948a which is restricted to the Three Kings Islands north of New Zealand and is probably a close relative of *Monoscutum titirangiense* (Forster 1948a).

Because only a single character has previously been used to diagnose the Monoscutidae (Martens 1976; Hunt & Cokendolpher 1991), no phylogenetic analysis of the family could be conducted without also testing its monophyly. Therefore, a number of representatives of other phalangoid families have been included. Each of the three subfamilies included in Neopilionidae by Cokendolpher (2007a) has been represented by a single exemplar—*Neopilio australis* Lawrence 1931 (Neopilioninae), *Ballarra longipalpus* (Ballarrinae) and *Thrasychirus* sp. (Enantiobuninae). The entapophyseate clade proposed by Hunt & Cokendolpher (1991) is represented by *Nelima doriae* (Sclerosomatidae), *Phalangium opilio* and *Opilio parietinus* (Phalangiidae). Both Caddoidea and Dyspnoi have been used as outgroup taxa, with Caddoidea represented by *Caddo agilis* and Dyspnoi by *Ischyropsalis kollari* (Ischyropsalididae), *Taracus* sp. (Sabaconidae), *Nipponopsalis yezoensis* (Nipponopsalididae) and *Nemastoma triste* (Nemastomatidae). Dyspnoi is

therefore represented by members of each of its two constituent subfamilies, Ischyropsalidoidea (*Ischyropsalis* and *Taracus*) and Troguloidea (*Nipponopsalis* and *Nemastoma*).

Wherever possible, characters have been coded using actual specimens. The only species tested for which specimens were unavailable was *Neopilio australis* whereas only female specimens were on hand for *Caddo agilis* and *Thrasychirus* sp. Characters that could not be coded from available specimens were taken from Lawrence (1931) and Hunt & Cokendolpher (1991) for *Neopilio australis*, Gruber (1974) for *Caddo agilis*, and Cokendolpher & Lanfranco (1985) and Hunt & Cokendolpher (1991) for *Thrasychirus* sp. Data on spiracle morphology has been taken from Hunt (1990) for *Megalopsalis serritarsus* and *Neopantopsalis camelus*. Unless otherwise indicated, all characters have been coded based on male specimens. In those species exhibiting male dimorphism, characters have been coded using major males.

The presence of male intrasexual dimorphism in Monoscutidae has been established for the genus *Pantopsalis* in New Zealand (Taylor 2004), and is here described for *Intutoportula*, *Neopantopsalis* and *Scissorestis* as well. As in *Pantopsalis*, dimorphic males of these genera are recognisable as conspecific due to sympatric distribution, identity of characters such as colour pattern, and similar genitalia. However, the pattern of dimorphism differs between the genera. In *Pantopsalis*, the two morphs present show similar size and development of characters related to sexual dimorphism, such as sclerotisation and armature, and differ only in the development of the chelicerae. These are long and slender in one form and shorter and more robust in the other (Taylor 2004). In contrast, in the Australian genera individuals of one morph (referred to as “minor males”) are considerably smaller than individuals of the standard morph, as well as showing reduction in prominence of the secondary sexual characters, notably length of the chelicerae and size of the hypertrophied proventral spine row on femur I if present. The minor form is considerably rarer in collections than the major form for *Neopantopsalis pentheter*, *N. psile* and *N. quasimodo* whereas in the cases of *Intutoportula minima* and *Scissorestis nigricans* the minor form is noticeably more abundant.

Members of the Opiliones clade Grassatores have recently been shown to possess two reproductively mature, morphologically distinct instars (Gnaspini *et al.*

2004). It is possible that the distinct male morphs present in some Monoscutidae may also be explainable in this way but it does not presently seem likely. Juveniles of *Pantopsalis* have been observed moulting directly into both long-chelicerate and short-chelicerate adults (S. Pollard, personal communication). The apparent much higher abundance of major males in *Neopantopsalis* is also inconsistent with their identification as second-instar adults.

Male dimorphism has not yet been recorded in *Megalopsalis* or in the Monoscutinae. In light of the differences between male dimorphism in *Pantopsalis* and *Neopantopsalis/Spinicrus*, it is currently an open question whether male dimorphism is homologous between the two groups, or has arisen polyphyletically within Monoscutidae. The differences in the mode of male dimorphism suggests that it may have developed independently on at least two occasions (depending on whether or not *Neopantopsalis* and *Spinicrus* are monophyletic in relation to *Pantopsalis*), but characters relating to male dimorphism have not been included in the current analysis. One reason is the difficulty of deciding whether *Pantopsalis*-type and *Neopantopsalis*-type dimorphism should be treated as different forms of the same character or as individual characters—either way requires making a potentially unjustified assumption about homology. The other reason is that very few monoscutid species are yet known from enough specimens to be well-studied for male dimorphism. Many species from which male dimorphism has not yet been recorded may prove to do so when further examples are studied. It is also for this latter reason that coding for male-dimorphic species has been restricted to major males, rather than coding such species as polymorphic.

## Characters used in analysis

Characters with more than two character states have been treated as ordered in the order given unless otherwise indicated.

0: *Suprachelicerale lamellae*: (0) absent; (1) present.

1: *Elongate anterior propeltidial area, sloping downwards anteriorly*: (0) absent; (1) present (fig. 161).

2: *Ozopore position*: (0) flush with lateral margin of prosoma; (1) raised on protruding lobes.

3: *Ozopore shape*: (0) small and circular; (1) large and oval or oblong.

4: *Raised humps on either side of ocularium*: (0) absent; (1) present (fig. 131).

5: *Raised postocularial hump*: (0) absent; (1) present (fig. 131).

6: *Mesopeltidium*: (0) distinct; (1) merged with propeltidium. In the majority of taxa examined, the mesopeltidium is fused to the propeltidium to form the dorsal prosomal plate, but remains clearly distinguishable due to the presence of a dividing groove or as a raised ridge. In those taxa where the mesopeltidium is coded as merged with the propeltidium, the two sections are indistinguishable.

7: *Position of anterior margin of mesopeltidium relative to ocularium*: (0) mesopeltidium immediately behind ocularium; (1) distinct space between ocularium and anterior margin of mesopeltidium.

8: *Metapeltidium*: (0) non-sclerotised; (1) sclerotised.

9: *Dorsal junction between prosoma and opisthosoma*: (0) free; (1) fused.

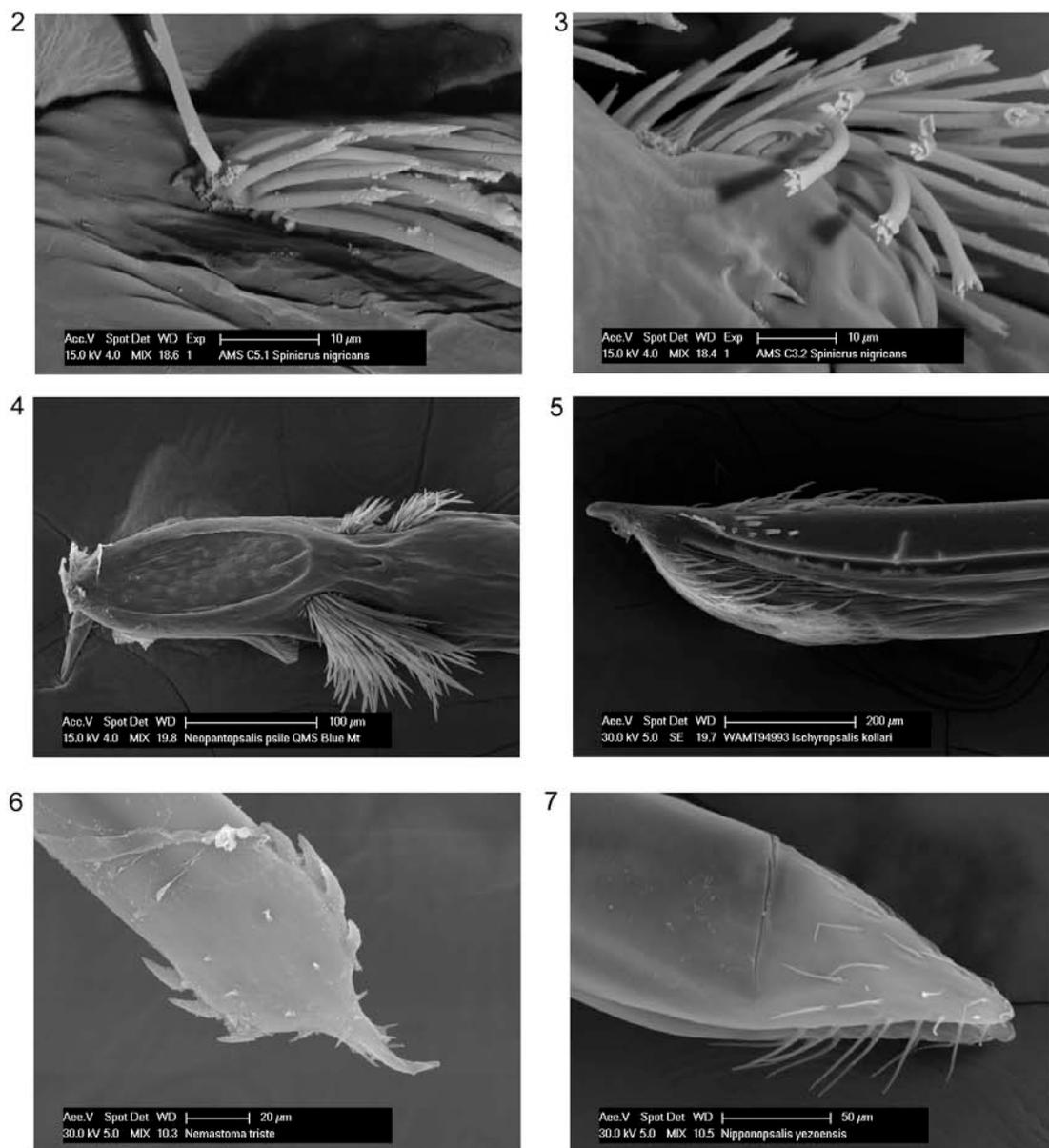
10: *Dorsum of opisthosoma*: (0) non-sclerotised; (1) sclerotised. Species of *Australiscutum*, *Taracus*, *Phalangium* and *Opilio* possess armature of spines or spinose setae on the opisthosoma, but the underlying dorsum remains coriaceous.

11: *Penis tendon*: (0) long; (1) short.

12: *Angular ventral junction between shaft and glans*: (0) absent; (1) present. A strong ventral corner between the shaft and glans of the penis is characteristic of most Eupnoi (including *Caddo*) whereas Dyspnoi exhibit a continuous, non-angled transition between shaft and glans. *Ballarra* differs from other Eupnoi considered herein in lacking an angled junction. Though not included in this analysis, *Protolophus* and some Sclerosomatidae also lack this character (Cokendolpher 2007b). Hunt & Cokendolpher (1991) only illustrated the penis of *Thrasychirus* sp. in ventral view, and *Thrasychirus* has been coded as unknown for this character.

13: *Lateral processes behind shaft-glans articulation*: (0) absent; (1) present. Members of both Eupnoi and Dyspnoi exhibit lateral processes on the penis. However, Monoscutidae, Enantiobuninae and Ballarrinae possess lateral processes behind the shaft-glans junction but lack them on the glans whereas Dyspnoi possess the reverse. Whether genital processes in the former are homologous with those of the latter is unknown, and they are treated here as separate characters.

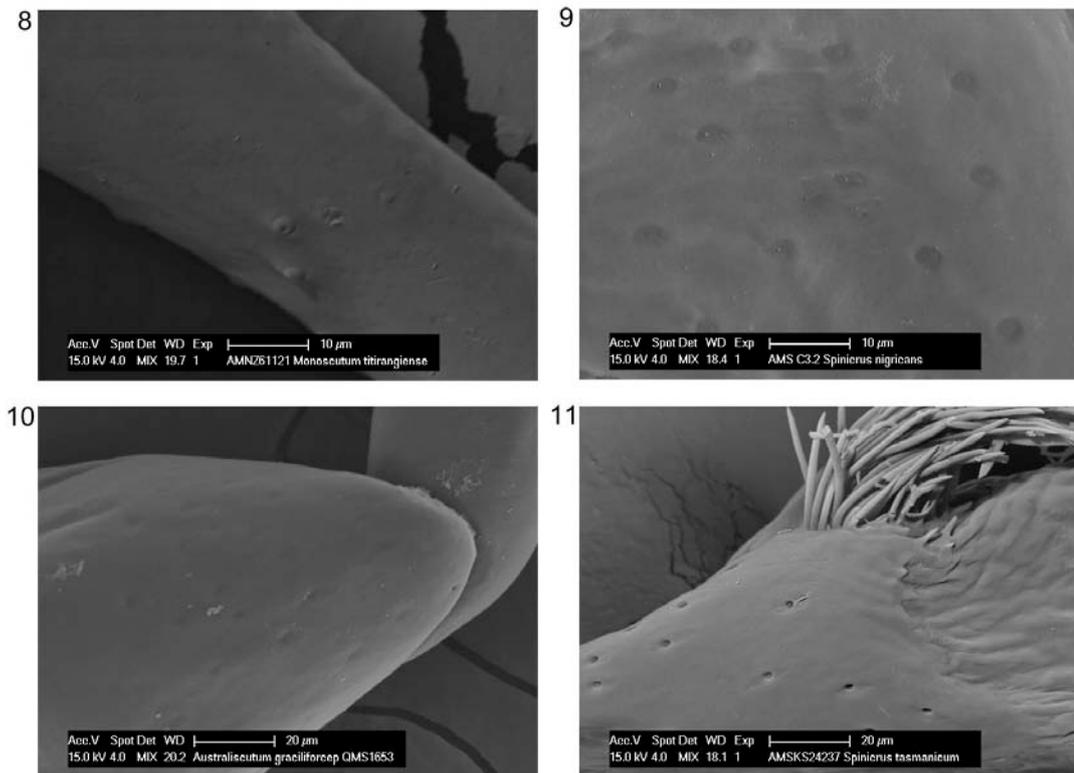
14: *Bristle groups as lateral processes of penis*: (0) absent; (1) present.



**FIGURES 2–7.** Genitalia of Monoscutidae and Dyspnoi, SEM. 2. *Spincerus nigricans*, close-up of fused base of anterior bristle group on penis. 3. *Spincerus nigricans*, multifurcate terminations of bristles on penis. 4. *Neopantopsalis psile*, ventral view of glans to show central concavity. 5–7. Glans of Dyspnoi specimens, showing accessory setae: 5. *Ischyropsalis kollari*. 6. *Nemastoma triste*. 7. *Nipponopsalis yezoensis*.

15: *Asymmetry of penis bristle groups*: (0) both sides present; (1) left bristle groups absent.

16: *Fused base to lateral bristles on penis*: (0) absent; (1) present. *Spincerus nigricans* differs from other species of Enantiobuninae in possessing bristle groups with multi-pointed bristles emerging from a fused base (figs 2–3). Extension of such fusion could potentially have given rise to the barbed lateral process characteristic of



**FIGURES 8–11.** Close-up images of monoscutid glans to show differing pore morphologies. 8. *Monoscutum titirangiense* with raised rimmed pores. 9. *Spinicrus nigricans* with level rimmed pores. 10. *Australiscutum graciliforceps* with shallowly recessed rimless pores. 11. *Spinicrus tasmanicum* with deeply recessed pores.

most Ballarrinae (Hunt & Cokendolpher 1991). *Spinicrus nigricans* also resembles Ballarrinae in possessing a pedipalp with a longer patella than tibia. To test the possibility of a relationship between these two taxa, *Ballarra longipalpus* has been coded as lacking bristle groups (character 13), but as possessing this character.

17: *Dorsal edge of glans*: (0) in same plane as shaft; (1) directed dorsad relative to shaft. Representatives of Phalangiidae have the glans reflexed back towards the shaft; for the purposes of this analysis, they have been assigned state 1. Also, genital characters below have been coded in *Phalangium* and *Opilio* relative to the homologous positions in other taxa—i.e. prodorsal edge coded as “ventral” and retroventral as “dorsal”.

18: *Glans length*: (0) short (fig. 62); (1) long (fig. 136).

19: *Glans shape in ventral view*: (0) subparallel edges (rectangular; fig. 136); (1) edges converging (triangular; fig. 62).

20: *Central concavity on ventral face of glans*: (0) absent; (1) present. A central dish with raised edges on the ventral face of the glans (fig. 4) is characteristic of Megalopsalidinae except for *Megalopsalis linnaei*.

21: *Shape of distal end of glans*: (0) not dorsoventrally flattened; (1) distinctly dorsoventrally flattened.

22: *Setae or bristles on glans*: (0) absent; (1) single lateral setae; (2) numerous setae or bristles. Dyspnoi species possess numerous setae or bristles on the glans (figs 5-7) whereas *Caddo*, *Phalangium* and *Nelima* possess isolated setae on the glans (the “Sinnesborsten” of Martens, 1987). Monoscutidae and Neopilionidae have a glans devoid of setae.

23: *Triangular dorsolateral keel on glans*: (0) absent; (1) present. A triangular dorsolateral keel on the glans, with the apex of the triangle at the distal end of the glans, is characteristic of *Pantopsalis*. The keel is much smaller in *P. luna* than in *P. albipalpis* and other species of *Pantopsalis* not included in this analysis; in Taylor (2004) this was misinterpreted as a different point of insertion of the stylus for *P. luna*.

24: *Sharp dorsal papillae on glans*: (0) absent; (1) present.

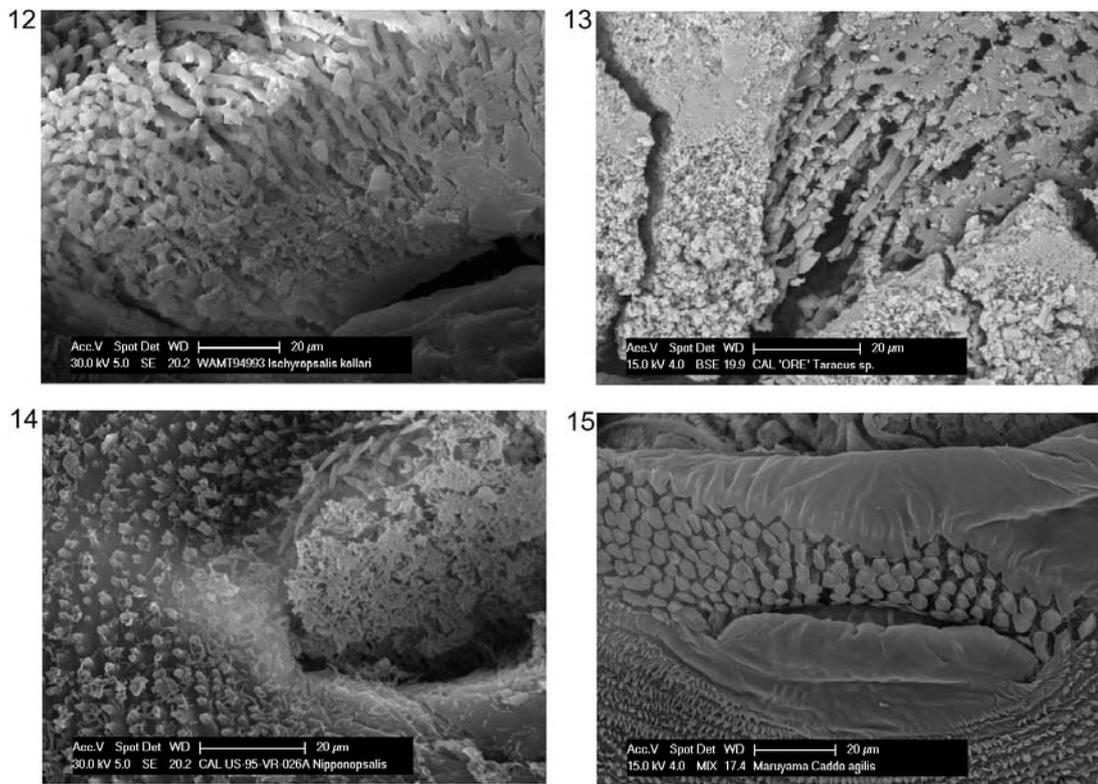
25: *Pores on glans of penis*: (0) absent; (1) present. All species of Dyspnoi examined in this study lack pores on the glans whereas they are present in all examined Phalangioidea. Unfortunately, the unavailability of male specimens for *Caddo agilis* prevented any investigation of this character for Caddoidea. The distribution of this character may be worthy of further investigation to establish whether it represents a synapomorphy of Phalangioidea or Eupnoi, or whether its absence is a synapomorphy of Dyspnoi. The function of these pores is currently unknown; it is notable that their presence correlates with a reduction in the distribution of accessory processes on the glans.

26: *Morphology of pores*: (0) raised with rim (fig. 8); (1) level with rim (fig. 9); (2) shallowly recessed without rim (fig. 10); (3) deeply recessed (fig. 11).

27: *Inflated stylus*: (0) absent; (1) present (figs 55–56). A distinctive inflated stylus is characteristic of *Australiscutum* species.

28: *Number of seminal receptacles*: (0) two; (1) four.

29: *Microsculpture anterior to spiracle*: (0) unornamented; (1) ornamented. In the majority of Eupnoi, ornate cuticular microsculpture is only present posterior to the spiracle whereas in front of the anterior border of the spiracle the cuticle is

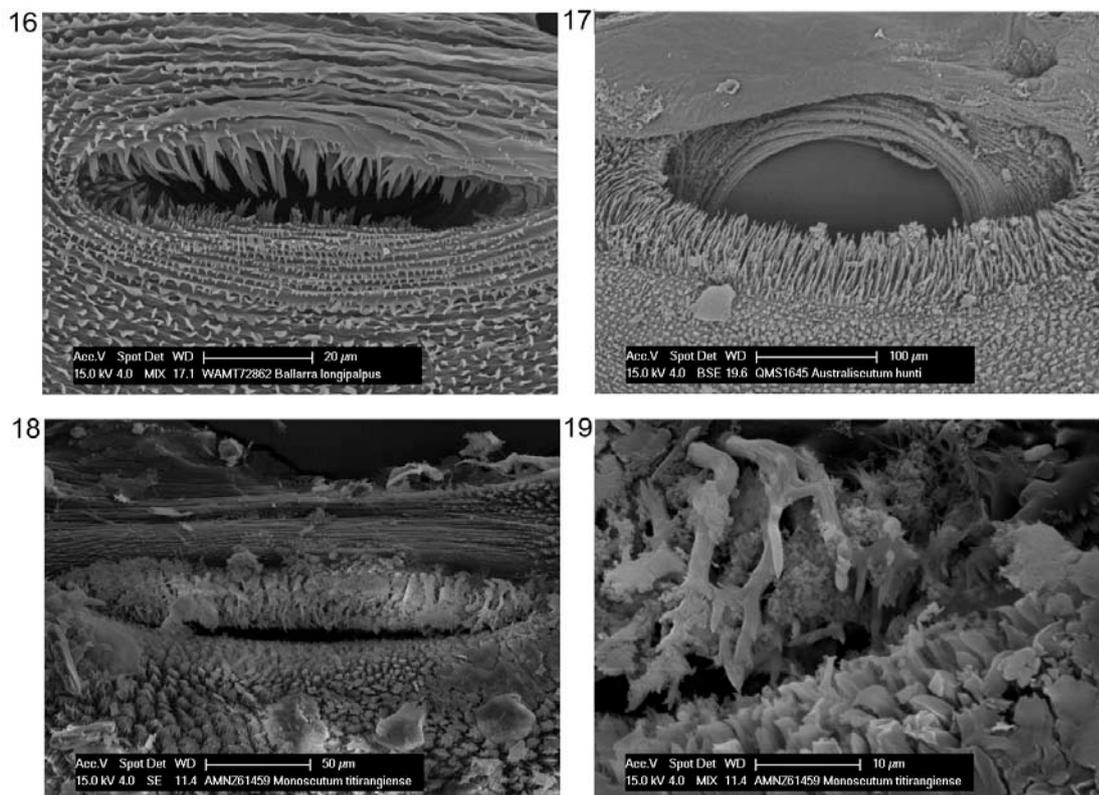


**FIGURES 12–15.** Spiracles of outgroup taxa. 12–14. Dyspnoi spiracles with multiple rows of short spines over covering plate: 12. *Ischyropsalis kollari*. 13. *Taracus* sp. 14. *Nipponopsalis yezoensis*. 15. Spiracle of *Caddo agilis*, with multiple rows of flat-topped, laterally reticulate ‘pedestal spines’.

unornamented. Dyspnoi (fig. 14), *Neopilio* (fig. 6d in Hunt & Cokendolpher, 1991), *Ballarra* (fig. 16) and *Thrasychirus* (figs 20–21) have the same cuticular ornamentation surrounding the cuticle. In *Caddo*, the distinctive spiracular spine rows extend anterior from the spiracle margin, but with an unornamented region further anterior. *Caddo agilis* has therefore been coded as unornamented.

30: *Spiracular entapophysis*: (0) absent; (1) present.

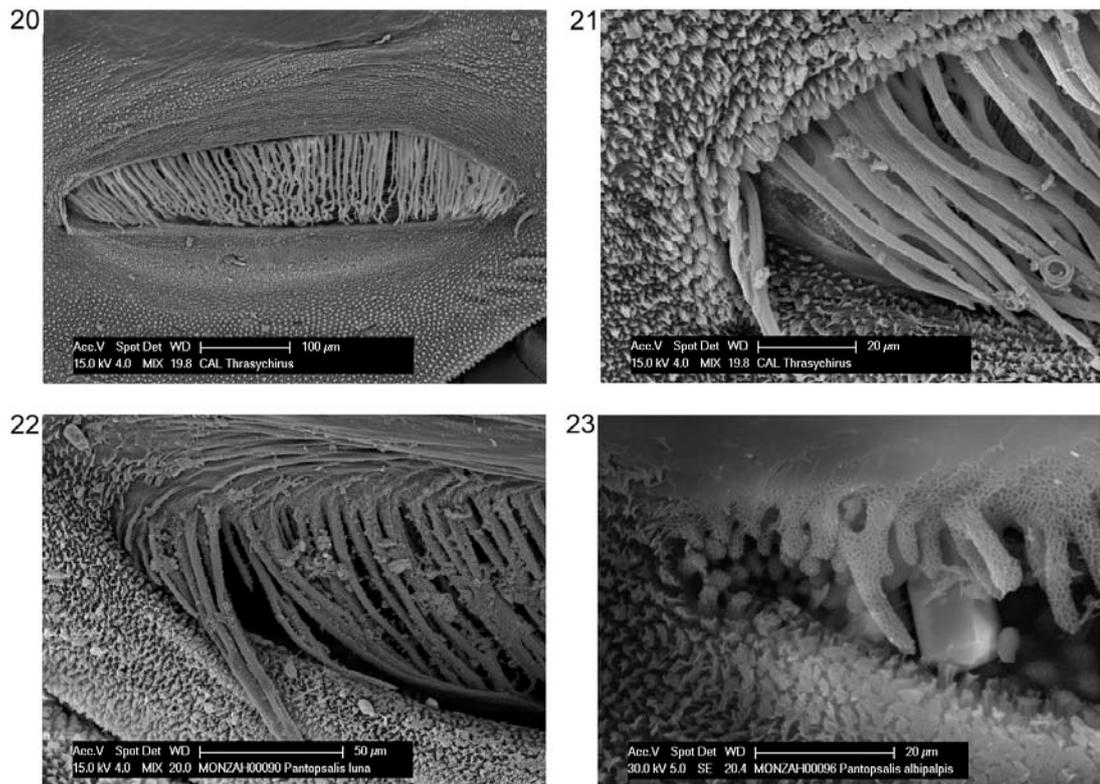
31: *Anterior spines at spiracular aperture*: (0) absent; (1) Dyspnoi-form spines; (2) *Ballarra*-form spines; (3) *Thrasychirus*-form spines or lace tubercles. Anterior spiracular ornamentation is completely absent in *Nelima*, *Phalangium* and *Australiscutum* (fig. 17). Remaining species whose spiracles were examined possessed either spinose anterior ornamentation or clear homologues thereof. Spiracles of *Opilio*, *Neopantopsalis thaumatopios*, *Megalopsalis hoggi* and *M. pilliga* could not be examined due to shortage of material. Members of different families of Eupnoi and Dyspnoi show great variation in the ornamentation of the spiracle, and establishing homologies (or otherwise) is by no means simple. Three



**FIGURES 16–19.** Neopilionid and monoscutid spiracles. 16. *Ballarra longipalpus*, showing spines derived from hypertrophied surrounding ornamentation. 17. *Australiscutum huntii*, with no anterior ornamentation and hypertrophied posterior ornamentation. 18. *Monoscutum titirangiense*, with multiple spine rows over covering plate. 19. Same, close-up of individual spines.

basic morphologies have been recognised in this analysis, but the character has been treated as unordered.

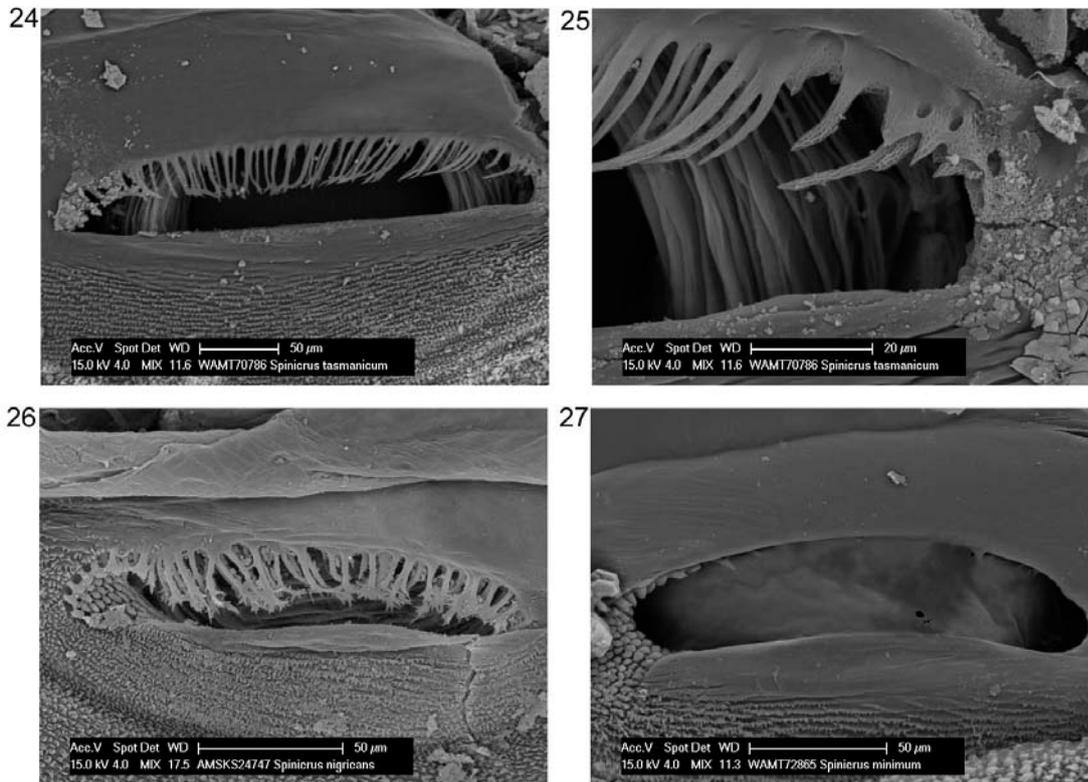
Thick, densely-placed spines in numerous rows on an anterior covering plate (character state 1) are found in *Dyspnoi* (figs 12–14) and *Monoscutum titirangiense* (figs 18–19). In the *Dyspnoi* species examined, the spines are relatively short and unbranched whereas *Monoscutum* has long, elbowed spines with side-branches. *Caddo agilis* has a unique spiracular ornamentation with numerous pedestal-like structures (fig. 15); because of their arrangement in numerous rows anterior to the spiracle, it has been coded as having *Dyspnoi*-form ornamentation. In *Ballarra longipalpus*, the spines are hypertrophied extensions of the surrounding cuticular ornamentation (fig. 16; character state 2). *Megalopsalidinae* and *Thrasychirus* possess elongate, often anastomosing spines in a curtain of only one or two rows, arising from along or just inside the lip of the spiracle (figs 20–26, 28–39; character state 3). *Thrasychirus*-form spines are often covered by a reticulated micro-



**FIGURES 20–23.** Spiracles of *Thrasychirus* and *Pantopsalis*. 20. *Thrasychirus*, entire spiracle. 21. Same, close-up to show reticulation on spines. 22. *Pantopsalis luna*, showing reticulation of spines extending onto surrounding cuticle. 23. *Pantopsalis albipalpis*, close-up of lateral corner of spiracle showing gradation between spines and lace tubercles.

ornamentation that demonstrates their homology with lace tubercles as described by Hunt (1990) and Hunt & Cokendolpher (1991); continuity between the reticulation of spines and tubercles is visible in figs 23 and 37. Therefore, *Spinicrus minimum* and *S. porongorupense* (which lack spiracular spines but possess lace tubercles; fig. 27) have been coded as possessing *Thrasychirus*-form spines. In some *Neopantopsalis* species (fig. 29) and *Megalopsalis leptekes* (fig. 35) the reticulations on the spines have been reduced or lost.

Whether the three basic spine morphologies observed are homologous is currently an open question. *Ballarra*-form spines are most likely not homologous to either of the other morphologies—the cuticular micro-ornamentation of which they are a clear extension is found around the spiracle in the other species examined, and does not intermingle with the spiracular spines. In contrast, *Thrasychirus*-form spines could potentially be derived from *Dyspnoi*-form spines through regression of the covering plate and reduction in the number of rows. The distinctive pedestal spines of *Caddo*

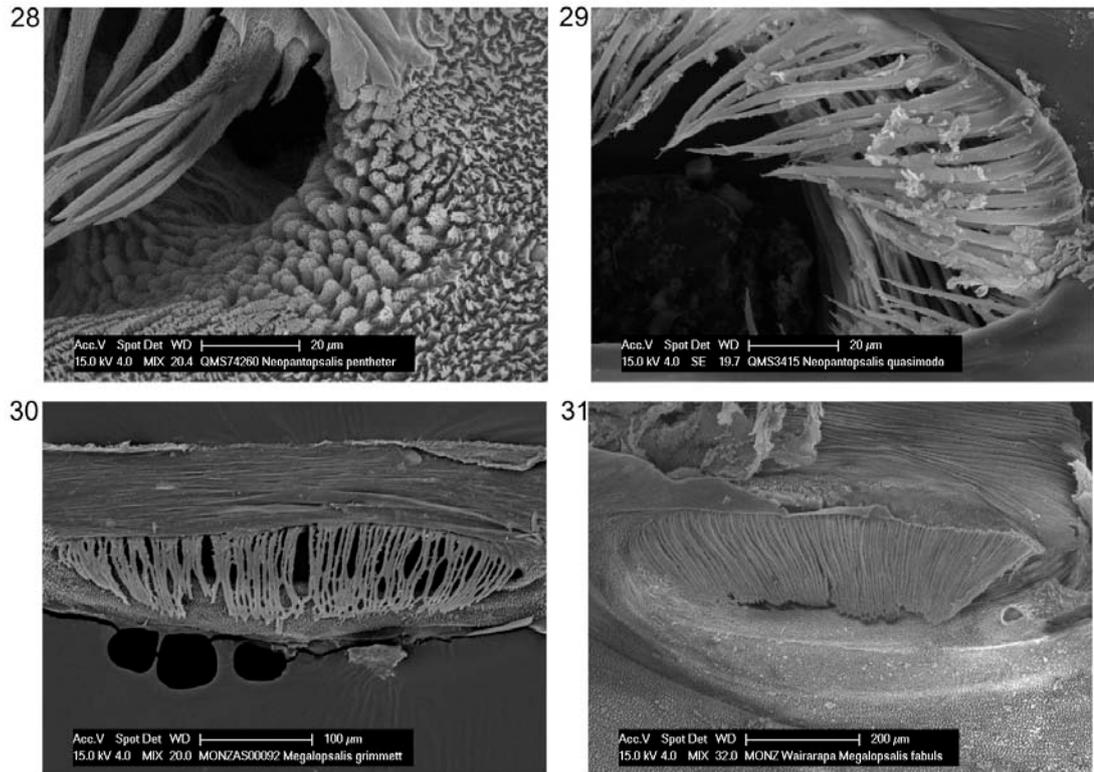


**FIGURES 24–27.** Spiracles of *Spinicrus* species. 24. *Spinicrus tasmanicum*, entire spiracle. 25. Same, close-up of lateral corner showing reticulate spines with reticulations fading medially. 26. *Spinicrus nigricans*, with broad palmate terminations on spines. 27. *Spinicrus minimum*, with medial spines absent and lateral lace tubercles only.

may support such a scenario in that they have a reticulate micro-ornamentation similar to that found in many *Thrasychirus*-form spines.

I have been unable to decide to which of these morphologies the spiracular spines illustrated for *Neopilio australis* by Hunt & Cokendolpher (1991, fig. 6d) should be assigned. In form they are reminiscent of Dyspnoi-form spines as seen in *Monoscutum*, but their position on the spiracle lip is more similar to *Thrasychirus*-form spines. In the main analysis, *Neopilio* has been coded as unknown for this character; successive analyses coding it as possessing either Dyspnoi-form or *Thrasychirus*-form spines did not return different results from the reported analysis.

A spiracle of the female paratype of *Templar incongruens* was examined, but unfortunately was mostly obscured by grit. Honeycomb-like reticulations visible on one broad process suggest a *Thrasychirus*-form spiracle ornamentation, but probably a very distinct one. Examination of further specimens is necessary to confirm the codings for *T. incongruens* used in this analysis.



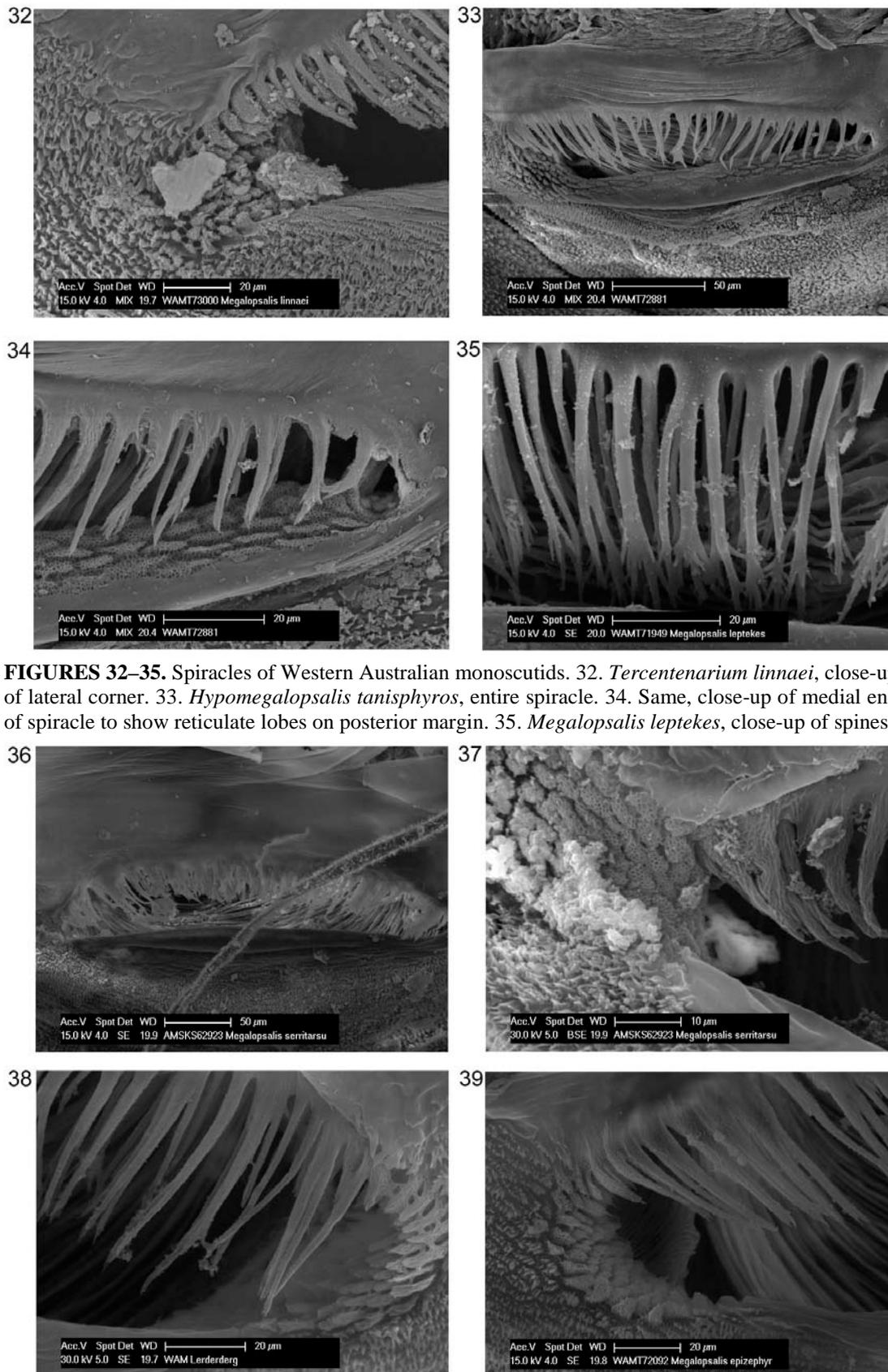
**FIGURES 28–31.** Spiracles of *Neopantopsalis* and New Zealand *Megalopsalis*. 28. *Neopantopsalis pentheter*, with multifurcate reticulate spines. 29. *Neopantopsalis quasimodo*, with non-reticulate spines briefly extending at lateral corner onto posterior margin of spiracle. 30. *Megalopsalis grimmetti*, with sparse, elongate reticulate spines. 31. *Megalopsalis fabulosa*, with dense curtain of elongate reticulate spines.

32: *Reticulate anterior spiracular spines*: (0) absent; (1) present. As noted above, the pedestal spines of *Caddo agilis* have a reticulate micro-ornamentation reminiscent of that found in many species with *Thrasychirus*-form spines. *Caddo* has therefore been coded as possessing reticulate spines whereas *Dyspnoi* species, *Neopilio*, *Ballarra* and *Monoscutum* have been coded as lacking them. However, characters 30–32 below have only been coded for those species definitely possessing *Thrasychirus*-form ornamentation.

33: *Extent of anterior spines over spiracle*: (0) absent; (1) halfway; (2) entire spiracle.

34: *Terminations of anterior spiracular spines*: (0) simple (fig. 38); (1) palmate (fig. 35).

35: *Lace tubercles at corner of spiracle*: (0) absent; (1) present. *Intutoportula suffugiens* possesses a patch of lace-like reticulation marking the position occupied by the lace tubercles in other taxa, and has been coded as possessing this character.



**FIGURES 32–35.** Spiracles of Western Australian monoscutids. 32. *Tercentenarium linnaei*, close-up of lateral corner. 33. *Hypomegalopsalis tanisphyros*, entire spiracle. 34. Same, close-up of medial end of spiracle to show reticulate lobes on posterior margin. 35. *Megalopsalis leptekes*, close-up of spines.

**FIGURES 36–39.** Spiracles of *Megalopsalis* species. 36. *Megalopsalis serritarsus*, entire spiracle. 37. Same, close-up of lateral corner. 38. *Megalopsalis eremiotis*, close-up of lateral corner. 39. *Megalopsalis epizephyr*, close-up of lateral corner.

36: *Posterior margin of spiracle*: (0) unornamented (fig. 27); (1) short ornamentation; (2) elongate spines (fig. 17).

37: *Male chelicerae compared to female*: (0) not enlarged; (1) enlarged. In three of the Dyspnoi species analysed herein (*Ischyropsalis kollari*, *Nipponopsalis yezoensis* and *Taracus* sp.), enlarged chelicerae are present in both sexes. These species have been coded as unknown for this character.

38: *Ventral spur at base of cheliceral segment I*: (0) absent; (1) present. This character has been coded from female specimens. In males with elongate denticulate chelicerae, the ventral spur (if present for that species) is lost or becomes indistinguishable from other denticles. This character was used by Hunt and Cokendolpher (1991).

39: *Ventrolateral row of enlarged denticles on cheliceral segment I*: (0) absent; (1) present (fig. 207).

40: *Cheliceral segment II compared to segment I*: (0) not significantly inflated; (1) inflated.

41: *Cheliceral finger length*: (0) short; (1) long. ‘Long’ fingers are here defined as those which are more than twice as long as the breadth across their base anteriorly.

42: *Mobile finger of chelicera*: (0) closes tightly against immobile finger of segment II; (1) bows away from immobile finger proximally.

43: *Setae on mobile finger of chelicera*: (0) absent; (1) present. Species of the genera *Pantopsalis*, *Forsteropsalis* and *Neopantopsalis* (except *N. quasimodo*) possess a congregation of setae near the large tooth on the mobile finger. Other species examined lack setae on the mobile finger except *Taracus* sp., which has setae spaced out all along the finger and not only around the tooth (but has been coded as possessing this character state nevertheless).

44: *Medial side of pedipalp coxae*: (0) unarmed; (1) with covering of blunt denticles.

45: *Plumose setae on pedipalp*: (0) absent; (1) present. This character appeared in the analysis of Hunt and Cokendolpher (1991).

46: *Length of pedipalp femur*: (0) shorter than or subequal to prosoma length; (1) more than 1.5 × as long than prosoma.

47: *Pedipalp patella vs tibia*: (0) patella shorter than tibia; (1) patella longer than tibia. This character was removed from the final analysis by Hunt and Cokendolpher (1991).

48: *Medial side of pedipalp patella*: (0) sparsely setose; (1) hypersetose (as described in Taylor 2004).

49: *Pedipalp patella apophysis in male*: (0) absent; (1) poorly developed (less than one-third patella length); (2) well-developed (about one-half patella length).

50: *Shape of pedipalp patella apophysis in male*: (0) rounded; (1) triangular.

51: *Pedipalp patella apophysis in female*: (0) absent; (1) poorly developed (less than one-third patella length); (2) well-developed (about one-half patella length).

52: *Shape of pedipalp patella apophysis in female*: (0) rounded; (1) triangular. This character is identical to character 50 in most species, but *Forsteropsalis grimmetti* is currently unique in possessing a triangular apophysis in the male and a rounded apophysis in the female.

53: *Shape of pedipalp tibia*: (0) straight; (1) bent mediad from patella.

54: *Distribution of microtrichia on pedipalp*: (0) absent; (1) distal half to third of tarsus only; (2) full length of tarsus; (3) tibia and tarsus.

55: *Pedipalp claw*: (0) absent; (1) present. Hunt and Cokendolpher (1991) coded *Neopilio* as lacking a pedipalp claw due to its reduction in size in that taxon; it is here coded as present.

56: *Teeth on pedipalp claw*: (0) absent or only one or two teeth; (1) tooth-comb. The coding of this character differs from Hunt and Cokendolpher (1991) who grouped taxa with one or two teeth with those with tooth-combs. However, in those taxa with one or two teeth the teeth are reduced to minute nubbins whereas taxa lacking ventral teeth may possess a ventral rugosity in place of the teeth (personal observation).

57: *Armature of coxa I*: (0) unarmed; (1) armed.

58: *Armature of trochanter I*: (0) unarmed; (1) prolateral denticles only; (2) prolateral and retrolateral denticles; (3) retrolateral denticles only. In various species of *Megalopsalis*, *Spinicrus* and *Neopantopsalis*, trochanter I bears a prolateral cluster of denticles (fig. 109). In some Dyspnoi, *Nelima*, Phalangiidae and *Monoscutum*, there is a single stout denticle prolaterally and retrolaterally. This character has been treated as unordered.

59: *Leg I length and shape*: (0) long and slender; (1) short and sturdy. ‘Long’ legs are those in which the femur is more than twice the length of the prosoma.

60: *Leg I armature in male*: (0) absent; (1) femur; (2) femur to patella; (3) femur to tibia; (4) femur to basitarsus; (5) femur to distitarsus.

61: *Leg I armature in female*: (0) absent; (1) femur; (2) femur to patella.

62: *Arrangement of denticles on leg I*: (0) scattered; (1) sublinear; (2) very linear. Taxa with ‘very linear’ denticles have all or almost denticles in strict longitudinal rows, as seen in Phalangidae such as *Phalangium* and *Opilio*. Taxa with ‘sublinear’ denticles have denticles predominantly in longitudinal rows, but also have a reasonable number of extra denticles scattered between the rows. Taxa with ‘scattered’ denticles lack indications of an arrangement into longitudinal rows.

63: *Prolateral longitudinal row of hypertrophied spines on leg I*: (0) absent; (1) present (fig. 154).

64: *Pseudoarticulations in femur II*: (0) absent; (1) present. *Nemastoma triste* and *Nipponopsalis yezoensis* have a number of closely spaced pseudoarticulations near the base of femur II whereas in Phalangioidea possessing pseudoarticulated femora II (Gagrellinae, some *Neopantopsalis* species) the pseudoarticulations are more widely spaced and not restricted to the base of the femur. As the homology of these two arrangements is uncertain, they have not been distinguished in the analysis. This character was removed from the final analysis by Hunt and Cokendolpher (1991).

65: *Accessory tracheal stigmata in tibiae*: (0) absent; (1) present. This has been regarded as one of the defining features of Phalangioidea, but is absent in *Monoscutum* and *Templar*.

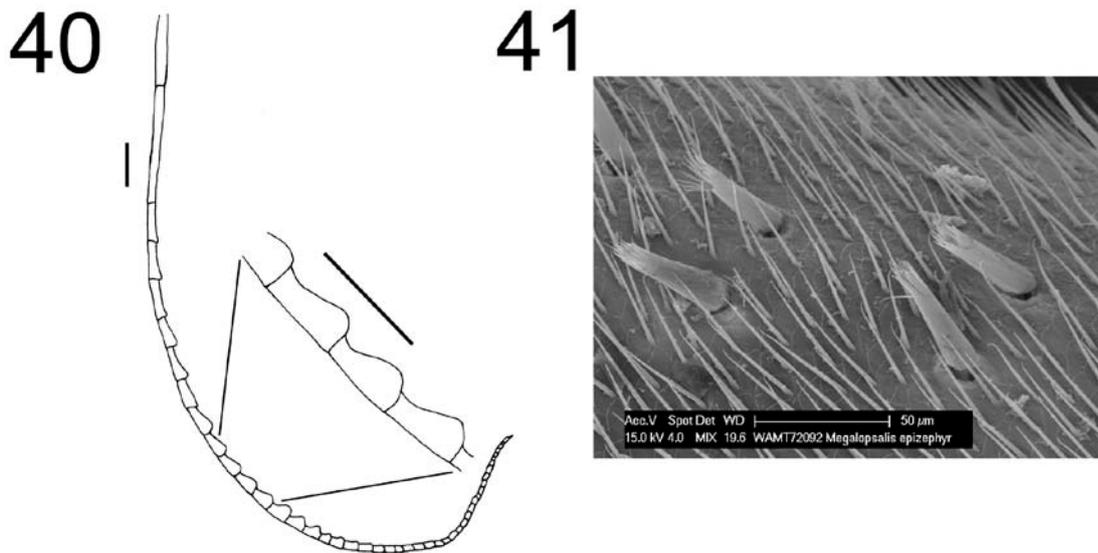
66: *Tibia II shape*: (0) cylindrical; (1) dilated along length.

67: *Pseudoarticulations in tibia II*: (0) absent; (1) present.

68: *Pseudoarticulations in tibia IV*: (0) absent; (1) present.

69: *Pseudoarticulations in basitarsi*: (0) absent; (1) present. Absence of pseudoarticulations is not directly connected to shortening of the basitarsus; some species such as *Megalopsalis leptekes* have an elongate but non-articulated basitarsus.

70: *Ventrodiscal spines on basitarsal pseudosegments*: (0) absent; (1) present. A ventral pair of large stiff spine-like distally-directed setae is present on the distal margin of each tarsal pseudosegment in many Opiliones. If these spines are present,



**FIGURES 40–41.** Modified distitarsi in *Megalopsalis* species. 40. *Megalopsalis serritarsus* (AMS KS63527), distitarsus II showing distoventral bulges on pseudosegments (scale bars = 1 mm). 41. *Megalopsalis epizephyr*, close-up of two pairs of brush-like setae on ventral side of distitarsus IV.

taxa differ as to whether they are present on pseudosegments of the distitarsus only or of both the basitarsus and distitarsus, and whether or not they are present at the junction of the basitarsus and distitarsus. Species in which the basitarsus is not pseudosegmented are coded as unknown for this character.

71: *Mobile hinge between basitarsus and distitarsus*: (0) absent; (1) present.

72: *Ventrodiscal spines on the junction of the basitarsus and distitarsus*: (0) absent; (1) present.

73: *Ventrodiscal swellings on pseudosegments of distitarsus II* (fig. 40): (0) absent; (1) present.

74: *Proximal part of distitarsi III and IV*: (0) not swollen with no brush-like setae; (1) not swollen with double row of brush-like setae; (2) swollen with double row of brush-like setae. Ventral rows of brush-like setae are found on distitarsus III and IV of *Opilio parietinus*, *Spinicrus stewarti*, *S. tasmanicum* and most Australian *Megalopsalis* species. In those *Megalopsalis* species with brush-like setae, the distitarsi bearing are also inflated proximally whereas in other taxa the distitarsus is similar in diameter to the basitarsus. When viewed under the SEM, the brush-like setae can be characterised as thick hollow setae in which the ends have become frayed (fig. 41). The function of these structures is unknown.

75: *Ventrodiscal spines on distitarsal pseudosegments*: (0) absent; (1) present. In those *Megalopsalis* species with modified tarsus II (character 73), the ventrodiscal

spines are absent on the ventrally swollen pseudosegments. However, they remain present on the tarsi of the other legs.

76: *Lateral extension on left side of glans*: (0) absent; (1) present. In *Spinicrus stewarti* and *S. sublucens*, the left side of the glans protrudes outwards above the anterior bristle group (figs 195–196).

**TABLE 1.** Character state matrix for phylogenetic analysis.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Ischyropsalis kollari</i>	0	0	1	0	0	0	1	?	1	0	1	0	0	0	0	?
<i>Taracus</i>	0	0	1	0	0	0	1	0	1	0	0	?	0	0	0	?
<i>Nemastoma triste</i>	0	0	0	0	0	0	1	?	1	1	1	?	0	0	0	?
<i>Nipponopsalis yezoensis</i>	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?
<i>Caddo agilis</i>	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
<i>Neopilio australis</i>	1	0	?	?	0	0	0	0	0	0	0	0	1	0	0	?
<i>Ballarra longipalpus</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	?
<i>Thrasychirus</i>	1	0	1	1	0	0	0	1	?	0	0	1	?	1	0	?
<i>Nelima doriae</i>	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	?
<i>Phalangium opilio</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	?
<i>Opilio parietinus</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	?
<i>Australiscutum huntii</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1
<i>Australiscutum graciliforceps</i>	1	0	1	1	0	0	1	1	1	0	1	0	1	1	1	1
<i>Australiscutum triplodaemon</i>	1	0	1	1	0	0	1	1	1	0	0	0	1	1	1	1
<i>Monoscutum titirangiense</i>	1	0	0	0	0	0	1	?	1	1	1	0	1	1	1	0
<i>Templar incongruens</i>	1	0	0	0	0	0	1	?	1	1	1	?	1	1	1	0
<i>Tercentenarium linnaei</i>	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0
<i>Hypomegalopsalis tanisphyros</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Megalopsalis serritarsus</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Megalopsalis epizephyros</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Megalopsalis eremiotis</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Megalopsalis hoggi</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Megalopsalis leptekes</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Megalopsalis pilliga</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Neopantopsalis quasimodo</i>	1	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1
<i>Neopantopsalis camelus</i>	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0
<i>Neopantopsalis pentheter</i>	1	1	1	1	1	1	0	0	1	0	0	0	1	1	1	0
<i>Neopantopsalis psile</i>	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0
<i>Neopantopsalis thaumatopoioides</i>	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0
<i>Forsteropsalis chiltoni</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Forsteropsalis fabulosa</i>	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Forsteropsalis grimmetti</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Forsteropsalis inconstans</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Pantopsalis albipalpis</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Pantopsalis luna</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Spinicrus tasmanicum</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Spinicrus stewarti</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Spinicrus sublucens</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Intutoportula minima</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Intutoportula porongorupensis</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Intutoportula suffugiens</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Intutoportula walpolensis</i>	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Scissorestis nigricans</i>	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0
<i>Spinibunus atrocidiana</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0
<i>Spinicrurellum coronatum</i>	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0
<i>Spinicrurellum puerile</i>	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0
<i>Spinicruroides caeruleomontium</i>	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0

**TABLE 1.** Continued.

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Ischyropsalis kollari</i>	?	0	0	1	0	0	2	0	0	0	?	0	1	1	0
<i>Taracus</i>	?	0	1	1	0	0	2	0	0	0	?	0	1	1	0
<i>Nemastoma triste</i>	?	0	0	0	0	0	2	0	0	0	?	0	?	?	0
<i>Nipponopsalis yezoensis</i>	?	0	0	0	0	0	2	0	0	0	?	0	0	1	0
<i>Caddo agilis</i>	?	1	1	1	0	0	1	0	0	?	?	0	1	0	0
<i>Neopilio australis</i>	?	1	1	1	0	0	0	0	?	?	?	0	0	1	0
<i>Ballarra longipalpus</i>	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0
<i>Thrasychirus</i>	?	?	1	1	0	0	0	?	?	?	?	0	0	1	0
<i>Nelima doriae</i>	?	0	1	0	0	1	1	0	0	1	2	0	1	0	1
<i>Phalangium opilio</i>	?	1	1	0	0	0	1	0	0	1	0	0	?	?	1
<i>Opilio parietinus</i>	?	1	1	0	0	0	1	0	0	?	?	0	0	?	1
<i>Australiscutum hunti</i>	0	1	0	1	1	0	0	0	0	1	2	1	1	0	0
<i>Australiscutum graciliforceps</i>	0	1	0	1	1	0	0	0	0	1	2	1	1	0	0
<i>Australiscutum triplodaemon</i>	0	1	0	1	1	0	0	0	0	1	2	1	?	0	0
<i>Monoscutum titirangiense</i>	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0
<i>Templar incongruens</i>	?	0	1	1	1	0	0	0	?	?	?	0	0	0	0
<i>Tercentenarium linnaei</i>	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Hypomegalopsalis tanisphyros</i>	0	0	0	1	1	1	0	0	0	1	3	0	?	0	0
<i>Megalopsalis serritarsus</i>	?	0	0	1	1	1	0	0	0	?	?	0	?	0	0
<i>Megalopsalis epizephyros</i>	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0
<i>Megalopsalis eremiotis</i>	0	0	0	1	1	1	0	0	0	1	3	0	0	0	0
<i>Megalopsalis hoggi</i>	?	0	0	1	1	1	0	0	0	?	?	0	?	?	?
<i>Megalopsalis leptekes</i>	0	0	0	1	1	1	0	0	0	1	2	0	?	0	0
<i>Megalopsalis pilliga</i>	0	0	0	1	1	1	0	0	0	1	2	0	?	?	?
<i>Neopantopsalis quasimodo</i>	0	0	1	1	1	0	0	0	0	1	1	0	?	0	0
<i>Neopantopsalis camelus</i>	?	0	1	1	1	0	0	0	0	?	?	0	?	0	0
<i>Neopantopsalis pentheter</i>	0	0	1	1	1	0	0	0	0	1	2	0	0	0	0
<i>Neopantopsalis psile</i>	0	0	1	0	1	0	0	0	0	1	2	0	0	0	0
<i>Neopantopsalis thaumatopios</i>	?	0	1	1	1	0	0	0	0	?	?	0	?	?	?
<i>Pantopsalis albipalpis</i>	0	1	1	0	1	0	0	1	1	1	1	0	1	0	0
<i>Pantopsalis luna</i>	0	0	1	0	1	0	0	1	1	1	1	0	1	0	0
<i>Forsteropsalis chiltoni</i>	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0
<i>Forsteropsalis fabulosa</i>	0	0	0	1	1	0	0	0	1	1	2	0	?	0	0
<i>Forsteropsalis grimmetti</i>	0	0	1	0	1	0	0	0	1	1	1	0	1	0	0
<i>Forsteropsalis inconstans</i>	0	1	1	0	1	0	0	0	0	1	0	0	?	0	0
<i>Spinicrus tasmanicum</i>	0	0	0	1	1	1	0	0	0	1	3	0	1	0	0
<i>Spinicrus stewarti</i>	0	0	0	1	1	1	0	0	0	1	2	0	1	0	0
<i>Spinicrus sublucens</i>	?	0	0	1	1	1	?	0	0	?	?	0	?	0	0
<i>Intutoportula minima</i>	0	0	0	1	1	0	0	0	0	1	3	0	?	0	0
<i>Intutoportula porongorupensis</i>	0	0	0	1	1	0	0	0	0	1	3	0	?	0	0
<i>Intutoportula suffugiens</i>	0	0	0	1	1	0	0	0	0	1	2	0	1	0	0
<i>Intutoportula walpolensis</i>	0	0	0	1	1	0	0	0	0	1	3	0	?	0	0
<i>Scissorestis nigricans</i>	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0
<i>Spinibunus atrocidiana</i>	?	0	1	0	1	1	?	0	0	?	?	0	0	0	0
<i>Spinicrurellum coronatum</i>	0	0	0	0	1	1	0	0	0	1	1	0	?	0	0
<i>Spinicrurellum puerile</i>	0	0	0	0	1	1	0	0	0	1	3	0	?	0	0
<i>Spinicruroides caeruleomontium</i>	0	0	0	1	1	1	0	0	0	1	2	0	?	0	0

**TABLE 1.** Continued.

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Ischyropsalis kollari</i>	1	0	?	?	?	0	?	0	1	0	1	0	0	0	0
<i>Taracus</i>	1	0	?	?	?	0	?	0	0	0	1	0	1	0	1
<i>Nemastoma triste</i>	?	?	?	?	?	?	0	1	0	0	0	0	0	0	1
<i>Nipponopsalis yezeensis</i>	1	0	?	?	?	0	?	0	0	0	0	0	0	0	0
<i>Caddo agilis</i>	1	1	?	?	?	0	0	0	0	0	0	0	0	0	1
<i>Neopilio australis</i>	?	0	?	?	?	0	0	0	0	0	0	0	?	?	1
<i>Ballarra longipalpus</i>	2	0	?	?	?	2	0	0	0	0	0	0	0	0	1
<i>Thrasychirus</i>	3	1	2	0	0	1	1	1	0	1	?	?	0	?	1
<i>Nelima doriae</i>	0	?	?	?	?	2	0	0	0	0	0	0	0	0	0
<i>Phalangium opilio</i>	0	?	?	?	?	1	0	0	0	0	0	0	0	1	0
<i>Opilio parietinus</i>	0	?	?	?	?	?	0	1	0	0	0	0	0	0	?
<i>Australiscutum huntii</i>	0	?	?	?	?	2	1	1	1	1	0	1	0	0	0
<i>Australiscutum graciliforceps</i>	0	?	?	?	?	2	1	1	1	1	0	0	0	0	0
<i>Australiscutum triplodaemon</i>	0	?	?	?	?	2	1	?	1	1	0	[01]	0	0	0
<i>Monoscutum titirangiense</i>	1	0	?	?	?	1	0	1	0	0	1	0	0	0	1
<i>Templar incongruens</i>	3	1	1	0	?	1	1	0	1	1	0	0	0	0	?
<i>Tercentenarium linnaei</i>	3	1	1	1	1	0	0	0	0	0	0	0	0	0	1
<i>Hypomegalopsalis tanisphyros</i>	3	0	2	1	1	0	0	0	0	0	1	0	0	0	1
<i>Megalopsalis serritarsus</i>	3	0	1	1	1	0	1	?	0	0	0	0	0	0	1
<i>Megalopsalis epizephyros</i>	3	1	1	0	1	0	1	0	0	0	0	0	0	0	1
<i>Megalopsalis eremiotis</i>	3	0	1	0	1	0	1	0	0	0	0	0	0	0	1
<i>Megalopsalis hoggi</i>	?	?	?	?	?	?	1	?	0	0	0	0	0	0	?
<i>Megalopsalis leptekes</i>	3	0	2	1	?	0	1	?	0	0	0	0	0	1	1
<i>Megalopsalis pilliga</i>	?	?	?	?	?	?	1	?	0	0	1	0	0	0	1
<i>Neopantopsalis quasimodo</i>	3	0	1	0	?	0	1	?	0	0	1	1	0	0	0
<i>Neopantopsalis camelus</i>	3	?	1	1	?	?	1	?	0	0	0	1	1	0	?
<i>Neopantopsalis pentheter</i>	3	1	1	0	1	0	1	0	1	0	1	1	1	0	0
<i>Neopantopsalis psile</i>	3	0	1	0	1	0	1	0	0	0	1	1	1	0	0
<i>Neopantopsalis thaumatopoius</i>	?	?	?	?	?	?	1	?	0	1	1	1	1	0	?
<i>Pantopsalis albipalpis</i>	3	1	2	1	1	0	1	1	0	[01]	0	0	1	0	0
<i>Pantopsalis luna</i>	3	1	2	0	0	1	1	1	0	0	0	0	1	0	0
<i>Forsteropsalis chiltoni</i>	3	1	2	1	0	1	1	?	0	0	1	1	1	1	0
<i>Forsteropsalis fabulosa</i>	3	0	2	1	0	1	1	1	0	1	1	1	1	1	0
<i>Forsteropsalis grimmetti</i>	3	1	2	1	0	1	1	1	0	1	0	1	1	1	0
<i>Forsteropsalis inconstans</i>	3	1	2	?	0	1	1	0	0	0	1	1	1	1	0
<i>Spinicrus tasmanicum</i>	3	1	1	1	0	0	1	1	0	0	0	0	0	0	0
<i>Spinicrus stewarti</i>	3	1	1	1	1	0	1	0	0	0	0	0	0	0	0
<i>Spinicrus sublucens</i>	3	?	2	1	0	1	0	1	0	0	0	0	0	0	0
<i>Intutoportula minima</i>	3	?	0	?	1	0	1	?	0	0	1	0	0	0	0
<i>Intutoportula porongorupensis</i>	3	?	0	?	1	0	1	?	0	0	0	0	0	0	0
<i>Intutoportula suffugiens</i>	3	?	0	?	1	0	1	0	0	0	0	0	0	0	0
<i>Intutoportula walpolensis</i>	3	?	0	?	1	0	0	?	0	0	0	0	0	0	0
<i>Scissorestis nigricans</i>	3	0	1	1	1	0	1	0	0	0	1	0	0	0	0
<i>Spinibunus atrocidiana</i>	3	1	1	0	1	0	1	1	0	0	0	0	0	0	1
<i>Spinicrurellum coronatum</i>	3	1	1	0	1	0	0	0	0	0	1	0	0	0	1
<i>Spinicrurellum puerile</i>	3	1	1	0	1	0	0	1	0	0	0	0	0	0	0
<i>Spinicruroides caeruleomontium</i>	3	1	1	0	1	0	1	0	0	1	1	1	1	0	0

**TABLE 1.** Continued.

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Ischyropsalis kollari</i>	0	0	0	0	?	0	?	0	3	0	?	0	0	0	0
<i>Taracus</i>	1	0	0	0	?	0	?	0	0	0	?	0	0	0	0
<i>Nemastoma triste</i>	0	1	0	0	?	?	?	0	0	0	?	1	2	1	0
<i>Nipponopsalis yezeensis</i>	1	1	0	0	?	0	?	0	0	0	?	1	2	0	0
<i>Caddo agilis</i>	0	0	1	0	?	0	?	0	0	1	0	0	0	0	?
<i>Neopilio australis</i>	0	1	1	0	?	0	?	0	2	1	0	0	0	0	0
<i>Ballarra longipalpus</i>	1	1	0	0	?	0	?	0	0	0	?	0	0	0	0
<i>Thrasychirus</i>	0	0	1	?	?	1	0	0	2	1	1	?	?	0	?
<i>Nelima doriae</i>	0	0	0	0	?	0	?	0	3	1	1	0	2	0	2
<i>Phalangium opilio</i>	1	0	0	0	?	?	?	0	1	1	0	0	2	0	5
<i>Opilio parietinus</i>	0	0	0	0	?	0	?	0	3	1	0	0	2	0	5
<i>Australiscutum hunti</i>	0	0	1	0	?	1	0	0	1	1	1	0	0	1	0
<i>Australiscutum graciliforceps</i>	0	0	1	1	0	1	0	0	1	1	1	0	0	1	1
<i>Australiscutum triplodaemon</i>	0	0	1	1	0	?	0	0	1	1	1	0	0	1	1
<i>Monoscutum titirangiense</i>	0	0	0	2	1	2	1	1	1	1	0	0	2	1	0
<i>Templar incongruens</i>	0	0	1	1	0	2	0	1	1	1	0	0	3	1	3
<i>Tercentenarium linnaei</i>	0	0	1	2	0	2	0	0	1	1	0	0	0	0	0
<i>Hypomegalopsalis tanisphyros</i>	0	0	1	2	0	?	?	0	1	1	1	0	0	0	0
<i>Megalopsalis serritarsus</i>	0	0	1	2	0	?	?	0	1	1	1	1	1	0	3
<i>Megalopsalis epizephyros</i>	0	0	1	2	0	2	0	0	1	1	1	0	1	0	3
<i>Megalopsalis eremiotis</i>	0	0	1	2	0	2	0	0	1	1	1	1	1	0	3
<i>Megalopsalis hoggi</i>	0	0	1	2	0	?	?	0	1	1	1	1	1	0	3
<i>Megalopsalis leptekes</i>	0	0	1	2	0	?	?	0	1	1	1	0	0	0	2
<i>Megalopsalis pilliga</i>	0	0	0	2	0	?	?	0	1	1	1	0	0	0	3
<i>Neopantopsalis quasimodo</i>	0	0	0	0	?	?	?	0	2	1	1	0	1	0	3
<i>Neopantopsalis camelus</i>	0	0	0	0	?	?	?	0	2	1	1	0	0	0	1
<i>Neopantopsalis pentheter</i>	0	0	0	0	?	0	?	0	2	1	1	0	1	0	3
<i>Neopantopsalis psile</i>	0	0	0	0	?	0	?	0	2	1	1	0	1	0	3
<i>Neopantopsalis thaumatopios</i>	0	0	0	0	?	?	?	0	2	1	1	0	0	0	2
<i>Pantopsalis albipalpis</i>	0	0	1	0	?	1	0	0	1	1	0	0	0	0	1
<i>Pantopsalis luna</i>	0	0	1	0	?	1	0	0	1	1	0	0	0	0	1
<i>Forsteropsalis chiltoni</i>	0	0	0	1	1	1	1	0	1	1	0	0	0	0	1
<i>Forsteropsalis fabulosa</i>	1	0	1	1	1	1	1	0	2	1	0	0	0	0	1
<i>Forsteropsalis grimmetti</i>	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1
<i>Forsteropsalis inconstans</i>	0	0	0	1	1	1	1	0	2	1	0	0	0	0	1
<i>Spinicrus tasmanicum</i>	0	0	1	0	?	0	?	0	2	1	1	0	1	0	1
<i>Spinicrus stewarti</i>	0	0	1	0	?	1	0	0	2	1	1	0	1	0	4
<i>Spinicrus sublucens</i>	0	0	0	0	?	?	?	0	2	1	1	0	0	0	0
<i>Intutoportula minima</i>	0	0	0	0	?	?	?	0	2	1	1	0	1	0	[12]
<i>Intutoportula porongorupensis</i>	0	0	0	0	?	?	?	0	2	1	1	0	1	0	2
<i>Intutoportula suffugiens</i>	0	0	1	0	?	0	?	0	2	1	1	0	0	0	1
<i>Intutoportula walpolensis</i>	0	0	0	0	?	?	?	0	1	1	1	0	1	0	1
<i>Scissorestis nigricans</i>	1	1	0	0	?	0	?	0	1	1	1	0	0	0	0
<i>Spinibunus atrocidiana</i>	0	0	0	0	?	1	0	0	2	1	1	0	1	0	2
<i>Spinicrurellum coronatum</i>	0	0	0	0	?	?	?	0	2	1	1	0	0	0	2
<i>Spinicrurellum puerile</i>	0	0	0	0	?	?	?	0	1	1	1	0	0	0	1
<i>Spinicruroides caeruleomontium</i>	0	0	0	0	?	0	?	0	2	1	1	0	0	0	1

**TABLE 1.** Continued.

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
<i>I. kollari</i>	0	?	0	0	0	0	0	0	1	0	1	1	0	0	0	0
<i>Taracus</i>	0	?	0	0	0	0	0	0	1	0	1	1	0	0	0	0
<i>N. triste</i>	?	?	0	1	0	0	0	0	1	0	1	0	0	0	0	0
<i>N. yezoensis</i>	0	?	0	1	0	0	1	0	1	0	1	0	0	0	0	0
<i>C. agilis</i>	0	?	0	0	0	?	0	0	1	0	1	1	?	?	0	0
<i>N. australis</i>	0	?	0	0	1	?	0	0	?	?	?	?	0	0	?	0
<i>B. longipalpus</i>	0	?	0	0	1	0	1	0	1	0	1	1	0	0	1	0
<i>Thrasychirus</i>	0	?	?	1	1	?	?	?	1	1	1	1	?	?	1	0
<i>N. doriae</i>	2	1	0	0	1	0	1	0	1	1	1	1	0	0	1	0
<i>P. opilio</i>	?	2	1	0	1	0	0	0	1	1	1	1	0	0	1	0
<i>O. parietinus</i>	1	2	0	0	1	0	0	0	1	1	1	1	0	1	1	0
<i>A. hunti</i>	0	?	0	0	1	0	0	0	0	?	1	1	0	0	1	0
<i>A. graciliforceps</i>	1	2	0	0	1	0	0	0	0	?	1	1	0	0	1	0
<i>A. triplodaemon</i>	?	1	0	0	1	0	0	0	0	?	1	1	0	0	1	0
<i>M. titirangiense</i>	0	?	0	0	0	0	1	0	1	0	0	0	0	0	1	0
<i>T. incongruens</i>	2	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
<i>T. linnaei</i>	0	?	0	0	1	0	0	0	0	?	0	0	0	0	1	0
<i>H. tanisphyros</i>	?	?	0	0	1	0	1	0	0	?	0	0	0	0	1	0
<i>M. serritarsus</i>	?	1	1	0	1	1	1	0	0	?	0	0	1	2	1	0
<i>M. epizephyros</i>	0	1	1	0	1	1	1	0	0	?	0	0	1	2	1	0
<i>M. eremiotis</i>	0	1	1	0	1	1	1	0	0	?	0	0	1	2	1	0
<i>M. hoggi</i>	?	1	1	0	1	0	1	0	0	?	0	0	0	2	1	0
<i>M. leptekes</i>	?	1	0	0	1	0	0	0	0	?	0	0	0	0	1	0
<i>M. pilliga</i>	?	2	0	0	1	0	1	0	0	?	0	0	1	2	1	0
<i>N. quasimodo</i>	?	2	1	0	1	0	1	1	1	0	0	0	0	0	1	0
<i>N. camelus</i>	?	2	1	1	1	0	1	1	1	1	0	0	0	0	1	0
<i>N. pentheter</i>	2	2	1	0	1	0	1	1	1	0	0	0	0	0	1	0
<i>N. psile</i>	2	2	1	0	1	0	1	1	1	0	0	0	0	0	1	0
<i>N. thaumatopoiios</i>	?	2	1	1	1	0	1	?	1	0	0	0	0	?	1	0
<i>P. albipalpis</i>	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0
<i>P. luna</i>	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0
<i>F. chiltoni</i>	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0
<i>F. fabulosa</i>	0	0	0	0	1	0	1	1	[01]	1	0	0	0	0	1	0
<i>F. grimmetti</i>	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0
<i>F. inconstans</i>	1	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0
<i>S. tasmanicum</i>	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0
<i>S. stewarti</i>	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	1
<i>S. sublucens</i>	?	?	0	0	1	0	1	1	0	?	0	0	0	1	1	1
<i>I. minima</i>	?	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0
<i>I. porongorupensis</i>	?	0	0	0	1	0	1	0	0	?	0	0	0	0	1	0
<i>I. suffugiens</i>	1	[01]	0	0	1	0	1	1	1	0	0	0	0	0	1	0
<i>I. walpolensis</i>	?	1	0	0	1	0	1	0	0	?	0	0	0	0	1	0
<i>S. nigricans</i>	0	?	0	0	1	0	1	0	1	0	0	0	0	0	1	1
<i>S. atrocidiana</i>	2	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0
<i>S. coronatum</i>	?	0	0	0	1	0	1	1	[01]	0	0	0	0	0	1	0
<i>S. puerile</i>	?	1	0	0	1	0	1	1	[01]	0	0	0	0	0	1	0
<i>S. caeruleomontium</i>	2	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1

## Results and Discussion

The parsimony analysis produced two equally supported trees of 372 steps (CI = 0.261, RI = 0.628), the consensus of which is shown in figs 42–43. The only disagreement between the trees was in the position of *Forsteropsalis grimmetti*, which either remained the sister to the other *Forsteropsalis* species or became the sister to *Pantopsalis*.

The results are consistent with the monophyly of both Eupnoi and Phalangioida. Eupnoi are separated from Dyspnoi by the presence of cheliceral lamellae, the presence of an angular ventral junction between the penile shaft and glans, and the presence of pores and absence of extensive setae on the glans. Though not the primary focus of the analysis, the results are also consistent with monophyly of the two Dyspnoi superfamilies. Bremer supports were low across the entire tree, with only five clades receiving support values of four or more (the entapophyseate clade, Phalangiidae, *Australiscutum*, *Neopantopsalis*, and *Monoscutum* + *Templar*), and homoplasy affects the majority of characters analysed. Neither Monoscutidae nor Neopilionidae as currently defined are supported as monophyletic due to the nesting of *Thrasychirus* (Enantiobuninae) within the Monoscutidae clade whereas *Ballarra* and *Neopilio* are positioned as successive outgroups to Monoscutidae + *Thrasychirus*. A close relationship between Enantiobuninae and Monoscutidae is particularly supported by the unique character of *Thrasychirus*-form spines in *Thrasychirus* and Megalopsalidinae. Enforcing the monophyly of *Neopilio* + *Ballarra* + *Thrasychirus* adds nine steps to the tree length and retains a clade of Neopilionidae + Monoscutidae in the resulting majority rule consensus tree. The position of Enantiobuninae in Neopilionidae has previously been considered suspect, and its recognition as a distinct family has been recommended but not formally established (Hunt & Cokendolpher 1991; Cokendolpher *et al.* 2007). The failure of the current analysis to conclusively separate Enantiobuninae from Monoscutidae suggests that the most appropriate approach would be to combine Enantiobuninae and Monoscutidae into a single family. However, if this family were to be regarded as distinct from Neopilionidae, a new name would have to be established at the family level as Enantiobuninae Mello-Leitão 1931 holds precedence over Monoscutinae Forster 1948. Instead, I propose that Monoscutidae be synonymised

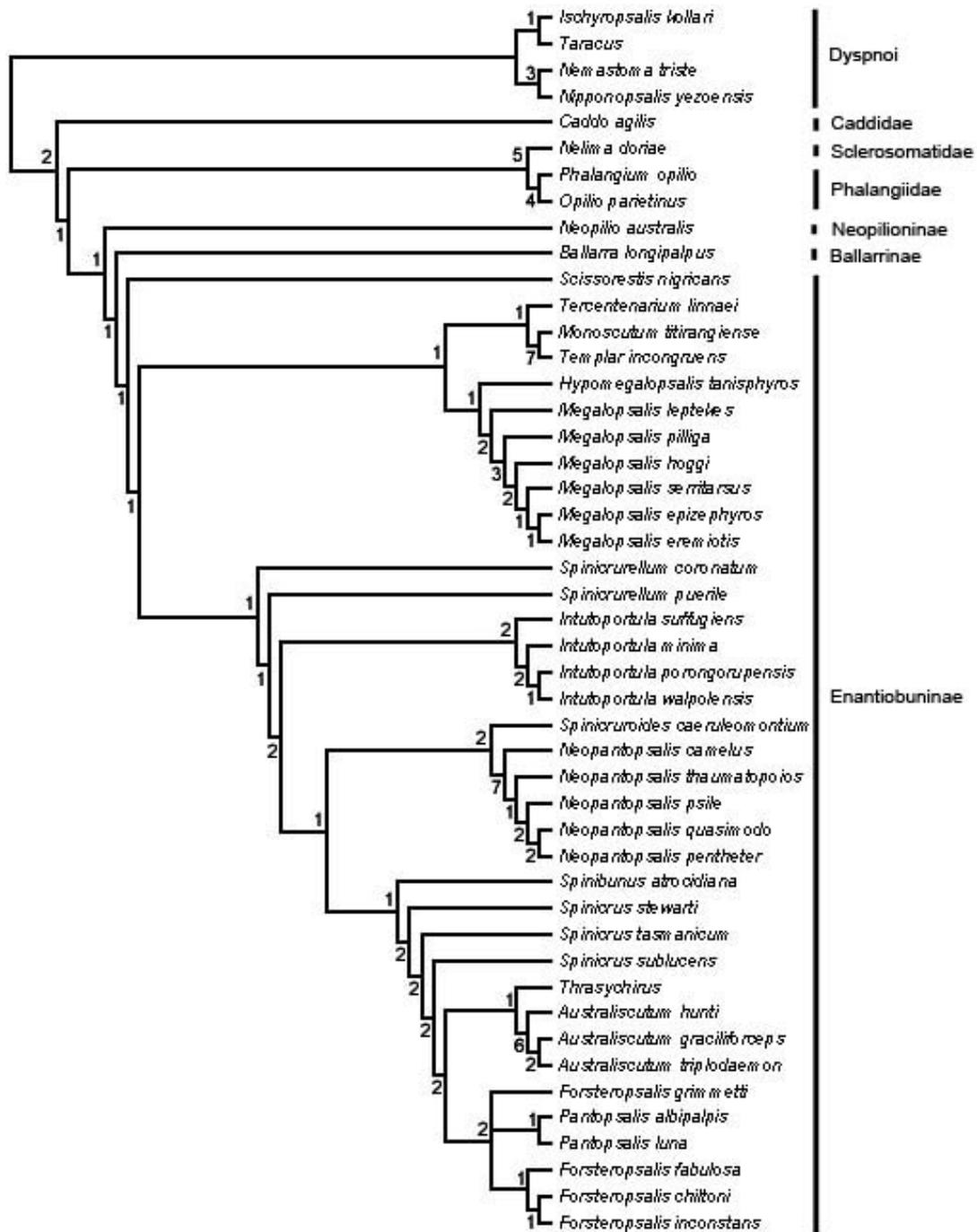
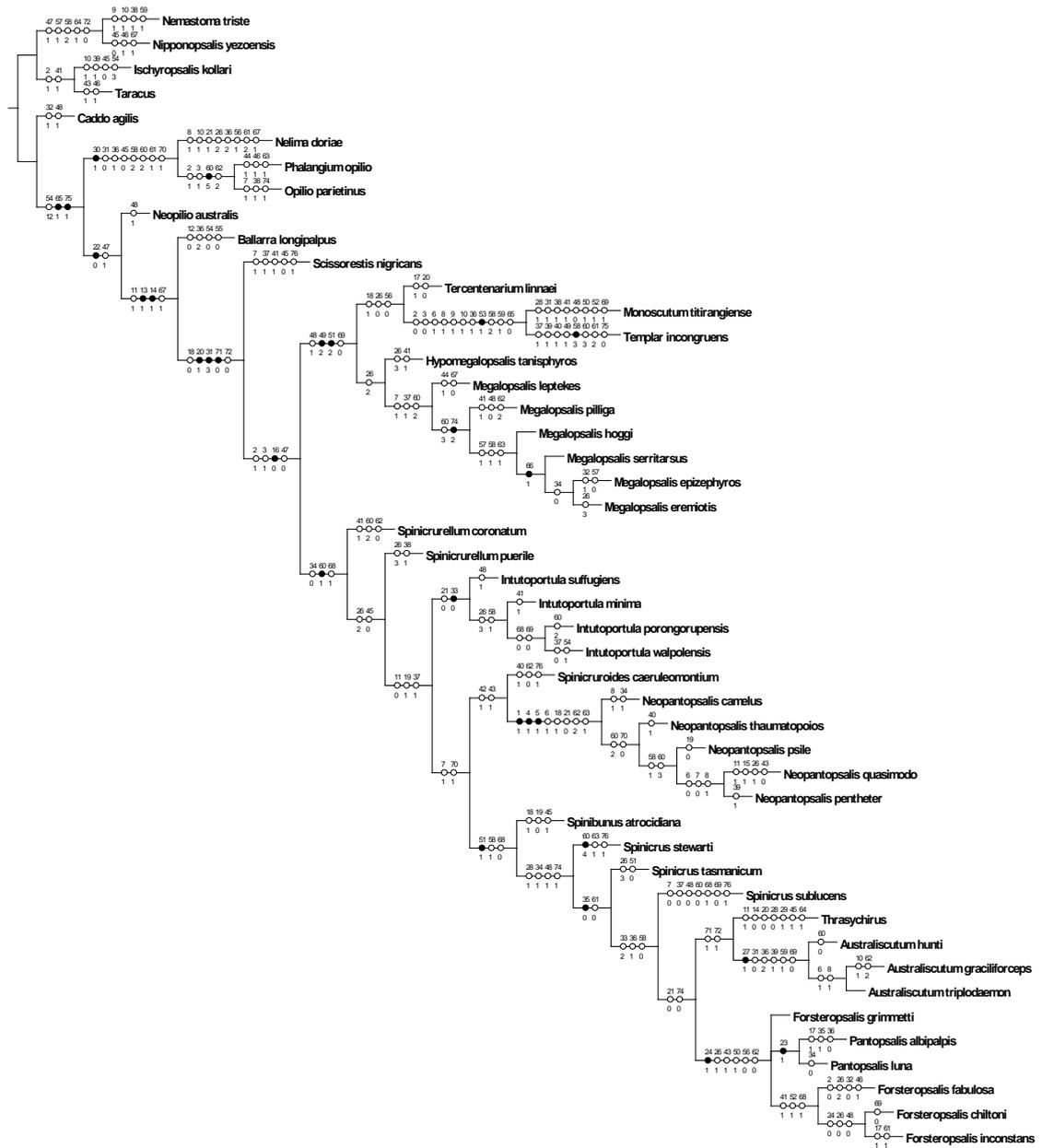
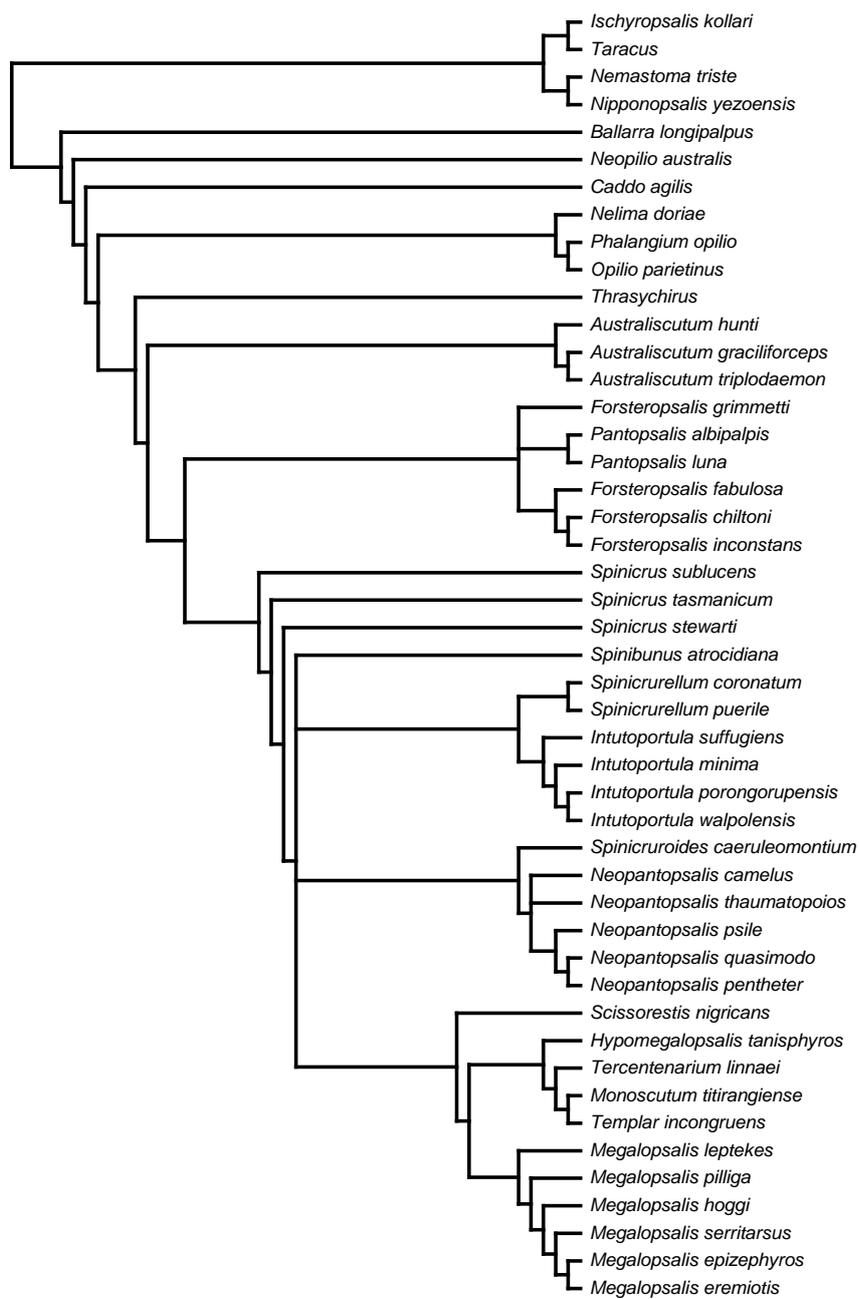


FIGURE 42. Strict consensus tree of Palpatores from parsimony analysis (source trees 372 steps, CI = 0.261, RI = 0.628). Numbers next to nodes are Bremer support values.



**FIGURE 43.** Strict consensus of Palpatores, with mapped synapomorphies. Black circles indicate unique synapomorphies; open circles indicate homoplastic synapomorphies. Numbers above circles are character numbers; numbers below circles represent character states.

with Neopilionidae, returning it to the position used by Šilhavý (1970). A potential synapomorphy of this expanded Neopilionidae is the absence of lateral setae on the glans, in contrast to the *Sinnesborsten* present in *Caddo* and the entapophyseate clade. In order to reflect the closer relationship between *Thrasychirus* and Monoscutidae than *Neopilio*, and to better reflect the uncertain position of *Thrasychirus*, I also synonymise the subfamilies Monoscutinae and Megalopsalidinae with Enantiobuninae. For the sake of convenience, the names



**FIGURE 44.** Strict consensus of eight most parsimonious trees for Palpatores resulting from analysis constrained for monophyly of Monoscutidae (375 steps, CI = 0.259, RI = 0.624).

Monoscutidae, Monoscutinae and Megalopsalidinae will continue to be used in the following discussion for those taxa associated under those names to date.

Forcing monophyly of Monoscutidae adds three steps to the tree length and *Thrasychirus* remains the sister taxon to Monoscutidae (fig. 44). Forcing the monophyly of Megalopsalidinae (i.e. a clade uniting all Enantiobuninae except *Thrasychirus*, *Australiscutum*, *Monoscutum* and *Templar*) adds seven steps to the tree length.

Biogeographic connections between southern South America and Australasia have been suggested for a number of organisms to the extent that an ‘Antarctic’ floral region has been proposed uniting southern South America and New Zealand with Antarctic elements also present in eastern Australia, especially Tasmania (Cox 2001). Examples of taxa exhibiting close biogeographic relationships between southern South America and Australia and/or New Zealand include Embothriaceae (Proteaceae; Weston & Crisp 1994), *Nothofagus* (Nothofagaceae; Linder & Crisp 1995; Swenson *et al.* 2001), *Abrotanella* (Asteraceae; Swenson & Bremer 1997); Luzuriagaceae (Vinnersten & Bremer 2001), tardigrades (McInnes & Pugh 1998), Paracolletini (Hymenoptera; Michener 1979) and Eucnemidae (Coleoptera; Muona 1991). The suggested position of *Thrasychirus* nested among, rather than sister to, Australasian taxa is also not incredible. Though the fossil record for Opiliones is relatively sparse, it seems likely that many of the modern higher taxa diverged some time during the Palaeozoic (Dunlop 2007). A recently described species from the Jurassic of China, *Mesobunus martensi* Huang *et al.* 2009, was assigned by its authors to the modern family Sclerosomatidae (Huang *et al.* 2009). This identification is not certain, but is very likely – none of the characters cited by Huang *et al.* (2009) are unique to Sclerosomatidae, but Sclerosomatidae is the only known family to exhibit all those characters in concert. Presence of Sclerosomatidae, and hence the entapophyseate clade, in the Middle Jurassic would also necessitate that the lineage leading to Neopilionidae had diverged by that time. Separation of South America and Australia from the connecting, non-glaciated Antarctica had begun by the end of the Cretaceous, but did not become complete until the end of the Eocene, at which time the establishment of the South Circumpolar Current allowed the development of the Antarctic ice sheet (McLoughlin 2001). Without a fossil record, the diversity of Neopilionidae at that time remains unknown, but specimens of other families of Opiliones from Eocene Baltic amber are similar enough to modern taxa of

other families to have been assigned to modern genera (Staręga 2002; Dunlop 2006, 2007). If Neopilionidae evolved at a comparable rate, then divergence of the Enantiobuninae crown group prior to the loss of a land connection between South America and Australia is quite believable. The presence of Ballarrinae in South Africa, South America and Australia also supports neopilionid divergence prior to the break-up of Gondwana (Hunt & Cokendolpher 1991). It is also noteworthy that Tasmania was the very last section of Australia to separate from Antarctica (McLoughlin 2001) which is also consistent with the position of *Thrasychirus* in the most parsimonious trees among eastern Australian and New Zealand taxa. Western Australia was also identified as the outgroup to a cluster including South America, New Zealand and eastern Australia in a biogeographic analysis of gymnosperms (Contreras-Medina & Luna Vega 2002). The cestode genus *Linstowia*, which is parasitic on marsupials and monotremes, has been recorded from South America and eastern Australia but not from western Australia (Gardner & Campbell 1992), despite the presence of presumably suitable hosts in the latter region.

The topology of the most parsimonious trees suggests that the single paired bristles on the penis of *Thrasychirus* could be derived via reduction from the bristle groups of other Enantiobuninae. Unfortunately, the genitalia have not yet been described for the only other South American genus previously assigned to Enantiobuninae, the monotypic *Thrasychiroides brasiliensis* Soares & Soares 1947. It would be of interest to see whether *Thrasychiroides* possesses a similar genital morphology to *Thrasychirus*.

The recently described genus *Australiscutum* (Taylor, in press) very likely corresponds to the 'new Australian genus' of Monoscutinae referred to by Hunt & Cokendolpher (1991). *Australiscutum* has a strong superficial resemblance to Monoscutinae with relatively short, sturdy legs and a highly ornamented dorsum. However, the dorsum is less sclerotised in *Australiscutum* than in Monoscutinae, the dorsal ornamentation is comprised of spinose setae rather than denticles, and the genital and spiracle morphology is distinct (Taylor 2009b). The current analysis does not support a close relationship between *Australiscutum* and Monoscutinae and indicates that their similar appearance is the result of convergence. Elsewhere among Opiliones, the combination of a sclerotised, often ornate dorsum and relatively short legs has evolved among numerous Dyspnoi and Laniatores, as well as being universal for Cyphophthalmi (Pinto-da-Rocha & Giribet 2007), and is associated

with a cryptic, soil-dwelling lifestyle (Curtis & Machado 2007). The analysis also supports the previously proposed close relationship of *Australiscutum graciliforceps* and *A. triplodaemon* to the exclusion of *A. hunti* (Taylor, in press).

Both the most parsimonious and constrained topologies support the polyphyly of species currently assigned to the genera *Megalopsalis* and *Spinicrus*, as has been suggested in the past (Hunt 1990; Taylor & Hunt 2009). The monophyly of *Neopantopsalis* Taylor & Hunt 2009 is strongly supported by the distinctive morphology of the dorsal prosomal plate, the bowed cheliceral fingers (shared with *Forsteropsalis*) with setae on the mobile finger (shared with *Pantopsalis* and *Forsteropsalis*, lost in *Neopantopsalis quasimodo*), the linear arrangement of denticles on the legs with elongate spine row on leg I, and the elongate glans. *Neopantopsalis camelus* and *N. thaumatopoius* are together resolved as the sister clade to the remaining taxa due to the more extensive leg armature and different spiracle spine morphology (unknown for *N. thaumatopoius*) in the remaining three species. The inferred phylogeny for *Neopantopsalis* also correlates with the biogeography of the genus: *N. camelus* and *N. thaumatopoius* have a more southerly distribution than the remaining species (Taylor & Hunt 2009).

Species previously assigned to *Megalopsalis* are divided between three genera in the systematic section below: *Megalopsalis*, *Tercentenarium* and *Forsteropsalis*. The New Zealand species of *Megalopsalis* included in the analysis (transferred below to the new genus *Forsteropsalis*) form a clade with *Pantopsalis*, supported by the presence of setae on the mobile finger of the chelicera, the reduction of the tooth-row on the pedipalp claw, and the non-linear arrangement of denticles on the legs. The analysis therefore indicates only two origins for New Zealand Enantiobuninae, Monoscutinae and the *Pantopsalis* + *Forsteropsalis* clade. The continental block that includes New Zealand became separated from Australia during the late Cretaceous (McLoughlin 2001). Forster (1964) suggested transfer of at least the New Zealand species of *Megalopsalis* to *Pantopsalis*, but in light of the distinct differences between the two groups (listed as differences between *Pantopsalis* and *Megalopsalis* in Taylor 2004) and their separate resolution in the current analysis, I recognise two genera within this clade. *Pantopsalis* is supported by the triangular dorsolateral keel on the glans whereas *Forsteropsalis* is supported by the bowed cheliceral fingers and denticles on the medial side of the pedipalp coxa.

*Megalopsalis* has been defined in the past primarily by the presence of an apophysis on the pedipalp patella (Sørensen 1886; Roewer 1923; Forster 1944), later redefined to specify its presence in both sexes (Taylor 2004). In all Australian species assigned to *Megalopsalis* the pedipalp patella apophysis is elongate, more than half the length of the main body of the patella, in contrast to *Pantopsalis* and *Spinicrus* where the apophysis is shorter or absent (Forster 1949a; Taylor 2004). However, the current analysis resolves an elongate apophysis as a synapomorphy for a larger clade including *Megalopsalis* and Monoscutinae. *Megalopsalis* as redefined below is supported by three synapomorphies but all three (the presence of a space between the ocularium and the mesopeltidium, elongate chelicerae in the males, and armature from the femur to at least the patella on leg I) must be regarded as weak due to homoplasy elsewhere. Further investigation would therefore be required to confirm the association between *M. leptekes* and the remaining *Megalopsalis* species. *Megalopsalis* species other than *M. leptekes* form a clade well-supported by a unique synapomorphy, the presence of a ventral paired row of brush-like bristles on enlarged distitarsi III and IV. In the species of this clade other than *M. hoggi*, distitarsus II has also been modified with distoventral bulges on the pseudosegments. The current analysis does not support monophyly for those species with modified distitarsus II, but as all synapomorphies excluding *M. pilliga* from the clade uniting *M. hoggi* with the remaining species are related to armature, this may be the result of a secondary reduction in armature in the former. Forcing the species with modified distitarsus II to form a clade adds two steps to the tree length. *Hypomegalopsalis tanisphyros* is the sister taxon to *Megalopsalis* in the most parsimonious tree, but becomes sister to *Tercentenarium* + Monoscutinae in the constrained tree.

Polyphyly of the species assigned to *Spinicrus* has been suggested by previous authors due to the heterogeneity of that genus (Hunt 1990; Taylor & Hunt 2009). This suggestion is confirmed by the current analysis, and consequently *Spinicrus*-like species are here divided between a number of genera. However, establishing an appropriate generic division has not been straightforward. Apart from a clade of four Western Australian species united by their unique spiracle morphology (recognised below as the genus *Intutoportula*), none of the other species form monophyletic clusters excluding members of other genera. Other than the possibility of synonymising pre-existing genera, a classification based on strict monophyly would require recognition of a separate genus for each species. Whereas

there are convincing arguments supporting the exclusive use of monophyletic taxa in formal classifications (Platnick 1978; Farris 1979; Fink 1979), I have felt the need to take a more flexible approach herein. Firstly, the diagnostic differences between some of the resulting genera would be very minor and in some cases difficult to distinguish, so there may be pragmatic advantages in recognising larger phenetic groupings as genera. Secondly, and more significantly, the nodes separating the various *Spinicrus*-like species in the analysis results are poorly supported, and the true paraphyly of the genera recognised herein cannot be regarded as conclusive. It is possible that future investigations may argue for further revisions to the current classification; however, this possibility applies to the classification of any organism.

With these factors in mind, monotypic genera are here established for the morphologically distinct species *Scissorestis nigricans* (Hickman 1957), *Spinicruroides caeruleomontium* and *Spinibunus atrocidiana*. *Scissorestis nigricans*, as explained above, is potentially the sister taxon to all other Enantiobuninae. *Spinicruroides caeruleomontium* is placed as the sister taxon to *Neopantopsalis*, with which it shares the presence of setae on the mobile finger of the chelicerae and cheliceral fingers that are bowed apart proximally. The distribution of *S. caeruleomontium* in mid-eastern New South Wales further supports the possibility of a southern origin followed by northern dispersal for *Neopantopsalis* (Taylor, in press).

Two species placed in the new genus *Spinicrurellum*, *S. coronatum* and *S. puerile*, share a distinct genital morphology but are placed by the analysis as successive basal branches in the clade of Enantiobuninae excluding *Scissorestis* and the elongate-apophysis clade. Constraining *Spinicrurellum* as monophyletic adds a single step to the tree length.

Species assigned herein to *Spinicrus* are morphologically heterogeneous but share the presence of ventral brush-like bristles on distitarsi III and IV whereas *Spinicrus stewarti* and *S. sublucens* also have a similar genital morphology. Constraining the monophyly of *Spinicrus* adds three steps to the tree length.

The classification of Phalangioida has been revised on numerous occasions (Roewer 1923; Šilhavý 1970; Martens 1976; Crawford 1992; Cokendolpher *et al.* 2007); unfortunately, the need for revision does not yet seem to have passed. Further investigation of *Thrasychirus* and its putative sister taxon *Thrasychiroides* is required to confirm its position in the current analysis whereas *Neopilio* and Ballarrinae

require further investigation to determine whether the enlarged Neopilionidae as recognised herein is truly a monophyletic unit. The support in this analysis for a monophyletic entapophyseate clade is in conflict with the results of Giribet *et al.* (2009). The latter study sampled a much broader range of taxa in Phalangiidae and Sclerosomatidae and the addition of further entapophyseate taxa could potentially affect the current results. Phalangioidea have a reputation for presenting relatively few taxonomically reliable characters (Crawford 1992). However, the current analysis demonstrates that members of the superfamily are not intractable to phylogenetic studies.

## Key to Genera of Enantiobuninae

'*Megalopsalis*' *triascuta* Forster 1944 is a New Zealand species of doubtful affinity, probably not a member of *Megalopsalis sensu stricto*. Unfortunately, the holotype (MONZ) is a juvenile (personal observation, 2001) and the position of this species cannot yet be established. It is keyed out separately below.

*Thrasychiroides brasiliicus* has had to be omitted from the following key, as it has not been redescribed since its original description (Soares & Soares 1947) and most of the characters used in the key remain unknown for it. *Thrasychiroides* is the only genus of Enantiobuninae described from South America other than *Thrasychirus*, from which Soares & Soares (1947) distinguished it by the lack of an apophysis on the pedipalp patella.

1. Legs relatively short, femur I less than twice length of prosoma; dorsum of opisthosoma usually conspicuously ornamented...2  
Legs long, femur I more than twice length of prosoma ...5
2. Bristle groups on right side of shaft-glans junction only; stylus conspicuously inflated (figs. 51–56; eastern Australia)...*Australiscutum*  
Bristle groups on both sides of shaft-glans junction; stylus not inflated (New Zealand)...3
3. Opisthosoma with large flanking spines (Three Kings Islands)...*Acihasta*  
Opisthosoma without large flanking spines...4
4. Dorsal ornamentation simple round nodules; ocularium with promedial projecting nodule (South Island)...*Templar*  
Dorsal ornamentation complex nodules with lateral projections; ocularium with large promedial projecting nodule (North Island)...*Monoscutum*
5. Dorsum of opisthosoma with transverse rows of spines (fig. 165; Queensland)...*Spinibunus*  
Dorsum of opisthosoma unarmed...6
6. Mobile hinge between leg basitarsus and distitarsus (South America)...*Thrasychirus*  
Junction between basitarsus and distitarsus straight, not hinged (Australasia)...7

7. Pedipalp patella with distinct elongate (longer than broad) medial apophysis (fig. 91)...8  
 Apophysis on pedipalp patella absent or, if present, not distinctly longer than broad...11
8. Pedipalp patella apophysis much longer than main body of patella (North Island, New Zealand)... '*Megalopsalis*' *triascuta*  
 Pedipalp patella apophysis shorter than main body of patella (Australia)...9
9. Dorsal prosomal plate denticulate; male chelicerae greatly elongate, projecting above level of dorsum (Western Australia to New South Wales)...*Megalopsalis*  
 Dorsal prosomal plate unarmed; male chelicerae not greatly elongate...10
10. Male chelicerae with distinct dorsodistal bulge (fig. 215); glans significantly longer than wide, bent distinctly dorsad from shaft, with vertical plate-like lateral process on left side of shaft-glans junction (figs 224–225; Western Australia)...*Tercentenarium*  
 Male chelicerae without dorsodistal bulge; glans not longer than wide, triangular in dorsal view (figs 61–62), not bent significantly dorsad from shaft, no platelike lateral process (Western Australia)...*Hypomegalopsalis*
11. Ozopores small, circular, without flanking lobes (Tasmania)...*Scissorestis*  
 Ozopores large, oval or oblong, with flanking lobes...12
12. Pedipalp claw with ventral tooth-comb (Australia)...13  
 Pedipalp claw without or with only one or two minute ventral teeth (New Zealand)...17
13. Distitarsi III and IV with ventral rows of brush-like bristles (fig. 41; New South Wales to Tasmania)...*Spinicrus*  
 Distitarsi III and IV without ventral brush-like bristles...14
14. Dorsum of male prosoma often raised in humps; proventral row of hypertrophied spines along femur I; glans elongate, more than twice as long as wide, oval or oblong in ventral view (New South Wales, Queensland)...*Neopantopsalis*  
 Dorsum of male prosoma never raised in humps; glans less than twice as long as wide...15
15. Mobile finger of chelicerae with setae (New South Wales)...*Spinicruroides*  
 Mobile finger of chelicerae without setae...16

16. Chelicerae unarmed; spiracle with covering spines; sides of glans subparallel in ventral view (figs 185–186; Queensland)...*Spinicrurellum*  
Chelicerae at least partially denticulate; spiracle without covering spines; glans triangular in ventral view, sides converging (fig. 73; Western Australia)...*Intutoportula*
17. Fingers of male chelicerae closing tightly against one another; male pedipalp patella entirely without apophysis...*Pantopsalis*  
Fingers of male chelicerae bowed apart proximally; male pedipalp with small triangular apophysis...*Forsteropsalis*

## Taxonomic Descriptions

### Neopilionidae Lawrence 1931

Neopilioninae Lawrence 1931: 473 (type genus *Neopilio* Lawrence 1931).

Neopilionidae Lawrence—Kauri 1961: 141–143; Šilhavý 1970: 171; Martens 1978: 55, 229; Shear 1982: 110; Hunt & Cokendolpher 1991: 138–139; Crawford 1992: 4, 9; Cokendolpher, Tsurusaki *et al.* 2007: 111; Cokendolpher 2007a: 121, 123.

**Included taxa.** Ballarrinae Hunt & Cokendolpher 1991, Enantiobuninae Mello-Leitão 1931, Neopilioninae Lawrence 1931.

**Definition.** Eupnoi sharing a more recent common ancestor with *Neopilio australis* than *Phalangium opilio*, *Phalangium quadridentatum* Cuvier 1795 (= *Homalenotus quadridentatus*) or *Caddo agilis*.

**Description.** Dorsum of opisthosoma usually coriaceous, rarely sclerotised. Glans of penis lacking lateral setae; lateral processes often present at shaft-glans junction. Spiracle lacking entapophysis, often with occluding spines. Pedipalp small, leg-like, without large spinose setae; tarsus longer than tibia.

**Comments.** The priority of Neopilioninae over Enantiobuninae was confirmed by Hunt and Cokendolpher (1991) and Crawford (1992).

### Enantiobuninae Mello-Leitão 1931

Enantiobuninae Mello-Leitão 1931: 92 (type genus *Enantiobunus* Mello-Leitão 1931); Šilhavý 1970: 171, 175; Hunt & Cokendolpher 1991: 134–135; Crawford 1992: 4, 8; Cokendolpher 2007a: 121, 123.

Monoscutinae Forster 1948a: 313 (type genus *Monoscutum* Forster 1948a; new synonym herein); Crawford 1992: 4, 9; Cokendolpher & Taylor 2007: 119–120; Taylor 2008a: 176.

Megalopsalinae Forster 1949a: 60 (incorrect original spelling; type genus *Megalopsalis* Roewer 1923; new synonym herein); Šilhavý 1970: 175; Gruber & Hunt 1973: 384.

Megalopsalididae Forster—Martens 1976: 64; Shear 1982: 109–110.

Megalopsalidinae—Hunt 1990b: 193–194; Crawford 1992: 4, 9; Cokendolpher & Taylor 2007: 119–120; Taylor 2008a: 176.

Monoscutidae Forster—Crawford 1992: 4, 9; Cokendolpher, Tsurusaki *et al.* 2007: 110–111; Cokendolpher & Taylor 2007: 118–120; Taylor 2008a: 176.

**Included taxa.** *Acihasta* Forster 1948a, *Australiscutum* new genus, *Forsteropsalis* new genus, *Hypomegalopsalis* new genus, *Intutoportula* new genus, *Megalopsalis* Roewer 1923, *Monoscutum* Forster 1948a, *Neopantopsalis* Taylor & Hunt 2009, *Pantopsalis* Simon 1879, *Scissorestis* new genus, *Spinibunus* new genus, *Spinicrurellum* new genus, *Spinicruroides* new genus, *Spinicrus* Forster 1949a, *Templar* Taylor 2008, *Tercentenarium* new genus, *Thrasychiroides* Soares & Soares 1947, *Thrasychirus* Simon 1884.

**Definition.** Eupnoi sharing a more recent common ancestor with *Enantiobunus spinulosus* Mello-Leitão 1931 (= *Thrasychirus gulosus* Simon 1884) than *Phalangium opilio*, *Phalangium quadridentatum*, *Caddo agilis*, *Neopilio australis* or *Ballarra drosera* Hunt & Cokendolpher 1991.

**Description.** Lateral processes (bristle groups or isolated bristles) at junction between glans and shaft of penis, usually in anterior and posterior pairs. No lateral processes on glans. Spiracle usually with covering grill of slender, anastomosing spines in one or few rows, arising from anterior margin of spiracle. Pedipalp with well-developed claw; dorsal angle between patella and tibia 180° or more; patella (excluding apophysis if present) usually shorter than tibia (only slightly longer if otherwise); tarsus longer than patella or tibia.

**Comments.** The phylogenetic analysis reported on above found both Enantiobuninae and Monoscutinae as recognised by Crawford (1992) nested within Megalopsalidinae; the three taxa are therefore united herein as a single subfamily for which the name Enantiobuninae Mello-Leitão 1931 takes priority.

#### ***Acihasta* Forster 1948a**

*Acihasta* Forster, 1948a: 315; Crawford, 1992: 10.

**Type (and only) species.** *Acihasta salebrosa* Forster 1948a by original designation.

**Diagnosis.** *Acihasta* is distinguishable from all other Enantiobuninae except *Monoscutum* and *Templar* by the heavily sclerotised dorsum of the opisthosoma. It is

distinguishable from all Enantiobuninae including the latter two genera by the presence of large flanking spines on the lateral margins of the opisthosoma (Forster 1948a).

**Distribution.** Three Kings Islands, New Zealand.

**Comments.** The penis and seminal receptacles of *Acihasta salebrosa* were illustrated by Hunt and Cokendolpher (1991: figs 2b, 3b). *Acihasta salebrosa* was not included in the current phylogenetic analysis due to an absence of specimens; however, its genital and overall morphology (sclerotised opisthosoma, elongate pedipalp patella apophysis) is suggestive of a relationship with *Monoscutum* and *Templar*.

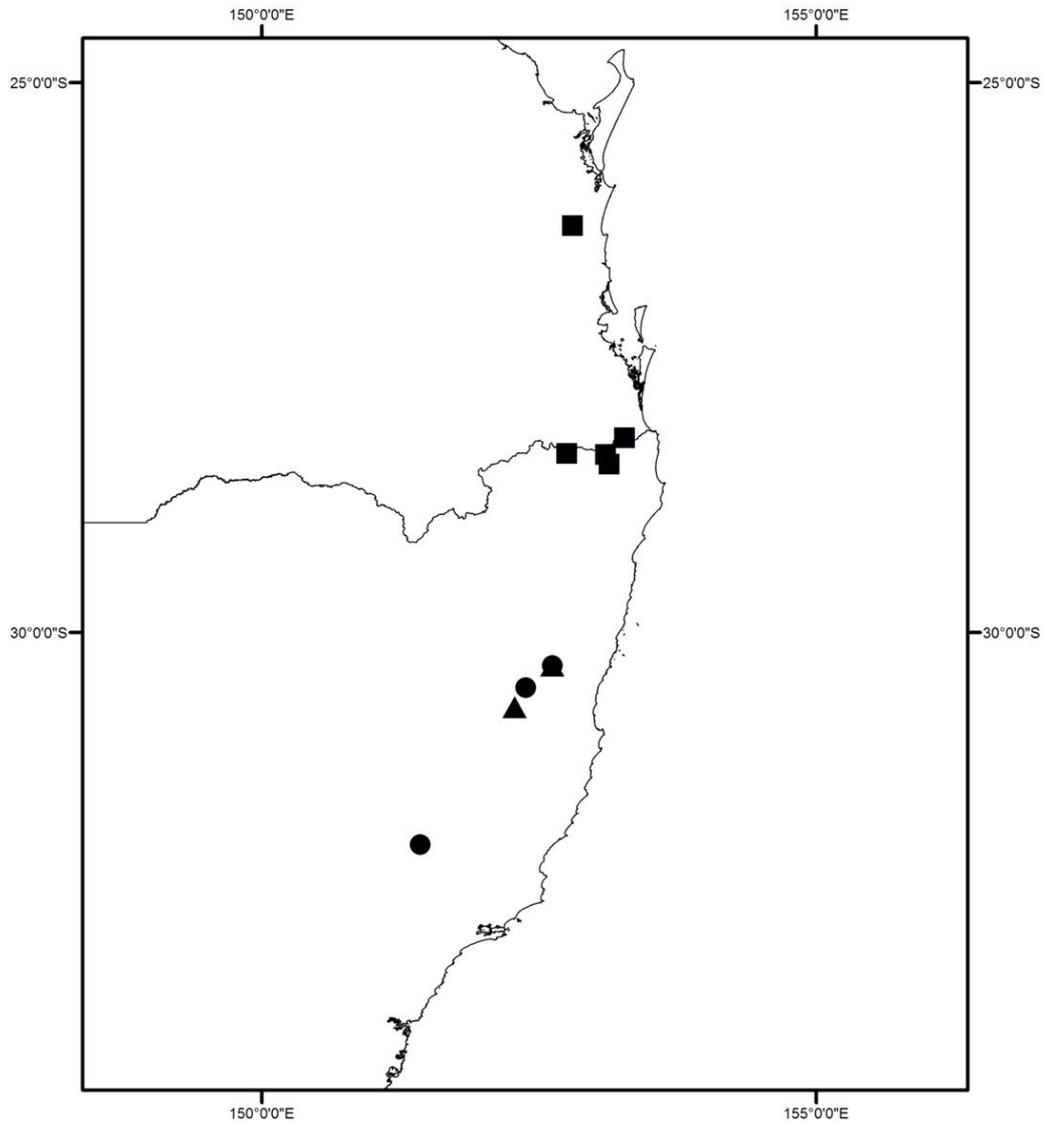
### ***Australiscutum* new genus**

*Australiscutum* Taylor, 2009b: 321-324.

**Type species.** *Australiscutum hunti* new species by present designation.

**Diagnosis.** *Australiscutum* is distinguishable from all other Enantiobuninae except for species attributed to Monoscutinae by Forster (1949a) and Taylor (2008a) by the presence of ornamentation on the dorsum of the opisthosoma and the shorter legs (femur I less than twice the length of the prosoma in “Monoscutinae” versus more than twice the length of the prosoma in “Megalopsalidinae”). It is distinguished from *Acihasta* Forster 1948 by the absence of flanking spines on the opisthosoma. It is distinguished from *Monoscutum* by the enlarged chelicerae in the male, and from *Monoscutum* and *Templar* Taylor 2008a by the ornamentation being spinose setae rather than sclerotised nodules, the much smaller pedipalp patellar apophysis, the absence of bristle groups on the left side of the penis, the glans of the penis being deep rather than attenuated, and the enlarged stylus wing.

**Description.** Dorsum evenly ornamented with short spinose setae set on small nodules. Orange-brown or reddish-brown stripe between anterior margin of prosoma and ocularium; remainder of anterior propeltidium dull gold, forming two stripes between ocularium and anterior margin. Ocularium low with eyes angled outwards and lower margins flush with dorsal prosomal plate, bearing spinose setae. Remainder of dorsal prosomal plate orange- or grey-brown with dull gold spots or mottling. Mesopeltidium not distinct from propeltidium. Raised ridge along posterior margin of dorsal prosomal plate, narrower medially behind ocularium, broadening



**FIGURE 45.** Records of distribution for *Australiscutum* species: square = *A. hunti*; circle = *A. graciliforceps*; triangle = *A. triplodaemon*.

and becoming less distinct laterally. Ozopores visible from above, protruding with spinose flanking lobes, flanking lobes and margin of ozopores dull golden. Distinct spinose lobes on lateral shelves above either side of leg III. Metapeltidium distinctly separate from dorsal prosomal plate, more or less distinctly so from opisthosoma. Metapeltidium and first three segments of opisthosoma with broad light median stripe flanked by much darker stripes, laterally lighter. Mouthparts cream; coxae brown with dull gold distal margins. Chelicerae enlarged in males, segment II may or

may not be significantly inflated. Cheliceral segment I dorsally denticulate with ventrolateral and ventromedial denticle rows present or absent, segment II evenly denticulate. Pedipalp femur, patella and tibia each dark brown proximally, yellow-brown distally; tarsus yellow-brown; black setae on pedipalp distomedially denser on patella and tibia. Small rounded patellar apophysis may or may not be present; if present, at most barely extending beyond patella-tibia junction. Claw with ventral tooth-comb. Legs banded or patched brown and dull gold; spinose setae on all trochanters to tibiae; trochanters unarmed except spinose setae. Leg I femur to tibia distinctly inflated relative to other legs. Tibiae II and IV undivided. Metatarsus with larger diameter than remainder of tarsus. Penis with tendon long, muscles attached to proximalmost part of shaft only. Bristle-groups absent on left side of shaft-glans junction, two well-developed bristle groups on right side. Glans short, deep, triangular in dorsal view. Stylus relatively large, with well-developed wing.

**Etymology.** From the Latin *australis*, southern (indicating Australia), and *scutum*, shield, by comparison with *Monoscutum*. Gender neuter.

**Distribution** (fig. 45). Southeast Queensland and northeast New South Wales.

**Comments.** Separate measurements for right and left chelicerae are given for males of each species; a single set of cheliceral measurements is given for females. The three species of *Australiscutum* described herein are very similar in external appearance, even sharing more or less the same dorsal colour pattern. Females of *A. hunti* can be distinguished from females of the other two species by the colour pattern on the genital operculum, but females of *A. graciliforceps* and *A. triplodaemon* cannot be distinguished from each other. Therefore, females of the latter two species are treated conjointly below as ‘*Australiscutum* female type A’. *Australiscutum hunti* is also distinguished from the other two species by such features as the less heavily sclerotised dorsal prosomal plate, less developed armature in front of the ocularium, and less developed pedipalp apophysis in the male, suggesting that it may be the most distantly related of the three species. *Australiscutum graciliforceps* and *A. triplodaemon*, in contrast, are almost identical save for the male chelicerae, which provide the only reliable means of distinguishing the two species.

The possibility cannot be excluded that the forms described here as ‘*A. graciliforceps*’ and ‘*A. triplodaemon*’ do not represent distinct species, but dimorphs

of a single species. They are indistinguishable in all characters other than the chelicerae, the females of the two species cannot be distinguished from among specimens of '*Australiscutum* female type A', and they have overlapping ranges (fig. 44), to the extent that males of both species have been collected in association (AMS KS62234). Male dimorphism has been recorded in a number of species of Opiliones (Forster 1954, Suzuki 1973, Hunt 1981), including other species of Monoscutidae (Taylor 2004). However, if *A. graciliforceps* and *A. triplodaemon* do represent dimorphs of the one species, the pattern of dimorphism exhibited would be unique within the Opiliones. The conservative approach is therefore to treat them as separate species until their relationship can be more closely examined.

Colour descriptions for the species below are taken from those specimens that retain the most contrast in their colour patterns. Other specimens within each species may show less distinct colour patterns—this may reflect individual variation, or it may be due to loss of coloration in alcohol.

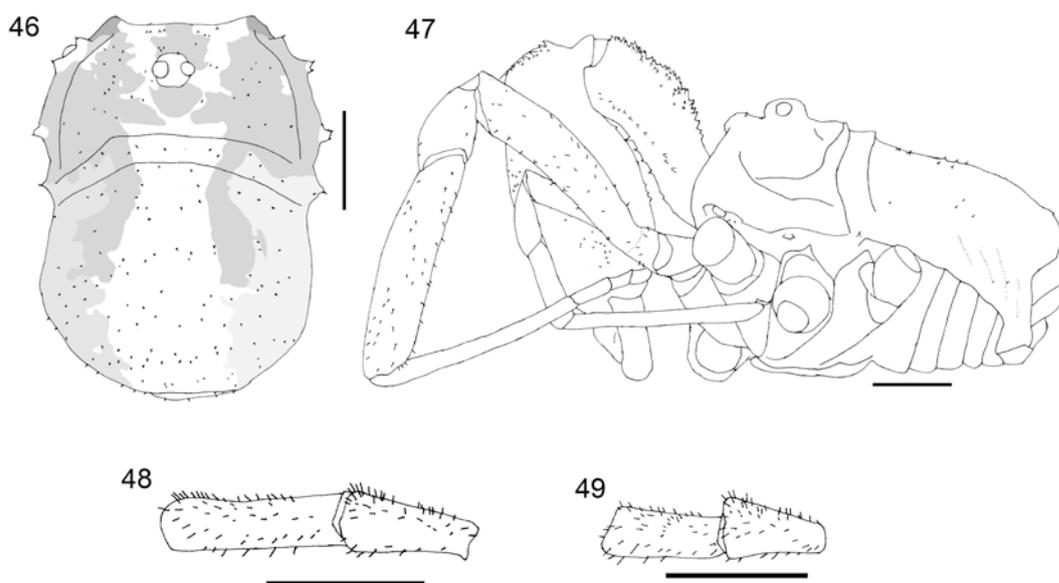
#### ***Australiscutum hunti* new species**

(Figs 17, 46–50a, 51–53)

*Australiscutum hunti* Taylor, 2009b: 324–327, figs 2–6a, 7–9.

**Material examined.** *Male holotype.* Dingo Ck, via Traveston, south-east Queensland, 26°18'S 152°48'E, 30[?] m, 1974–1975, G. B. & S. R. Monteith (QM S74226; measured).

*Paratypes.* 1 male, Bar Mountain, Wiangaree State Forest, New South Wales, 28°23'S 153°06'E, 1977–1978, G. B. Monteith, pitfall, rainforest (QM S1651; measured); 4 females, McPherson Range, New South Wales, 28°22'S 152°45'E, 500–600m, 16 February 1989, Smith, Hines, Pugh & Webber, pitfall, wet sclerophyll forest, Mt Warning Caldera Survey, UNE (AMS KS57171); 1 female, Repeater Station, Springbrook, south-east Queensland, 28°15'S 153°16'E, 1000m, 22 March–25 May 1975, G. B. & S. R. Monteith, pitfall, rainforest (QM S1646; measured); 1 male, ditto, 26 October–14 December 1974, G. B. & S. R. Monteith, pitfall, rainforest (QM S1647; measured); 1 female, ditto, 14 December 1974–22 March 1975, G. B. Monteith (QM S1648); 2 males, 2 females, ditto, 14 December 1974–22 March 1975, G. B. & S. R. Monteith, pitfall, rainforest (QM S1649; both males measured); 2 females, ditto, 2 December 1991–1 January 1992, D. J. Cook, pitfall,



**FIGURES 46–49.** *Australiscutum hunti*. 46. Male, dorsal view of body (QM S1647). 47. Male, lateral view of body, showing chelicera, pedipalp and leg I (QM S1651). 48. Patella and tibia of left male pedipalp, dorsal view (QM S1651). 49. Patella and tibia of left female pedipalp, dorsal view (QM S1645). Scale bars equal 1 mm.

rainforest (QM S25017); 2 females, ditto, 19 February–6 April 1995, G. B. Monteith, pitfall (QM S74232; both measured); 2 females, ditto, 9 January–19 February 1995, G. B. Monteith, intercept traps (QM S74323; both measured); 2 males, 1 female, ditto, 28°14'S 153°16'E, 1000 m, 31 October–31 December 1997, G. Monteith, pitfall, rainforest (QM S74326; both males measured); 1 female, Tweed Lookout, Wiangaree State Forest, via Kyogle, New South Wales, 27 December 1974–23 March 1975, G. B. & S. R. Monteith, pitfall, rainforest (QM S1645); 2 females, Tweed Range, New South Wales, 28°28'S 153°08'E, 1000–12000m, 17 February 1989, Smith, Hines, Pugh & Webber, pitfall, subtropical rainforest, Mt Warning Caldera Survey, UNE (AMS KS57734); 1 male, locality unknown (QM S74320; measured).

**Diagnosis.** Both males and females of *Australiscutum hunti* can be distinguished from the other two species of *Australiscutum* by the reversed colour pattern on the genital operculum. Males of *A. hunti* are also readily distinguished from males of the other species by the distinct form of the chelicera.

**Description.** MALE (figs 46–48, 50a, 51–53; N = 8). Body length 4.23 (0.35); prosoma length 1.68 (0.13), width 2.89 (0.73). Dorsum little sclerotised; evenly ornamented by short, spinose setae seated on small nodules. Small denticles

on median section of anterior margin of prosoma in front of ocularium. Medial part of prosoma between anterior margin and ocularium light reddish grey-brown, remainder of anterior propeltidium golden-cream, forming two broad stripes between ocularium and anterior margin. Anterior corners of prosoma black, unarmed. Ocularium low with eyes angled outwards and lower margins flush with dorsal prosomal plate, golden cream, with few spinose setae. Remainder of dorsal prosomal plate and lateral shelves reddish grey-brown with dull golden spots at bases of spinose setae, and two mottled dull golden stripes extending from either side of ocularium and converging to median point on posterior margin of dorsal prosomal plate. No distinct postocularium. Mesopeltidium indistinct from propeltidium. Raised ridge along posterior margin of dorsal prosomal plate, very narrow medially behind ocularium, broadening and becoming less distinct laterally. Ozopores visible from above, protruding with spinose flanking lobes, flanking lobes and margin of ozopores dull golden. Distinct spinose lobes on lateral shelves above either side of leg III. Metapeltidium distinctly separate from dorsal prosomal plate, less distinctly so from opisthosoma. Metapeltidium and first three segments of opisthosoma with broad median golden-cream stripe bordered with broad patches of reddish grey-brown, lightening to grey-brown laterally. Posterior part of opisthosoma golden-cream mottled with reddish grey-brown patches laterally. Mouthparts cream, coxae mottled reddish grey-brown with scattered cream patching and white-gold distal margins; medial dorsodistal spine on coxae I-III short, blunt. Genital operculum dark reddish grey-brown laterally, lighter grey-brown medially. Remainder of venter of opisthosoma grey-brown.

*Chelicerae* (fig. 50a). Segment I left 2.40 (0.22), right 2.39 (0.18); segment II left 3.88 (0.29), right 3.94 (0.33). Segment II greatly inflated, both segments robust with scattered black setae. Segment I dull gold dorsally, dark reddish-brown ventrally; densely covered with denticles dorsally, ventrally unarmed except dorsomedial and dorsolateral rows of denticles. Segment II mottled reddish-gold dorsally with dull golden patch above fingers, dark reddish-brown ventrally; densely covered with denticles. Cheliceral fingers reddish-brown with black margins; short, stout. Immobile finger straight with large blunt proximal tooth and distal serrula; mobile finger sickle-shaped with small pyramidal tooth opposite tooth on immobile finger and serrula along curved distal part, closes to leave space between mobile and immobile fingers.

*Pedipalps.* Femur 1.85 (0.16), patella 0.91 (0.04), tibia 1.08 (0.09), tarsus 2.28 (0.16). Proximal two-thirds of femur reddish black, distal third dull gold; patella mottled grey-brown with dorsolateral dull gold streak, distal margin white; tibia mottled grey-brown proximally, white distally; tarsus light grey-cream. Patella distally triangular, but no distinct apophysis; tibia straight (fig. 48). Setae black, denser distomedially on patella and tibia; aciculate ornamentation along entire tarsus. Claw with ventral tooth-comb.

*Legs.* Femora 2.85 (0.20), 5.14 (0.32), 2.29 (0.16), 3.59 (0.22); patellae 1.11 (0.05), 1.61 (0.11), 1.00 (0.06), 1.15 (0.06); tibiae 2.58 (0.17), 4.64 (0.33), 2.09 (0.15), 2.85 (0.20). All trochanters to tibiae bearing spinose setae. Trochanters grey-brown with white distal margins; unarmed. Femora mottled orange-brown to reddish-brown with white-gold patches. Patellae and tibiae with mottled orange-brown to black patches on gold-white background. Tarsi cream with small dorsal black patch below distal edge of metatarsus. Leg I femur to tibia distinctly inflated in comparison to other legs. Tibiae II and IV undivided. Metatarsi with slightly broader diameter than remainder of tarsi.

*Penis* (figs 51–53). Tendon long, muscles attached to proximalmost part of shaft only. Bristle-groups absent on left side of shaft-glans junction, two well-developed bristle groups on right side. Glans short, deep, triangular in dorsal view. Stylus relatively large, with well-developed wing.

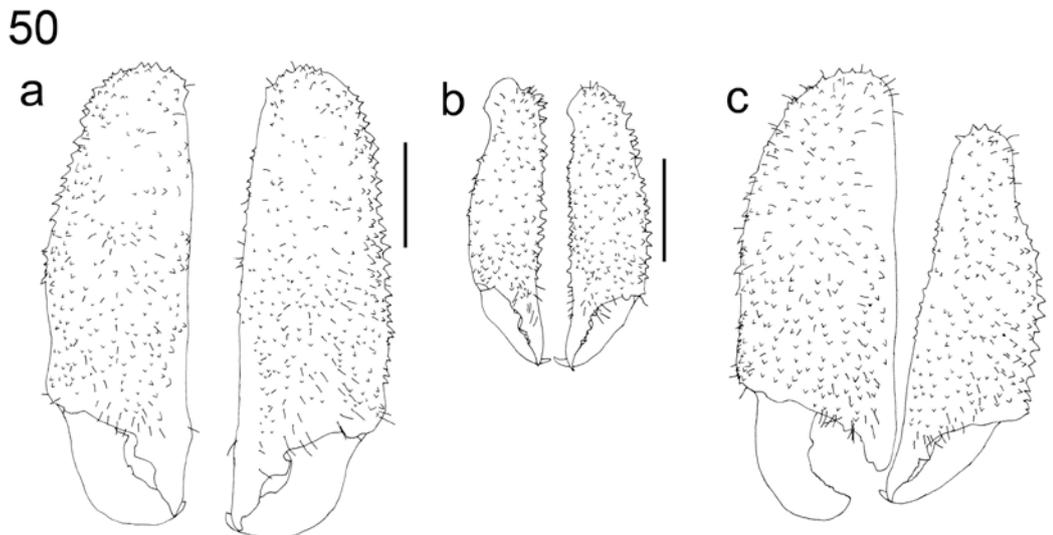
FEMALE (N = 5). As above, except for following. Body length 4.93 (0.43); prosoma length 1.72 (0.11), width 2.93 (0.13). No denticles on anterior margin of prosoma.

*Chelicerae:* Segment I 0.86 (0.07), segment II 1.80 (0.04). Smaller than in male; unarmed. Segment II not inflated, mobile finger crescent-shaped and closes tightly with immobile finger.

*Pedipalps:* Femur 1.22 (0.07), patella 0.62 (0.03), tibia 0.70 (0.05), tarsus 1.52 (0.04). Patella with small rounded apophysis, barely protruding past patella-tibia junction (fig. 49).

*Legs:* Femora 1.88 (0.14), 4.11 (0.16), 1.78 (0.13), 2.91 (0.14); patellae 0.89 (0.06), 1.36 (0.21), 0.83 (0.04), 0.97 (0.05); tibiae 1.79 (0.09), 3.76 (0.10), 1.58 (0.09), 2.34 (0.13).

**Etymology.** After the late Glenn Hunt, the most recent significant worker on Australian Opiliones.



**FIGURE 50.** Male chelicerae of *Australiscutum* species, frontal view: (a) *A. hunti* (QM S1647); (b) *A. graciliforceps* (QM S1653); (c) *A. triplodaemon* (AMS KS62234). Scale bars equal 1 mm.

***Australiscutum graciliforceps* new species**

(Figs 10, 50b, 54–55)

*Australiscutum graciliforceps* Taylor, 2009b: 327-329, figs 6b, 10–11.

**Material examined.** *Male holotype.* Nothofagus, New England National Park, New South Wales, 30°30'S 152°23'E, 1400m, G. B. Monteith, 11 November 1980–16 March 1981, pitfall, rainforest (QM S1653; measured).

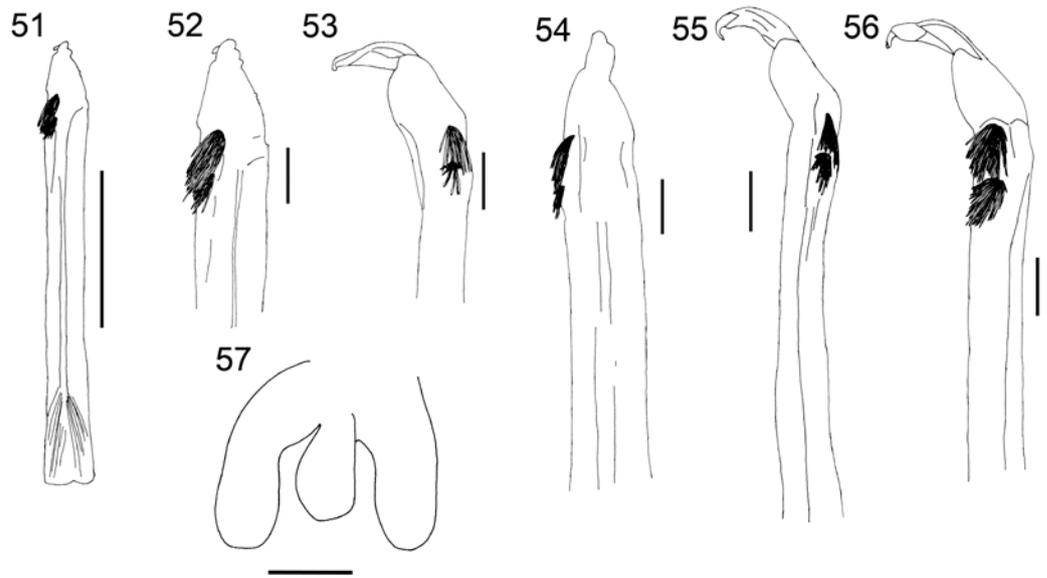
*Paratypes.* 2 males, Christophersons Mountain, 2 km SSW of Bostobrick, New South Wales, 30°17'45"S 152°37'04"E, 9–23 November 1999, M. Gray, G. Milledge & H. Smith, pitfall (AMS KS62234); Sirazleki State Forest, 10 April 1978, collector unknown (AMS KS10639; measured); 6 males, 0.4 km S along Barrington Trail from southern Green Gap turnoff, Stewarts Brook State Forest, New South Wales, 31°56'S 151°26'E, 1460m, 4 Feb–9 Apr 1993, M. Gray, G. Cassis (AMS KS42918; 5 males measured); 1 male, ditto (AMS KS90936); 2 males, ditto (AMS KS95277; both males measured); 1 male, Tidbinbilla, New South Wales (AMS KS56253); 1 male, Wathingeroo, Boyd Plateau, New South Wales, 15 August 1972, G. S. Hunt (AMS KS56240); 1 male, ditto, 22 September 1972, G. S. Hunt (AMS KS56244); 1 male, locality unknown, January 1985 (AMS KS56254).

**Diagnosis.** *Australiscutum graciliforceps* can be distinguished from *A. hunti* by the reversed colour pattern on the genital operculum and the distinct form of the

chelicerae. It can only be distinguished from *A. triplodaemon* by the form of the chelicerae.

**Description.** MALE (N = 9). Body length 3.49 (0.70); prosoma length 1.33 (0.11), width 2.32 (0.20). Dorsum evenly ornamented with short spinose setae on small nodules, dorsal prosomal plate sclerotised and ornately rugose. Denticles on medial part of anterior margin of prosoma in front of ocularium. Median part of prosoma between anterior margin and ocularium orange-brown. Remainder of anterior propeltidium dull golden, forming two stripes between ocularium and anterior margin. Anterior corners of prosoma black, unarmed. Ocularium low with eyes angled outwards and lower margins flush with dorsal prosomal plate, dark grey longitudinally streaked with dull gold, bearing spinose setae. Remainder of dorsal prosomal plate and lateral shelves orange-brown with dull golden spots. Mesopeltidium not distinct from propeltidium. Slightly raised ridge along posterior margin of dorsal prosomal plate, narrower behind ocularium, becoming broader and less distinct laterally. Ozopores protruding laterally with spinose flanking lobes, lobes and margin of ozopores dull gold. Lateral shelves with spinose lobes above either side of leg III. Metapeltidium distinctly separate from both dorsal prosomal plate and opisthosoma. Metapeltidium and first three segments of opisthosoma with broad median mottled orange-brown and dull gold stripe, bordered by broad dark reddish-brown stripes; laterally orange-brown with dull gold spots. Remainder of opisthosoma mottled dull gold and orange-brown. Mouthparts cream; coxae orange-brown with dull gold distal margins. Dorsodistal spines on coxae I–III short, blunt. Genital operculum white-gold laterally, orange-brown medially. Remainder of venter of opisthosoma grey with white spots.

*Chelicerae* (fig. 50b). Segment I left 1.13 (0.17), right 1.20 (0.15); segment II left 2.03 (0.25), right 2.06 (0.19). Segment I slender, segment II only slightly inflated compared to segment I; scattered setae on both segments not very prominent. Segment I light orange dorsally with dull gold band around lateral and distal margins, dark orange-brown ventrally; heavily covered with denticles dorsally, ventrally unarmed except enlarged ventrolateral and smaller ventromedial rows of denticles. Segment II mottled dull gold and orange dorsally, dark orange-brown ventrally, distally dull gold above fingers; evenly denticulate both dorsally and ventrally. Fingers dull gold shading to orange distally; mobile finger crescent-shaped, closing tightly against immobile finger.



**FIGURES 51–57.** Genitalia of *Australiscutum* species. 51. *Australiscutum hunti*, penis, ventral view (QM S74226). 52. *Australiscutum hunti*, close-up of glans, ventral view (ditto). 53. *Australiscutum hunti*, glans, lateral view (ditto). 54. *Australiscutum graciliforceps*, penis, ventral view (AMS KS10639). 55. *Australiscutum graciliforceps*, penis, lateral view (ditto). 56. *Australiscutum triplodaemon*, penis, lateral view (AMS KS62234). 57. *Australiscutum* female type A, seminal receptacles, dorsal view (AMS KS95274). Scale bars on figures 51 and 57 equal 0.5 mm; on figures 52–56 equal 0.1 mm.

*Pedipalps.* Femur 1.01 (0.11), patella 0.53 (0.05), tibia 0.59 (0.07), tarsus 1.22 (0.11). Femur, patella and tibia each proximally orange-brown, distally dull yellow-brown; tarsus yellow-brown. Small rounded patellar apophysis, barely protruding past patella-tibia junction; tibia very slightly curved mediad. Setae black, denser on patellar apophysis and distomedially on tibia; ventral setae on femur raised on nodules; aciculate ornamentation restricted to distal third of tarsus. Claw with ventral tooth-comb.

*Legs.* Femora 1.69 (0.20), 2.89 (0.30), 1.40 (0.14), 2.31 (0.17); patellae 0.73 (0.06), 1.10 (0.10), 0.67 (0.07), 0.85 (0.07); tibiae 1.45 (0.16), 2.59 (0.26), 1.27 (0.08), 1.86 (0.12). All trochanters to tibiae bearing spinose setae. Trochanters orange with dull gold distal margins; unarmed but with strong spinose setae in place of denticles anteriorly and posteriorly. Femora orange-brown banded with dull gold; patellae and tibiae mottled orange-brown and dull gold; tarsi yellow-brown. Leg I femur to tibia distinctly inflated in comparison to other legs. Tibiae II and IV undivided. Metatarsi with slightly broader diameter than remainder of tarsi.

*Penis* (figs 54–55). Tendon long, muscles attached to proximalmost part of shaft only. Bristle-groups absent on left side of shaft-glans junction, two well-developed bristle groups on right side. Glans short, deep, triangular in dorsal view. Stylus relatively large, with well-developed wing.

**Etymology.** From the Latin *gracilis*, slender, and *forceps*, tweezers, reflecting the slender cheliceral fingers in contrast to those of *Australiscutum hunti*.

### ***Australiscutum triplodaemon* new species**

(Figs 50c, 56)

*Australiscutum triplodaemon* Taylor, 2009b: 329-330, figs 6c, 12.

**Material examined.** *Male holotype.* Christophersons Mountain, 2km SSW of Bostobrick, New South Wales, 30°17'45"S 152°37'04"E, 9–23 November 1999, M. Gray, G. Milledge & H. Smith, pitfall (AMS KS62234).

*Paratypes.* 1 male, ditto (AMS KS62234); 1 male, Boyd Plateau, New South Wales, 21 July 1970, G. S. Hunt (AMS KS56239); 1 male, Mt Edwards, Boyd Plateau, New South Wales, 24 October 1971, G. S. Hunt, under log (AMS KS56242); 1 male, Petroi Trail & Forest Camp, Lower Creek State Forest, New South Wales, 30°41'S 152°17'E, 800–900 m, 19–20 December 1998, D. Bickel, yellow pans, wet sclerophyll/rainforest (AMS KS56257); 2 males, locality unknown (AMS KS23139); 1 male, locality unknown (AMS KS23140); 1 male, locality unknown, October 1980 (AMS KS23141).

**Diagnosis.** *Australiscutum triplodaemon* can be distinguished from *A. hunti* by the reversed colour pattern on the genital operculum and the distinct form of the chelicerae. It can only be distinguished from *A. graciliforceps* by the form of the chelicerae.

**Description.** MALE (N = 9). Body length 4.07 (0.47); prosoma length 1.67 (0.16), width 3.16 (0.26). Dorsum evenly ornamented with short spinose setae on small nodules, dorsal prosomal plate sclerotised and ornately rugose. Denticles on medial part of anterior margin of prosoma in front of ocularium. Light orange-brown median stripe between anterior margin and ocularium bearing two black longitudinal stripes, bordered by dark orange-brown stripes. Remainder of anterior propeltidium dull golden, forming two stripes between ocularium and anterior margin. Anterior corners of prosoma black, unarmed. Ocularium low with eyes angled outwards and

lower margins flush with dorsal prosomal plate, white anteriorly and retrolaterally, dark orange-brown mediolaterally, with black margins around eyes, bearing spinose setae. Dorsal prosomal plate posterior to ocularium medially orange-brown with dark brown markings, remainder of dorsal prosomal plate and lateral shelves yellow grey-brown with dull gold and black patches. Mesopeltidium not distinct from propeltidium. Slightly raised ridge along posterior margin of dorsal prosomal plate, narrower behind ocularium, becoming broader and less distinct laterally. Ozopores protruding laterally with spinose flanking lobes, lobes and margin of ozopores dull gold. Lateral shelves with dull gold spinose lobes above either side of leg III. Metapeltidium distinctly separate from both dorsal prosomal plate and opisthosoma. Metapeltidium and first three segments of opisthosoma with broad median mottled yellow grey-brown and dull gold stripe, bordered by broad dark reddish-brown stripes; laterally yellow grey-brown with gold spots. Remainder of opisthosoma medially mottled dull gold and yellow grey-brown, laterally white-gold. Mouthparts cream; coxae orange-brown with dull gold distal margins. Dorsodistal spines on coxae I-III short, blunt. Genital operculum white-gold laterally, dark grey-brown medially. Remainder of venter of opisthosoma dark grey-brown with white spots.

*Chelicerae* (fig. 50c). Segment I left 2.02 (0.20), right 2.11 (0.31); segment II left 3.30 (0.32), right 3.56 (0.44). Segment I slender, left segment II only slightly inflated, right segment II greatly inflated and slightly longer than left segment II; scattered black setae on both segments. Segment I light orange dorsally with dull gold band around lateral and distal margins, slightly darker; heavily covered with denticles dorsally, ventrally unarmed except ventrolateral and ventromedial rows of large denticles. Both segments II with small dull gold patch dorsoproximally; left segment II dark reddish-brown dorsally, reddish-black ventrally; right segment II lighter than left, orange, spotted with dull gold dorsally and black both dorsally and ventrally; both sides evenly denticulate dorsally and ventrally. Fingers dark orange-brown, left fingers slender, right fingers more robust; left chelicera with mobile finger angular crescent-shaped, closing tightly against immobile finger; right chelicera with mobile finger crescent-shaped, closing to leave distinct gap between fingers, immobile finger reduced.

*Pedipalps*. Femur 1.56 (0.19), patella 0.75 (0.08), tibia 0.88 (0.10), tarsus 1.89 (0.20). Femur, patella and tibia each proximally orange-brown, distally yellow-brown; tarsus yellow-brown. Small round apophysis not protruding past patella-tibia

junction, slightly more developed on left pedipalp than on right; tibia very slightly curved mediad. Setae black, distomedially denser on patella and tibia; ventral setae on femur raised on nodules; aciculate ornamentation on distal two-thirds of tarsus. Claw with ventral tooth-comb.

*Legs.* Femora 2.48 (0.21), 4.07 (0.45), 1.88 (0.27), 2.99 (0.36); patellae 1.05 (0.10), 1.44 (0.17), 0.88 (0.11), 1.07 (0.09); tibiae 2.19 (0.26), 3.58 (0.35), 1.72 (0.19), 2.40 (0.25). All trochanters to tibiae bearing spinose setae. Trochanters orange with dull gold distal margins; unarmed but with strong spinose setae in place of denticles anteriorly and posteriorly. Femora dark orange-brown banded with dull gold; patellae and tibiae patched with orange-brown and dull gold; tarsi yellow-brown with dull gold patches. Leg I femur to tibia distinctly inflated in comparison to other legs. Tibiae II and IV undivided. Basitarsus with slightly broader diameter than distitarsus.

*Penis* (fig. 56). Tendon long, muscles attached to proximalmost part of shaft only. Bristle-groups absent on left side of shaft-glans junction, two well-developed bristle groups on right side. Glans short, deep, triangular in dorsal view. Stylus relatively large, with well-developed wing.

**Etymology.** After the Triple Demons of Compromise from Norton Juster's book *The Phantom Tollbooth*, in reference to the distinctive asymmetrical chelicerae of this species in comparison to the other two species in the genus. The Triple Demons included one member who was short and fat, one who was tall and thin, and one who looked exactly like the other two.

**Comments.** This species appears to represent the first recorded instance of asymmetrical chelicerae among the Opiliones, and the second among the Arachnida as a whole. Delle Cave (1979) described asymmetrical chelicerae in *Galeodes barbarus* (Solifugae), but the difference was not the size of the chelicerae, but the presence (left) or absence (right) of a flagellum. Asymmetrical pedipalps are present in the spider *Metagonia mariguitarensis* (González-Sponga 1998) (Pholcidae; Huber 2004), but the significantly different functions of spider pedipalps and harvestman chelicerae would mean that the two cases are probably not comparable. The best-known examples of asymmetrical chelae in arthropods are among the Decapoda, where they are found in numerous lineages. Observations of live specimens of *Australiscutum triplodaemon* have not yet been made, so the function of the asymmetrical chelae in this species is unknown. However, asymmetrical chelae in

decapods may reflect differential use of the two chelae while feeding or use in display (Govind & Blundon 1985; Mariappan *et al.* 2000). The absence of asymmetrical chelae in females assigned to 'Australiscutum female type A', which probably includes females of *A. triplodaemon*, indicates that, unless a significant difference in diet exists between males and females, a connection to reproductive behaviour is more likely (Lee 1995). The other two species of *Australiscutum* have chelicerae that are more or less symmetrical—specimens may occasionally show a slight difference in the size of the right and left chelicerae, but never to anywhere near the extent of *A. triplodaemon*, and they do not possess the distinction between the two sides in the shape of the cheliceral fingers.

### ***Australiscutum* female type A**

(Fig. 57)

**Material examined.** *Measured specimens.* 3 females, 0.4 km S along Barrington Trail from southern Green Gap turnoff, Stewarts Brook State Forest, New South Wales, 31°56S 151°26E, 1460m, 4 Feb–9 Apr 1993, M. Gray, G. Cassis (AMS KS42918).

*Illustrated specimen.* 1 female, Cliffs Trail (top end), New England National Park, New South Wales, 1350 m, 30°30'S 152°23'E, 4 Feb–9 Apr 1993, M. Gray, G. Cassis (AMS KS95274).

**Description.** FEMALE (N = 3). As for male of *Australiscutum graciliforceps* or *A. triplodaemon*, except for the following. Body length 4.49 (0.50); prosoma length 1.59 (0.06), width 2.49 (0.10).

*Chelicerae.* Segment I 0.59 (0.12), segment II 1.44 (0.07). Smaller than in male; unarmed. Segment II not inflated, mobile finger crescent-shaped and closes tightly with immobile finger.

*Pedipalps.* Femur 0.98 (0.02), patella 0.49 (0.02), tibia 0.56 (0.02), tarsus 1.19 (0.06). Patella with small rounded apophysis, barely protruding past patella-tibia junction.

*Legs.* Femora 1.63 (0.06), 2.97 (0.05), 1.44 (0.03), 2.38 (0.06); patellae 0.65 (0.03), 0.97 (0.01), 0.68 (0.05), 0.86 (0.02); tibiae 1.38 (0.04), 2.65 (0.06), 1.30 (0.04), 1.89 (0.01).

*Ovipositor* (fig. 57). Four sausage-shaped seminal receptacles of similar size to each other.

**Comments.** The specimens here referred to as ‘*Australiscutum* female type A’ represent the females of *A. graciliforceps* and/or *A. triplodaemon*. No character has been identified that would allow the distinction of females belonging to these two species, and as their ranges overlap, location is also insufficient.

### ***Forsteropsalis* new genus**

*Megalopsalis* Roewer 1923—Forster 1944: 184–185.

**Type species.** *Macropsalis chiltoni* Hogg 1910 by present designation.

**Other included species.** *Pantopsalis distincta* Forster 1964, *Macropsalis fabulosa* Phillipps & Grimmett 1932, *Pantopsalis grayi* Hogg 1920, *Megalopsalis inconstans* Forster 1944, *Megalopsalis marplei* Forster 1944, *Megalopsalis chiltoni nigra* Forster 1944, *Pantopsalis wattsi* Hogg 1920. *Megalopsalis turneri* Marples 1944 is probably also a member of this genus, but the published description is insufficient for its identification and its type specimen needs to be redescribed before its position can be established.

**Diagnosis.** *Forsteropsalis* can be distinguished from all other genera of Monoscutidae by the small pointed pedipalp patella apophysis present in both sexes except for females of *Forsteropsalis grimmetti* and males of *F. distincta*, and by the array of denticles on the medial side of the pedipalp coxa. It can be distinguished from *Megalopsalis* and *Spinicrus* by the more elongate, narrower glans on the penis. Females, including that of *F. grimmetti*, can be distinguished from *Megalopsalis* by possessing four rather than two seminal receptacles.

**Distribution.** New Zealand, including Auckland Island.

**Comments.** This genus contains the majority of the New Zealand species previously assigned to *Megalopsalis*. Characters listed as distinguishing *Pantopsalis* and ‘*Megalopsalis*’ in Taylor (2004) actually apply to *Pantopsalis* and *Forsteropsalis*, and those species transferred by Taylor (2004) to *Megalopsalis* on the basis of those characters are here transferred to *Forsteropsalis*.

This genus will be established in a forthcoming publication presenting the phylogenetic analysis of Enantiobuninae; however, it has not been included herein as the relevant descriptive work was not conducted as part of the current thesis project.

## ***Hypomegalopsalis* new genus**

**Type species.** *Hypomegalopsalis tanisphyros* new species by present designation.

**Diagnosis.** *Hypomegalopsalis* is distinguished from *Pantopsalis*, *Forsteropsalis*, *Spinicrus* and *Neopantopsalis* by the presence of a well-developed apophysis, longer than wide, on the pedipalp patella. It differs from *Monoscutum*, *Acihasta*, *Templar* and *Australiscutum* in having long, slender legs and from *Megalopsalis* in the lack of elongate chelicerae in the male. It differs from *Tercentenarium* in having a short glans that is triangular in ventral view.

**Description.** As for type and only known species.

**Etymology.** From the Greek prefix *hypo-*, less than, plus *Megalopsalis*, indicating the resemblance of this genus to *Megalopsalis*, albeit lacking sexual dimorphism. Gender feminine.

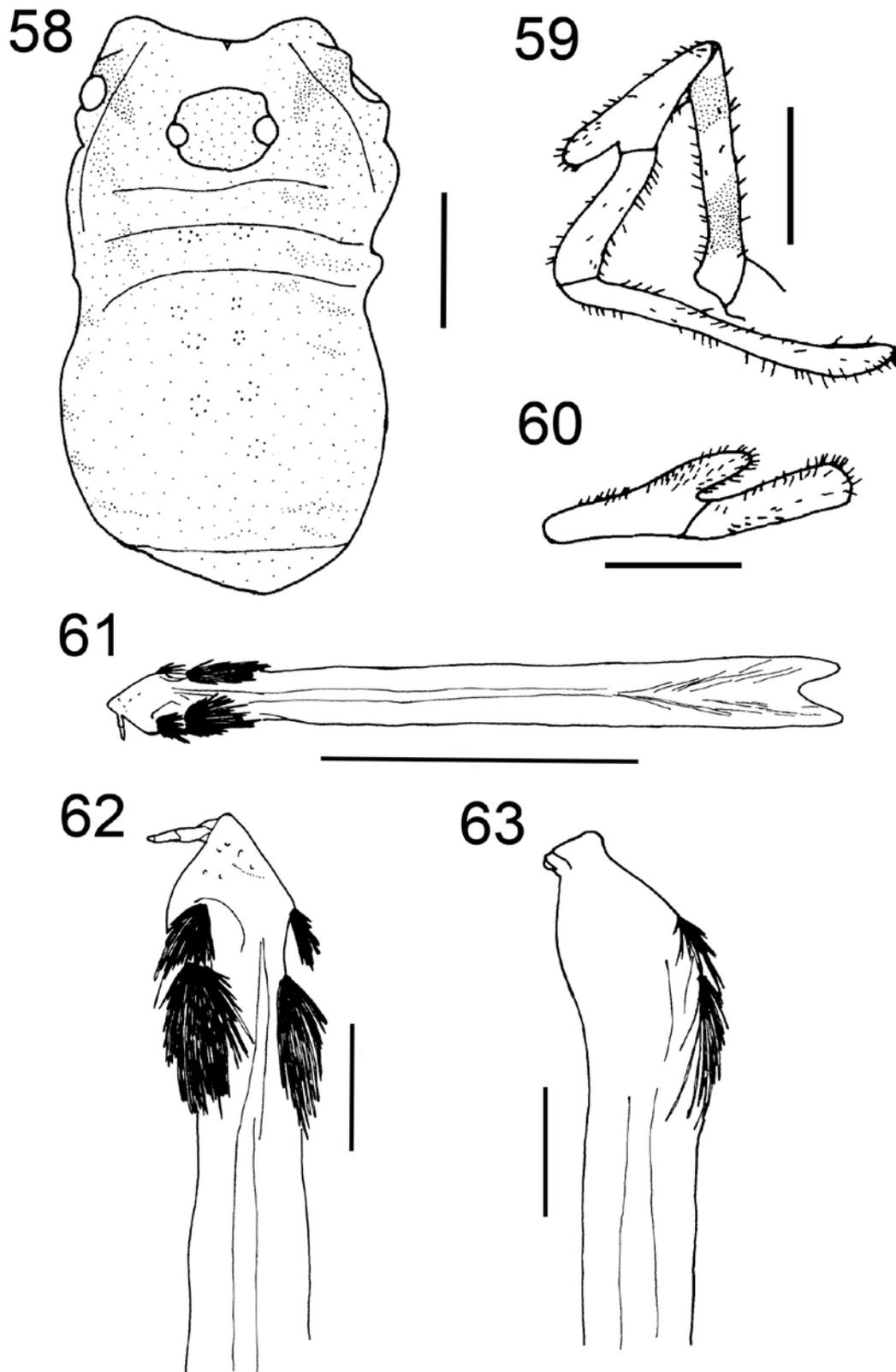
**Distribution** (fig. 87). Southwest Western Australia.

## ***Hypomegalopsalis tanisphyros* new species**

(Figs 33-34, 58-63).

**Material examined.** *Male holotype.* Cape Arid National Park, Mt Arid, south side nr summit, Western Australia, 33°57'45"S 123°13'01"E, 5 June 2007, M. L. Moir, M. C. Leng, under rock (WAM T80802; measured).

*Paratypes.* 1 male, Durokoppin Nature Reserve, Western Australia, 31°25'S 117°46'E, 23 June–4 August 1987, B. Y. Main, pitfall trap (WAM T42176); 1 male, Grasspatch, Western Australia, 33°14'S 121°43'E, 6 June 1989, A. F. Longbottom, on water tank, 'Clover Paddock' (WAM 90/1532); 1 male, Mt Cooke, Western Australia, 32°25'S 116°18'E, 18 September 1995, J. M. Waldock, Y. Konishi (WAM T71947; measured); 1 male, 2.5 km NE of Mt Lesueur, Western Australia, 30°10'S 115°12'E, 11 July 1989, K. Gaull *et al.*, wandoo woodland, leaf & twig litter (WAM 90/1680); 1 male, ditto, 16 July 1989, K. Gaull, under rocks (WAM 90/1682; measured); 1 male, ca. 4 km NNE of Mt Lesueur, Western Australia, 30°8'S 115°12'E, 9 July 1989, K. Gaull *et al.* (WAM 90/1675; measured); 1 male, Torndirrup National Park, Western Australia, 35°10'S 117°50'E, 6–13 July 1983, P. H. Dyer, J. Lyon, 4 yr burn, pitfall (WAM T72879; measured); 3 males, ditto, 13-20 July 1983, P. H. Dyer, J. Lyon, 4 yr burn, pitfall (WAM T72885; measured); 1 male,



**FIGURES 58–63.** *Hypomegalopsalis tanisphyros*, male (all WAM T80802). 58. Body, dorsal view. 59. Left pedipalp, retrolateral view. 60. Patella and tibia of right pedipalp, dorsal view. 61. Penis, ventral view. 62. Glans, ventral view. 63. Glans, dorsolateral view. Scale bars for figs 58–61 = 0.5 mm; figs 62–63 = 0.1 mm.

ditto, 27 July–3 August 1983, P. H. Dyer, J. Lyon, 17 year burn, pitfall (WAM T72881; measured); 1 male, ditto, 25 May–9 November 1983, P. H. Dyer, J. Lyon, pitfall trap (WAM 87/1287; measured).

**Description.** MALE (N = 9). Prosoma length 0.82 (0.10), width 1.30 (0.12); entire body length 2.27 (0.32). Anterior part of propeltidium white-tan, remainder of propeltidium and mesopeltidium light brown with iridescent silver patches; entire dorsum unarmed. Anterior corners of propeltidium silver; dark odoriferous glands readily visible through cuticle. Ocularium light brown, unarmed. Metapeltidium and opisthosoma mottled light brown medially, striped dark brown laterally, with pair of medial silver spots on each segment, tan punctures laterally. Venter white-tan with white spots on opisthosoma.

*Chelicerae.* Segment I 0.49 (0.07), segment II 1.06 (0.10). White-tan, dusted black shading dorsally on first segment; both segments unarmed with black setae. Cheliceral fingers medium length, slender; mobile finger crescent-shaped.

*Pedipalps* (figs 59–60). Femur 1.04 (0.16), patella 0.60 (0.11), tibia 0.72 (0.12), tarsus 1.30 (0.18). Femur banded white-tan and dusted black; patella, tarsus and tibia each proximally medium brown, distally light tan; entire pedipalp unarmed. Patella with long rounded apophysis, approximately half to two-thirds length of patella body (fig. 60); tibia with marked mediolateral swelling; medial side of patella and tibia densely setose. Microtrichia on distal half of tarsus; claw with ventral tooth-row.

*Legs.* Femora 2.65 (0.18), 4.75 (0.30), 2.55 (0.14), 4.48 (0.35); patellae 0.81 (0.05), 1.00 (0.09), 0.74 (0.05), 0.84 (0.07); tibiae 2.31 (0.11), 4.35 (0.26), 1.80 (0.14), 2.87 (0.21). All segments, including trochanters, tan, unarmed. Tibia II with four or five pseudosegments; distitarsus II without ventral swellings. Tibia IV undivided; tarsi III and IV not proximally broadened.

*Penis* (figs 61–63). Shaft elongate with long tendon. Well-developed bristle groups. Glans short, triangular in ventral view, distally dorsoventrally flattened; dorsal side of glans evenly convex without dorsolateral keel. Pores deeply recessed.

*Spiracle* (figs 33–34). Anterior spines thick, widely spaced, mostly lacking reticulations; terminations simple or broadly palmate. Dense array of lace tubercles at lateral corner, with reticulations from lace tubercles extending across array of reticulate lobes on posterior margin of spiracle.

**Etymology.** From the Greek *tanisphyros*, slender-ankled, referring to the delicate, wispy appearance of this species.

**Comments.** The possibility could be raised that *Hypomegalopsalis tanisphyros* might represent the minor male of an unidentified *Megalopsalis* species, similar to the minor males previously recorded for *Spinicrus* and *Neopantopsalis* (Taylor & Hunt 2009). As yet, *H. tanisphyros* can be distinguished from all known *Megalopsalis* species by its distinctly smaller genitalia and distinct spiracle morphology. The genitalia do not differ noticeably in size between morphs of previously identified dimorphic species (unpublished personal observations). The reticulate posterior spiracle margin of *H. tanisphyros* is unique among Enantiobuninae observed to date.

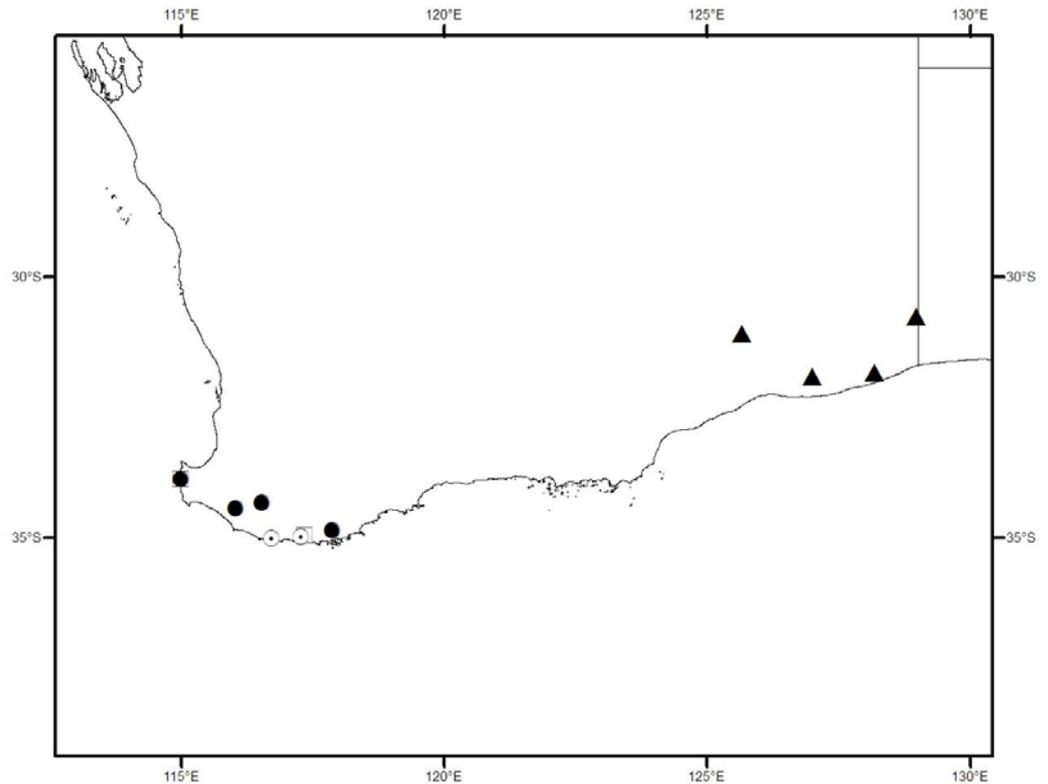
### ***Intutoportula* new genus**

**Type species.** *Spinicrus minimum* Kauri 1954 by present designation.

**Included species.** *Spinicrus porongorupense* Kauri 1954; *Intutoportula suffugiens* new species; *I. walpolensis* new species.

**Diagnosis.** *Intutoportula* is distinguished from *Megalopsalis*, *Hypomegalopsalis*, *Tercentenarium* and *Forsteropsalis* by the absence of an apophysis on the pedipalp patella. It is distinguished from *Scissorestis* by the presence of ozopore lobes and the simple, pointed terminations to the bristles on the penis. It is distinguished from *Pantopsalis*, *Neopantopsalis* and *Spinicrurellum* by its short and broad triangular glans. It differs from *Spinicruroides* in lacking setae on the mobile cheliceral finger, and from *Spinicrus* in lacking spines over the spiracle and brush-like bristles on distitarsi III and IV.

**Description.** Ozopores large, oblong. Dorsum of opisthosoma unarmed. Chelicerae denticulate; mobile finger crescent-shaped. Pedipalp patella shorter than tibia; no apophysis on patella; claw with ventral tooth-row. Femur I at least denticulate; distitarsus II without ventrodiscal bulges on pseudosegments; distitarsi III and IV not swollen proximally, without ventral brush-like bristles. Glans short, triangular in ventral view, not strongly flattened distally. Spiracle without covering spines (residual spine bases sometimes present); lace tubercles or lace-like reticulations in lateral corner.



**FIGURE 64.** Records of distribution for *Intutoportula* species in southern Western Australia: open square = *I. minima*; solid circle = *I. porongorupensis*; circle with dot = *I. walpolensis*; solid triangle = *I. suffugiens*.

**Etymology.** From the Latin words *intutus*, unguarded or defenseless, and *portula*, a small door, in reference to this genus' lack of covering spines over the spiracle.

**Distribution** (fig. 64). Southern Western Australia.

**Comments.** Unfortunately, the type specimens of *Spinicrus minimus* and *S. porongorupense* were not available for the present study. These species have been identified based on their original descriptions by Kauri (1954).

Females have been found in association with *Intutoportula minima*, *I. porongorupensis* and *I. walpolensis* (unpublished observations, specimens in WAM). However, as no distinct morphotypes have been distinguished among the likely *Intutoportula* females, though the ranges of these species overlap, it has not been possible as yet to determine which females are assignable to which species.

## Key to Species of *Intutoportula*

1. Dorsum of prosoma strongly denticulate...*Intutoportula minima*  
Dorsum of prosoma unarmed or with very few denticles...2
2. Legs unarmed or with sparse, relatively long and slender spines; body silvery...*Intutoportula suffugiens*  
Legs with numerous small denticles; opisthosoma with dark transverse stripes...3
3. Pedipalp with numerous denticles on femur and patella...*Intutoportula porongorupensis*  
Pedipalp unarmed...*Intutoportula walpolensis*

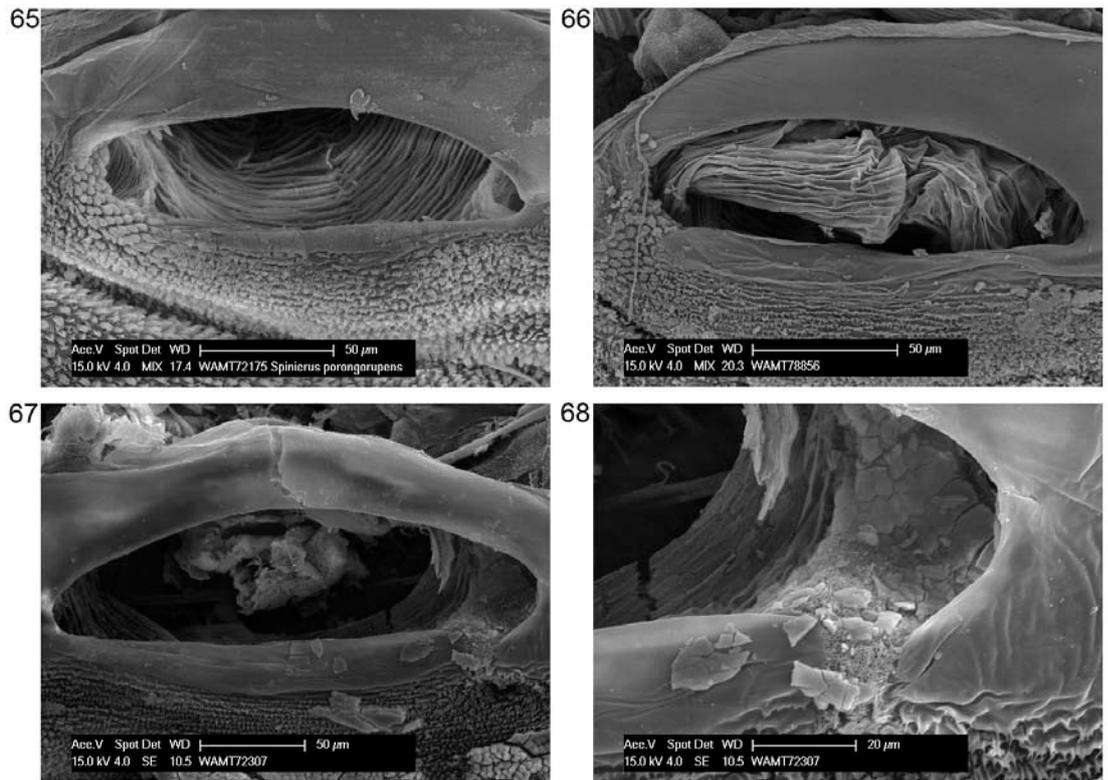
### *Intutoportula minima* (Kauri 1954) new combination

(Figs 27, 69–74)

*Spinicrus minimus* Kauri, 1954: 7–8, fig. 4a–b (incorrect original spelling).

*Spinicrus minimum* Kauri—Taylor, 2004: 76 (spelling therein emended by W. Starega).

**Material examined.** 1 minor male, Denmark, Western Australia, 34°57'S 117°21'E, 11 November 1990, A. F. Longbottom, under granite (WAM T72865); 3 minor males, Glenbourne farm, Old Ellensbrook Rd, S of Gracetown, Western Australia, 33°53'S 115°00'E, 27–28 October 1996, L. Marsh *et al.*, pitfall (WAM T72171, T72184 [2 measured]); 3 major males, ditto, 28–30 June 1997, L. Marsh *et al.*, dry pitfalls, base of cliff (WAM T72167–9; measured); 2 minor males, ditto, 13–15 September 1997, L. Marsh *et al.*, dry pitfall traps (WAM T72176 [measured], T72186); 1 minor male, ditto, 27–29 December 1997, L. Marsh *et al.*, dry pitfalls, site 3 (WAM T72160); 1 minor male, 33°54'28"S 115°00'49"E, 24–26 October 1998, L. Marsh *et al.*, dry pitfall traps (WAM T72172; measured); 2 minor males, ditto, 33°54'32"S 115°00'24"E, 24–26 October 1998, L. Marsh *et al.*, dry pitfall traps (WAM T72158); 2 minor males, ditto, 33°54'40"S 115°00'34"E, 30 October - 1 November 1999, L. Marsh *et al.*, dry pitfall traps (WAM T72144; 1 measured); 1 minor male, ditto, 20–22 October 2001, L. Marsh *et al.*, dry pitfall traps (WAM T72193; measured); 1 minor male, ditto, 33°55'08"S 115°00'44"E, 20–23 October 2000, L. Marsh *et al.*, dry pitfall traps (WAM T72187; measured).

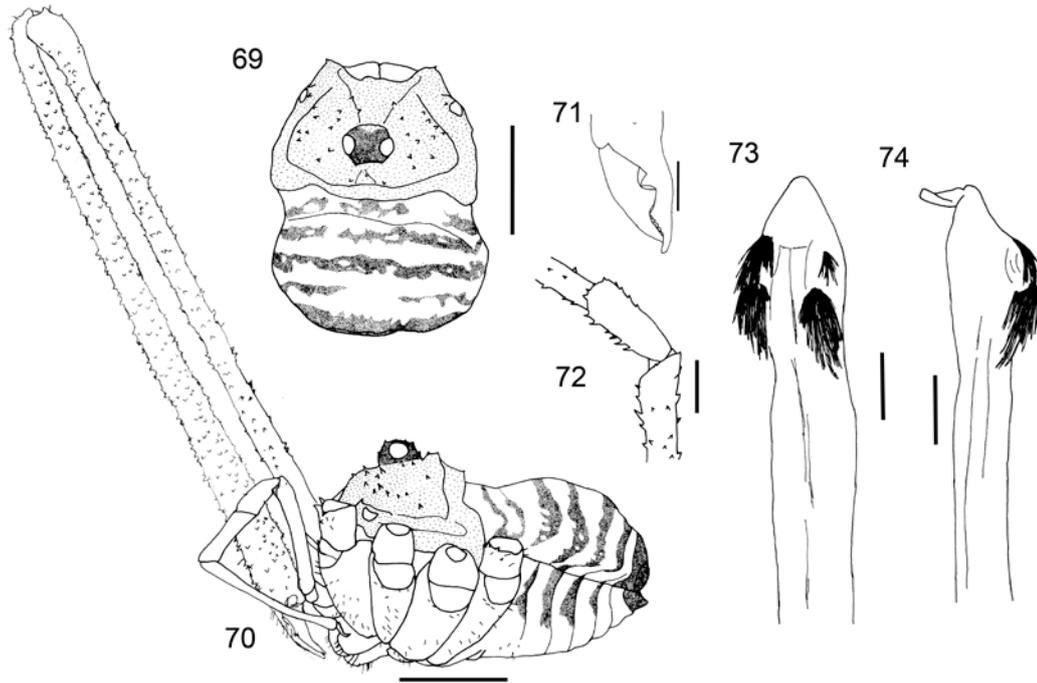


**FIGURES 65–68.** Spiracles of *Intutoportula* species. 65. *Intutoportula porongorupensis*. 66. *Intutoportula walpolensis*. 67. *Intutoportula suffugiens*. 68. Same, close-up of lateral corner showing area of reticulation.

**Diagnosis.** *Intutoportula minima* can be distinguished from other *Intutoportula* species by the heavier denticulation on the dorsal prosomal plate. The major males can also be distinguished from other species by the proportionately much longer chelicerae.

**Description.** MAJOR MALE (N = 3). Prosoma length 0.85 (0.06), width 1.86 (0.10); total body length 2.37 (0.27). Dorsal prosomal plate golden brown; median prosomal area strongly denticulate, fewer denticles on margins of anterior and posterior prosomal areas. Ocularium black with row of denticles along edge on each side. Ozopore large, lenticulate. Dorsum of opisthosoma with alternating tan and dark brown mottled with tan stripes, and scattered iridescent white patches. Coxae tan with medium brown distal ends; venter of opisthosoma dark brown medially; tan dusted with black laterally.

*Chelicerae.* Segment I 5.81 (1.03), segment II 6.83 (0.86). Chelicerae golden brown with second segment tan distad; evenly denticulate. Fingers long; mobile finger crescent-shaped (fig. 71).



**FIGURES 69–74.** *Intutoportula minima*, major male (all WAM T72169). 69. Body, dorsal view. 70. Body, lateral view, showing chelicera and pedipalp. 71. Right cheliceral fingers, frontal view. 72. Femur to tibia of right leg I, prolateral view. 73. Glans, ventral view. 74. Glans, dorsolateral view. Scale bars for figs 69–70 = 1 mm; fig. 71 = 0.25 mm; fig. 72 = 0.5 mm; figs 73–74 = 0.1 mm.

*Pedipalps.* Femur 0.96 (0.04), patella 0.44 (0.02), tibia 0.55 (0.03), tarsus 1.23 (0.08). Alternating tan and brown bands; femur without denticles. Femur to proximal part of tibia with longitudinal rows of large setae, distal tibia and tarsus with large setae interspersed among small setae. Inner dorsal distal patella with swelling but no distinct apophysis. Microtrichia on distal end of tibia and tarsus; claw with ventral tooth-row.

*Legs.* Femora 4.27 (0.37), 7.51 (0.50), 3.72 (0.24), 5.75 (0.31); patellae 0.87 (0.09), 0.96 (0.08), 0.81 (0.07), 0.95 (0.04); tibiae 3.96 (0.31), 8.15 (0.50), 3.67 (0.21), 5.79 (0.37). Femora with strong denticles. Patella I with two longitudinal rows of spines, one on each side; rows continue on tibia, dwindling distalwards (fig. 72). Patellae of other legs only lightly denticulate; tibiae smooth. Tibia II with 7–9 pseudosegments, tibia IV with two pseudosegments.

*Penis* (figs 73–74). Tendon long; waist in shaft behind bristle groups; left anterior bristle group reduced. Glans short, triangular in ventral view, not strongly flattened distally; dorsal side in line with shaft, evenly convex. Deep pores.

*Spiracle* (fig. 27). Spines almost entirely absent, residual reticulate bases only towards lateral corner; dense field of lace tubercles at lateral corner.

MINOR MALE (N = 7). Prosoma length 0.73 (0.06), width 1.82 (0.11); total body length 1.83 (0.30). As above, except for following.

*Chelicerae*. Segment I 0.96 (0.57), segment II 1.68 (0.63).

*Pedipalps*. Femur 0.84 (0.04), patella 0.37 (0.02), tibia 0.48 (0.04), tarsus 1.05 (0.11).

*Legs*. Femora 3.48 (0.22), 6.57 (0.23), 3.34 (0.18), 4.79 (0.18); patellae 0.72 (0.05), 0.83 (0.06), 0.72 (0.05), 0.83 (0.05); tibiae 3.46 (0.26), 7.02 (0.33), 3.26 (0.14), 4.74 (0.32). Patella I lightly denticulate, without longitudinal spine rows.

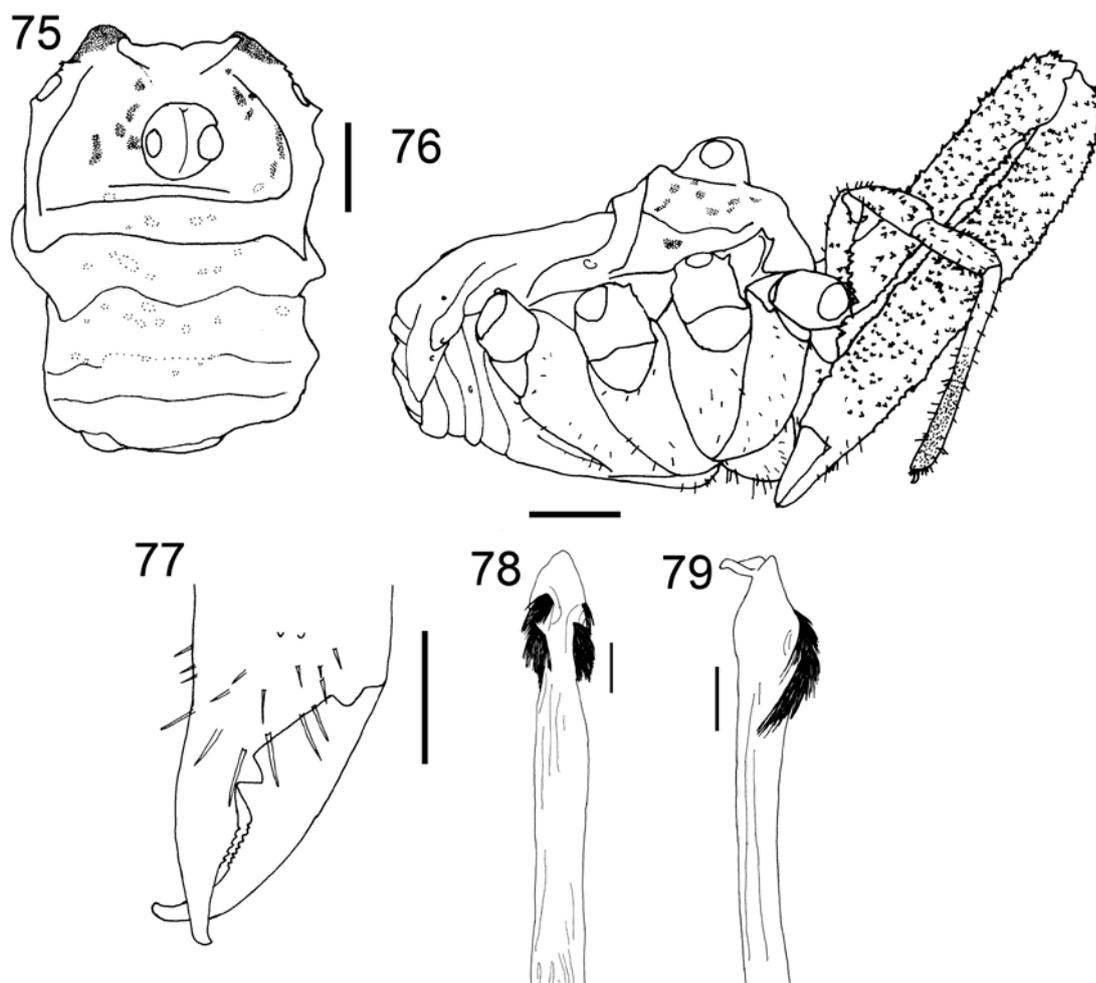
### ***Intutoportula porongorupensis* (Kauri 1954) new combination**

(Figs 65, 75–79)

*Spinicrus porongorupensis* Kauri, 1954:8–9, fig. 4c (incorrect original spelling).

*Spinicrus porongorupense* Kauri—Taylor, 2004: 76 (spelling therein emended by W. Starega).

**Material examined.** 5 males, Glenbourne, Old Ellensbrook Road, S of Gracetown, Western Australia, 33°53'S 115°00'E, 27–28 October 1996, L. Marsh *et al.*, pitfalls (WAM T72175 [2 measured]; T72184 [1 measured]); 2 males, ditto, 27–29 December 1997, L. Marsh *et al.*, dry pitfalls (WAM T72152-3; measured); 1 male, ditto, 33°54'50"S 115°00'57"E, 24–26 October 1998, L. Marsh *et al.*, dry pitfall traps (WAM T72161; measured); 1 male, ditto, 33°54'32"S 115°00'24"E, 20–23 October 2000, L. Marsh *et al.*, dry pitfall traps (WAM T72200); 1 male, ditto, 33°54'40"S 115°00'34"E, 24–26 October 1998, L. Marsh *et al.*, dry pitfall traps (WAM T72173); 1 male, ditto, 25–27 October 2003, L. Marsh *et al.*, dry pitfall traps (WAM T72198; measured); 1 male, ditto, 33°54'35"S 115°00'15"E, 30 October - 1 November 1999, L. Marsh *et al.*, dry pitfall traps (WAM T72155; measured); 3 males, ditto, 33°54'50"S 115°00'57"E, 30 October–1 November 1999, L. Marsh *et al.*, dry pitfall traps (WAM T72143; 2 measured); 1 male, Pemberton, Crowea Block, Western Australia, 240 m, 17 December 1976, S. J. Curry, pitfall trap (WAM 90/1319); 2 males, ditto, 24 October 1977, S. J. Curry, ridge site, pitfall traps (WAM 90/1321-2); 1 male, ditto, 31 October 1977, S. J. Curry, ridge site, pitfall trap (WAM 90/1335); 1 male, ditto, 11 November 1977, S. J. Curry, ridge site, pitfall trap (WAM 90/1326); 1



**FIGURES 75–79.** *Intutoportula porongorupensis*, male. 75. Body, dorsal view (WAM T72155). 76. Body, lateral view, showing chelicera and pedipalp (WAM T72161). 77. Left cheliceral fingers, frontal view (WAM T72175). 78. Penis, ventral view (WAM T72175). 79. Penis, dorsolateral view (WAM T72175). Scale bars for figs 75–76 = 0.5 mm; fig. 77 = 0.25 mm; figs 78–79 = 0.1 mm.

male, Porongurup Range, Western Australia, 20 January 1932, E. W. Bennett (WAM 32/217); 1 male, Porongurup National Park, Porongurups, Western Australia, 34°40'55.8"S 117°51'58.6"E, 570 m, 13 June 1996, S. Barrett, wet pitfalls (WAM T72214); 3 males, Mordalup Road, Unicup, Western Australia, 34°19'01"S 116°31'49"E, 15 Oct 1999–31 Oct 2000, P. van Heurck, wet pitfalls (WAM T73035).

**Diagnosis.** *Intutoportula porongorupensis* is distinguishable from other *Intutoportula* species by the presence of denticulation on the pedipalp.

**Description.** MALE (N = 10). Prosoma length 0.81 (0.08), width 1.55 (0.13); total body length 1.94 (0.22). Dorsal prosomal plate including ocularium tan with dark mottling; unarmed. Ozopore large. Dorsum of opisthosoma tan with iridescent white spots and broad white median stripe.

*Chelicerae*. Segment I 1.35 (0.52), segment II 2.04 (0.66). Tan; heavily and uniformly denticulate. Cheliceral fingers medium length; mobile finger crescent-shaped (fig. 77).

*Pedipalps*. Femur 0.83 (0.07), patella 0.38 (0.04), tibia 0.45 (0.03), tarsus 1.05 (0.06). Tan. Femur and patella heavily denticulate, few scattered large setae only; tibia lightly denticulate proximally. Inner dorsal distal patella slightly bulging but no distinct apophysis. Microtrichia on distal part of tibia and tarsus; claw with ventral tooth row.

*Legs*. Femora 3.46 (0.27), 6.68 (0.45), 3.24 (0.19), 5.20 (0.36); patellae 0.73 (0.06), 0.84 (0.09), 0.66 (0.08), 0.80 (0.11); tibiae 3.16 (0.19), 7.12 (0.52), 3.03 (0.18), 4.78 (0.46).

*Penis* (fig. 78–79). Glans short, dorsal edge in line with shaft; stylus at 90° to glans and shaft. Left anterior bristle group reduced; waist in shaft behind bristle groups. Deep pores.

*Spiracle* (fig. 65). Spines almost entirely absent, residual reticulate bases only towards lateral corner; dense field of lace tubercles at lateral corner.

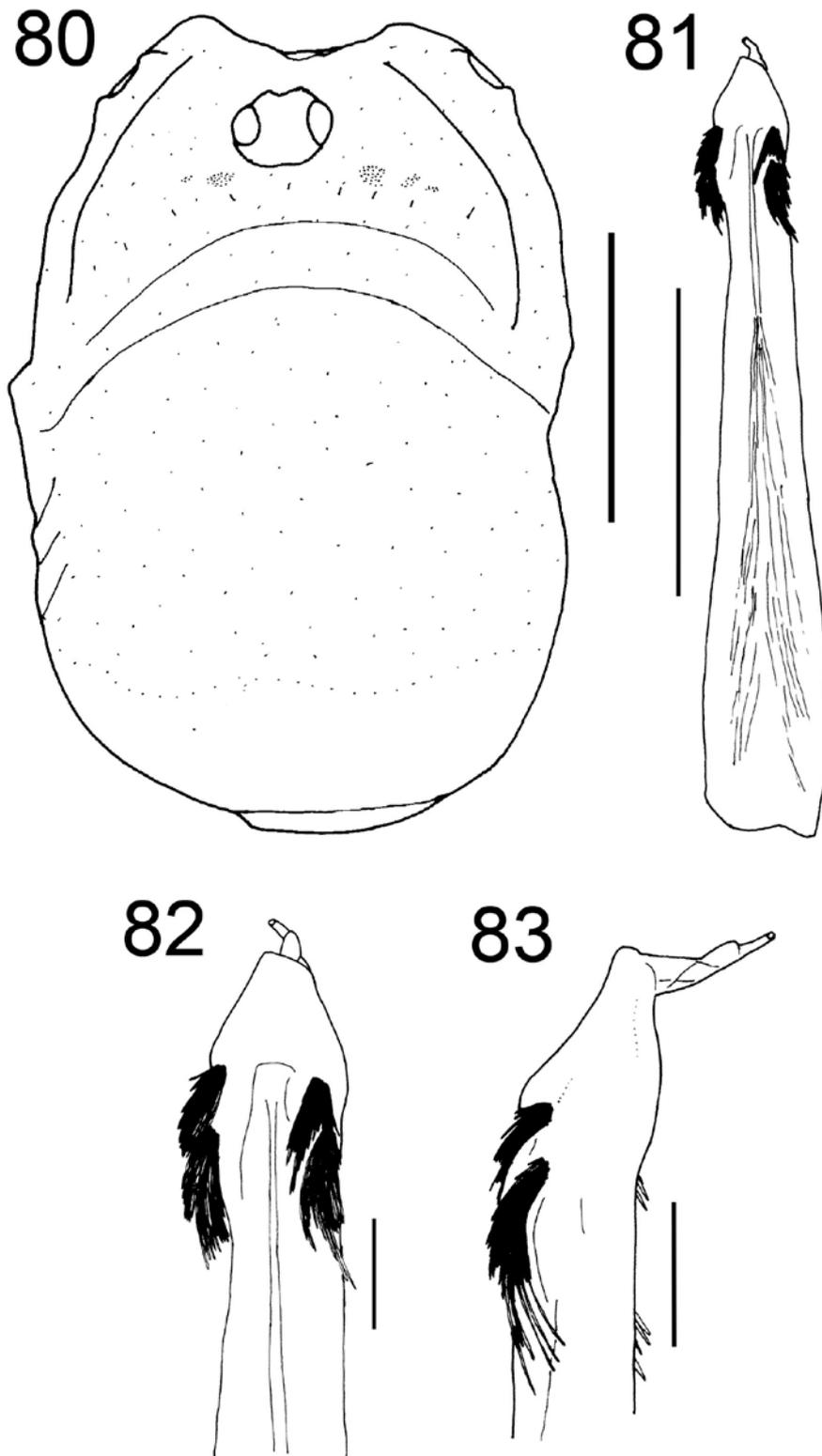
**Comments.** This species shows a relatively large degree of difference in cheliceral size between the largest and smallest individuals, but there is no clear clustering into a larger and a smaller morph.

### ***Intutoportula suffugiens* new species**

(Figs 67–68, 80–83)

**Material examined.** *Male holotype*. Balgair Station, cave 6N-612, Western Australia, 14 September 1999, N. Poulter, from ceiling adjacent to cave entrance (WAM T72303).

*Paratypes*. 1 male, Balgair Station, cave 6N-1536, Western Australia, 13 September 1999, N. Poulter, walking on damp earth floor (WAM T72299); 1 male, ditto, c. 11 m below cave entrance (WAM T72307); 1 female, Balgair Station, cave 6N-1616, Western Australia, 15 September 1999, P. Devine, N. Poulter, rockhole cave (WAM T72287); 2 males, 1 female, Hampton Tableland, Mundrabilla Station, cave 6N-326, 22 September 1999, P. Devine, N. Poulter, from cave walls in dark zone, largest [female] from entrance lip at night fall (WAM T72298); 1 female, Madura Plains



**FIGURES 80–83.** *Intutoportula suffugiens*, male (all WAM T72299). 80. Body, dorsal view. 81. Penis, ventral view. 82. Glans, ventral view. 83. Glans, lateral view. Scale bar for fig. 80 = 1 mm; fig. 81 = 0.5 mm; figs 82–83 = 0.1 mm.

Station (=Moonera Station), cave 6N-1617, 17 September 1999, R. Anderson, N. Poulter, from cave ceiling in dark zone (WAM T72305); 1 female, Nullarbor area, cave 6N-481, 1 October 1994, R. Foulds, from roof of entrance squeeze (WAM T72141).

**Diagnosis.** *Intutoportula suffugiens* is readily distinguished from other species of *Intutoportula* by its pale coloration without dark transverse bands on the opisthosoma. The spines on the legs (if present) are also proportionately longer and more slender than those found in other species. It can also be distinguished from *I. minima* by the lack of denticles on the ocularium and median propeltidial area and from *I. porongorupensis* by the lack of denticles on the pedipalps.

**Description.** MALE (figs 80–83; N = 5). Prosoma length 0.75 (0.06), width 1.69 (0.13); total body length 2.21 (0.10). Dorsal prosomal plate unarmed (Balgair Station specimens) or with few denticles on anterior propeltidial area (Hampton Tableland specimens); patched tan and iridescent white with scattered darker mottling. Mesopeltidium with distinct transverse row of black setae. Metapeltidium and anterior part of opisthosoma mottled tan and silver. Posterior part of opisthosoma silver with transverse bands of dark brown mottling.

*Chelicerae.* Segment I 1.47 (0.65), segment II 2.44 (0.73). Both segments tan; lightly denticulate with reduced denticulation distad on both segments. Segment II slightly inflated distad. Cheliceral fingers long, slender; mobile finger crescent-shaped.

*Pedipalps.* Femur 1.01 (0.09), patella 0.51 (0.02), tibia 0.57 (0.04), tarsus 1.27 (0.05). White with tan patches and black setae; femur with longitudinal rows of setae; patella and tibia with black setae laterally and medially, midline glabrous; no apophysis. Microtrichia over greater part of tarsus and tibia; claw with ventral tooth row.

*Legs.* Femora 3.83 (0.46), 7.14 (0.71), 3.10 (0.31), 4.94 (0.62); patellae 0.90 (0.06), 1.05 (0.07), 0.85 (0.06), 0.99 (0.08); tibiae 3.71 (0.31), 7.42 (0.55), 3.57 (0.45), 4.91 (0.62). Trochanters iridescent white; unarmed or with single anterior spine on trochanters I and III. Legs tan; femur I with sparse, slender spines, reduced to only a few dorsally in some specimens; femur II unarmed or with few spines near base; remaining segments unarmed. Femora and patellae with scattered black setae; tibiae and tarsi densely covered in small setae. Tibia II with 11 to 13 pseudosegments; tibia IV with two or three pseudosegments.

*Penis* (figs 81–83). Shaft broad, tendon relatively short; bristle groups well-developed. Glans short, broad, triangular in dorsal view; in line with shaft; dorsal side evenly convex; not significantly flattened distally. Pores shallowly recessed.

*Spiracle* (figs 67–68). No occluding spines; lace tubercles at lateral corner reduced to patch of reticulation.

FEMALE (N = 4). Prosoma length 1.16 (0.38), width 2.13 (0.16); total body length 3.83 (0.42). As for male, except for following: Dorsum unarmed.

*Chelicerae*. Segment I 0.75 (0.07), segment II 1.58 (0.03). Unarmed.

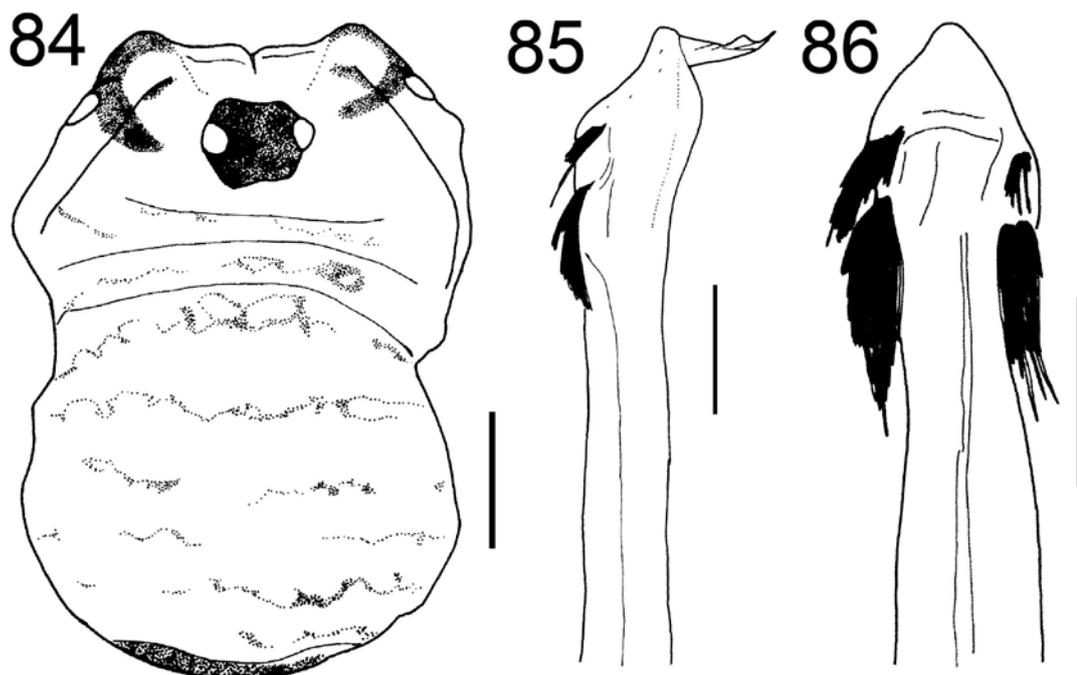
*Pedipalps*. Femur 1.31 (0.03), patella 0.68 (0.03), tibia 0.78 (0.04), tarsus 1.65 (0.02). Patella and tibia more densely setose medially than male.

*Legs*: Femora 4.68 (0.23), 9.28 (0.70), 4.01 (0.25), 5.95 (0.24); patellae 1.18 (0.07), 1.42 (0.10), 1.11 (0.07), 1.19 (0.05); tibiae 4.79 (0.13), 9.77 (0.56), 4.44 (0.15), 6.05 (0.18). Femora and patellae with longitudinal rows of small spines.

**Variation.** Males show a noticeable variation in the size of the chelicerae that correlates with the development of armature on the legs; however, the variation is not as large as that found in *Intutoportula minima*, and it is uncertain at present whether variation is continuous or a distinction occurs between major and minor males. Further specimens are also required to establish whether the difference in dorsal armature recorded above between Balgair Station and Hampton Tableland specimens indicate separate populations in these localities.

**Etymology.** From the Latin *suffugio*, to take shelter, to reflect the finding of specimens of this species within caves in the arid Nullarbor.

**Comments.** All specimens of *Intutoportula suffugiens* recorded to date were collected in caves; however, *I. suffugiens* does not show any obvious troglobitic adaptations. The eyes remain well-developed and the legs are proportionately only slightly longer than in other *Intutoportula* species. It seems more likely that *I. suffugiens* only uses the caves as damp refugia during the day, emerging at night to feed. This suggestion is supported by the collection of at least one specimen (WAM T72298) from a cave entrance at nightfall.



**FIGURES 84-86.** *Intutoportula walpolensis*, male (all WAM T78848). 84. Body, dorsal view. 85. Penis, lateral view. 86. Penis, ventral view. Scale bar for fig. 84 = 0.5 mm; figs 85-86 = 0.1 mm.

***Intutoportula walpolensis* new species**

(Figs 66, 84–86)

**Material examined.** *Male holotype.* Walpole-Nornalup National Park, Knoll Drive, Walpole, Western Australia, 34°59'43"S 116°43'12"E, 29 October 2006, M. L. Moir, A. Sampey (WAM T78848).

*Paratype.* 1 male, Mt Shadforth, Western Australia, 34°58'04"S 117°16'47"E, 6 November 2006, M. L. Moir, D. Jolly, in leaf litter (WAM T78856).

**Diagnosis.** The features of *Intutoportula walpolensis* appear intermediate between those of *I. minima* and *I. porongorupensis*. It differs from *I. minima* in lacking significant denticulation on the ocularium and propeltidium and from *I. porongorupensis* in lacking denticles on the pedipalps.

**Description.** MALE (N = 2). Prosoma length 0.65 (0.13), width 1.44 (0.13); total body length 2.22 (0.12). Anterior propeltidial area cream, remainder of propeltidium golden-brown with mottled black patches on anterior corners of dorsal prosomal plate and lateral shelves. Prosoma mostly unarmed, except few small scattered denticles on lateral edge of dorsal prosomal plate near odoriferous glands. Odoriferous glands visible as black patches through cuticle. Ocularium dark golden-brown, with row of small low denticles around each eye. Mesopeltidium,

metapeltidium and opisthosoma with transverse band of mottled black across golden-brown background of each segment, broken by tan or iridescent white spots. Coxae cream with mottled purple patches at distal ends; venter of opisthosoma cream dusted with purple, condensing to more solid patches laterally.

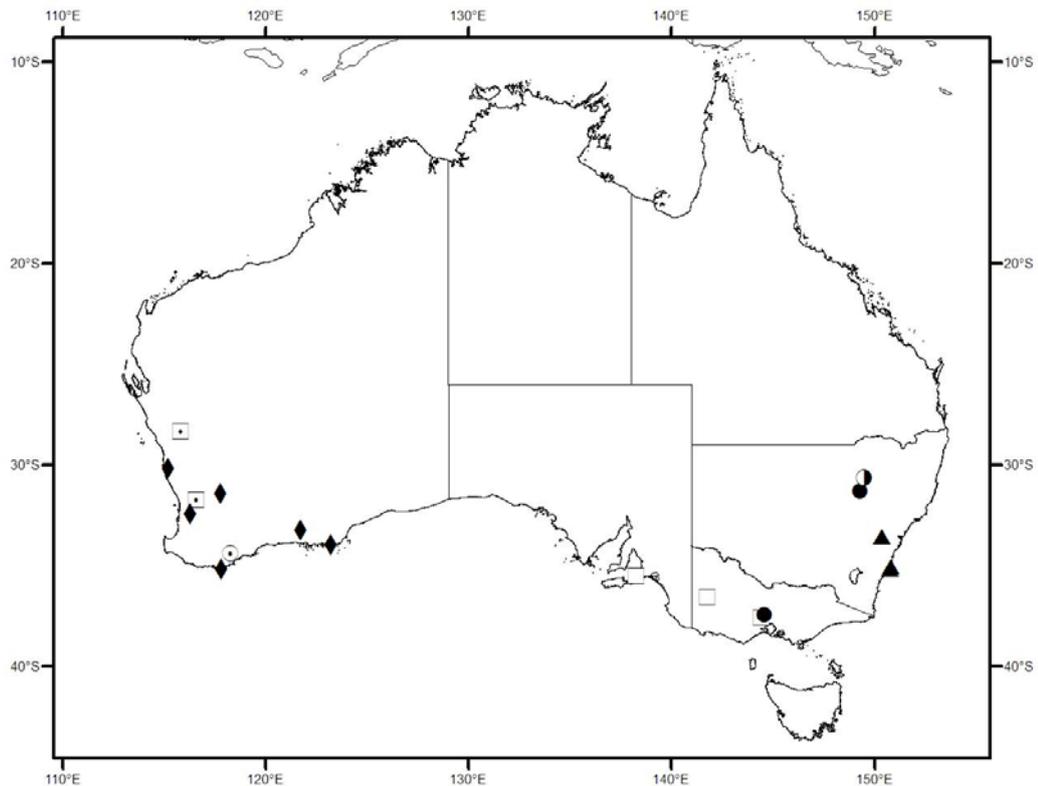
*Chelicerae*. Segment I 0.73 (0.08), segment II 1.42 (0.24). Segment I mottled purple on cream background with purple mottling more solid laterally than medially; scattered denticles dorsally. Segment II cream, mottled with purple proximally, densely denticulate proximally with denticles thinning until distal third is unarmed. Cheliceral fingers short, lateral margin evenly rounded.

*Pedipalps*. Femur 0.90 (0.01), patella 0.42 (0.03), tibia 0.50 (0.03), tarsus 1.11 (0.05). Cream banded with purple, with cream stripe down dorsal midline; unarmed. No patellar apophysis; black setae denser on medial side of patella but not hypersetose. Microtrichia on tarsus, except for proximal third, and distalmost end of tibia. Tooth-comb on claw.

*Legs*. Femora 3.48 (0.06), 6.20 (0.06), 3.33 (0.01), 5.05 (0.09); patellae 0.81 (0.04), 1.05 (0.02), 0.82 (0.01), 0.95 (0.00); tibiae 3.42 (0.03), 6.95 (0.02), 3.16 (0.04), 4.90 (0.08). Trochanters white-cream mottled with purple, unarmed. Femora golden-brown proximally, with cream band beginning distad of halfway, followed by purple band, then cream distal end. Patellae dark cream dusted with black, tibiae and metatarsi banded cream and dusty black, tarsi cream. Femora and distal ends of patellae with broken rows of dorsal denticles, remaining segments unarmed. Tibia II with seven pseudosegments, tibia IV undivided.

*Penis* (figs 85–86). Left anterior bristle group somewhat reduced, remaining bristle groups well-developed. Glans short, broad, triangular in dorsal view; roughly in line with shaft; dorsal side evenly convex; not significantly flattened distally. Deep pores.

*Spiracle* (fig. 66). Spines entirely absent; dense patch of lace tubercles at lateral corner.



**FIGURE 87.** Records of distribution for *Megalopsalis* and *Hypomegalopsalis*: solid triangle = *Megalopsalis serritarsus*, solid circle = *M. hoggi*, half-filled circle = *M. pilliga*, open square = *M. eremiotis*, circle with dot = *M. epizephyros*, square with dot = *M. leptekes*, solid diamond = *Hypomegalopsalis tanisphyros*.

### ***Megalopsalis* Roewer 1923**

*Macropsalis* Sørensen 1886: 54–55 (junior homonym of *Macropsalis* Sclater 1866); Pocock 1903a: 398; Hogg 1910: 277; Roewer 1911: 102, 1912: 278.

*Megalopsalis* Roewer 1923: 866 (replacement name for *Macropsalis* Sørensen); Crawford 1992: 28, 29.

Not *Megalopsalis* Roewer—Forster 1944: 184–185 (= *Forsteropsalis* new genus).

**Type species.** *Macropsalis serritarsus* Sørensen 1886 by monotypy.

**Diagnosis.** *Megalopsalis* is distinguished from *Pantopsalis*, *Forsteropsalis*, *Spinicrus* and *Neopantopsalis* by the presence of a well-developed apophysis, longer than wide, on the pedipalp patella. It differs from *Monoscutum*, *Acihasta*, *Templar* and *Australiscutum* in having long, slender legs and from *Hypomegalopsalis* and

*Tercentenarium* in the presence of elongate chelicerae in the male. It also differs from *Tercentenarium* in having a short glans that is triangular in ventral view.

**Description.** MALE. Dorsal prosomal plate denticulate; remainder of dorsum unarmed. Chelicerae elongate, heavily denticulate; cheliceral fingers closing tightly against each other. Pedipalp patella with well-developed hypersetose mediobasal apophysis; claw with ventral tooth-comb. Trochanters I and II usually with prolateral spines (except *Megalopsalis leptekes*). Femora I and II denticulate, femur I usually particularly so; patella and tibia I often denticulate. Penis with elongate shaft and long tendon; well-developed bristle groups at shaft-glans junction. Glans short, triangular in ventral view, bent only slightly dorsad from glans; dorsal side evenly convex, no dorsolateral keel; distal end of glans dorsoventrally flattened. Pores on glans shallowly or deeply recessed without distinct rim. Spiracle with anterior grill of slender spines, often only extending partway across; spines often reticulate (except *M. leptekes*), with simple or palmate terminations; cluster of lace tubercles present at lateral corner; posterior margin of spiracle unornamented.

**Distribution** (fig. 87). Southern Western Australia, southern South Australia, Victoria, eastern New South Wales.

### Key to Species of *Megalopsalis*

1. Distitarsus II without ventral swellings on pseudosegments...2  
Distitarsus II with ventral swellings on pseudosegments...3
2. Pedipalp femur heavily spinose; distitarsi III and IV not inflated without ventral brush-like setae...*Megalopsalis leptekes*  
Pedipalp femur unarmed; distitarsi III and IV inflated proximally with ventral rows of brush-like setae...*Megalopsalis hoggi*
3. Femur II with ventral spines...4  
Femur II unarmed...*Megalopsalis pilliga*
4. Pedipalp femur with dorsal spines...*Megalopsalis epizephyros*  
Pedipalp femur unarmed or with ventral spines only...5
5. Spiracle spines relatively robust, lace tubercles short and forming more extensive field; pedipalp femur never spinose (New South Wales)...*Megalopsalis serritarsus*

Spiracle spines more slender, lace tubercles more elongate but less extensive; pedipalp femur may have ventral spines (Victoria, South Australia)...*Megalopsalis eremiotis*

***Megalopsalis serritarsus* Sørensen 1886**

(Figs 36–37, 40, 88–94)

*Macropsalis serritarsus* Sørensen 1886: 55–56, pl. 5. fig. 1; Roewer 1911: 103, 1912: 279, pl. 4 figs 22–23.

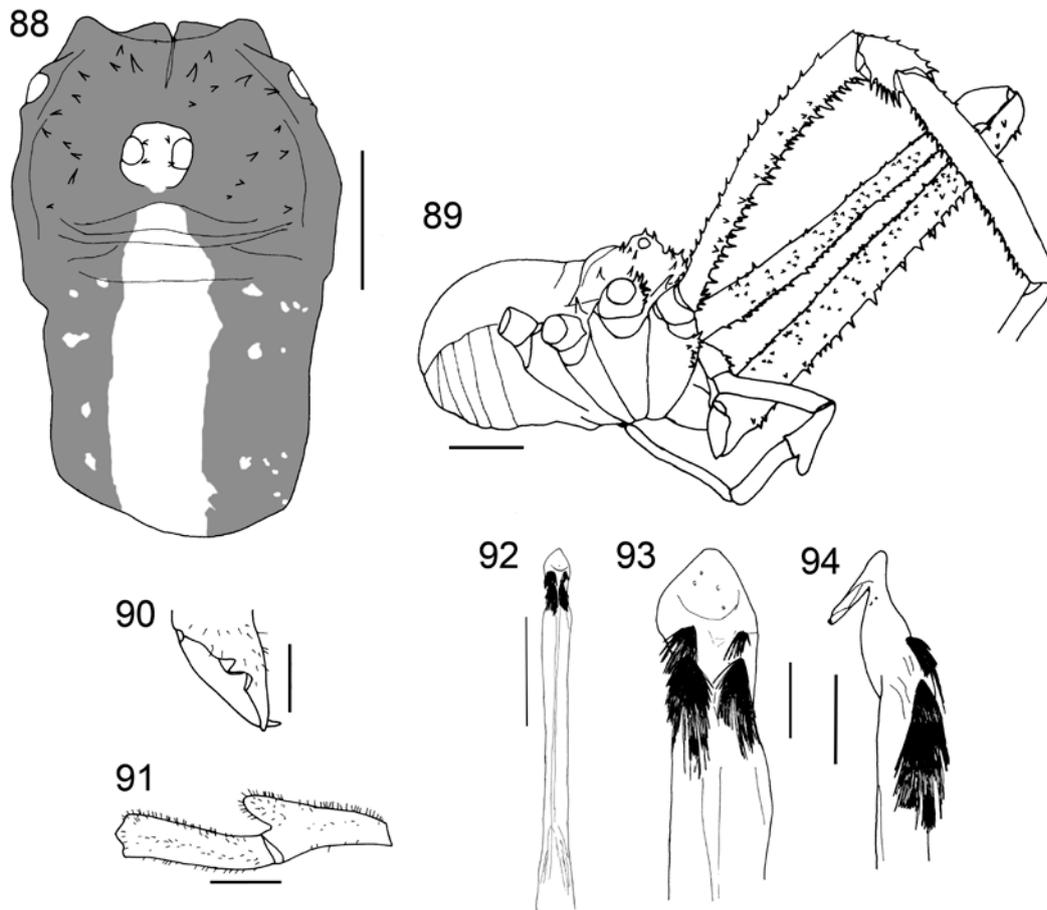
*Megalopsalis serritarsus* (Sørensen)—Roewer 1923: 867, fig. 1033, 1956: 267; Weidner 1959: 126; Hunt 1990: fig. 3d; Crawford 1992: 28 (by implication).

**Material examined.** *Male lectotype* (designated by Weidner 1959). Sydney, New South Wales (ZMH).

*Other material examined.* 1 male, 1 female, under rocks, Blackheath, Blue Mts, 6 June 1982, V. E. Davies (QM S2978); 1 male, Beecroft Peninsula, northern headland of Jervis Bay, New South Wales, 35°03'03"S 150°47'51"E, 11–15 August 1999, L. Gibson, pitfall traps (AMS KS63527); 1 male, Booderee National Park, southern headland of Jervis Bay, New South Wales, 35°08'49"S 150°45'05"E, 11–15 August 1999, L. Gibson, pitfall traps (AMS KS62923).

**Diagnosis.** *Megalopsalis serritarsus* can be distinguished from *M. leptekes* and *M. hoggi* by the presence of ventrodiscal bulges on the pseudosegments of distitarsus II, from *M. pilliga* by the presence of distinct armature on femur II, and from *M. epizephyros* by the lack of spines on the pedipalp femur. Distinguishing *M. serritarsus* from *M. eremiotis* for certain requires examination of the spiracle – *M. serritarsus* has less slender spines across the spiracle and the lace tubercles are shorter but more extensive. However, no specimens of *M. serritarsus* have been recorded with ventral spines on the pedipalp femur, as found in some specimens of *M. eremiotis*, and the two species have disjunct distributions.

**Description.** MALE (N = 3). Prosoma length 1.59 (0.17), width 2.07 (0.10), entire body length 3.49 (0.60). Dorsal prosomal plate and anterior half of lateral shelves mottled orange-brown with iridescent white reticulation on anterior propeltidium. Spines on anterior and posterior propeltidium, median propeltidium unarmed except few spines on lateral margin of dorsal prosomal plate. Ocularium white but with black eyes visible through cuticle. Ocularium spinose. Small



**FIGURES 88–94.** *Megalopsalis serritarsus*, male. 88. Body, dorsal view (AMS KS63527). 89. Body, including chelicera, pedipalp and leg I, lateral view (AMS KS63527). 90. Right cheliceral fingers, anterior view (AMS KS63527). 91. Left pedipalp patella and tibia, dorsal view (AMS KS63527). 92. Penis, ventral view (AMS KS62923). 93. Glans, ventral view (AMS KS62923). 94. Glans, lateral view (AMS KS62923). Scale bars for figs 88–89 = 1 mm; figs 90–92 = 0.5 mm; figs 93–94 = 0.1 mm.

iridescent white postocularial marking. Anterior margin of mesopeltidium medially curved anteriorly. Mesopeltidium, metapeltidium and opisthosoma with broad iridescent white medial stripe. Metapeltidium, posterior half of lateral shelves and opisthosoma laterally light grey-brown with irregular tan punctures. Mouthparts white; coxae light orange. Coxa I ventrally spinose. Venter of opisthosoma cream with purple median stripe on genital operculum.

*Chelicerae.* Segment I 4.66 (0.17), segment II 5.82 (0.23). Long, slender, with segment II slightly inflated distally; both segments tan with dark brown markings on segment II; evenly denticulate. Cheliceral fingers short; mobile finger angular crescent-shape (fig. 90).

*Pedipalps.* Femur 1.69 (0.03), patella 0.82 (0.02), tibia 1.04 (0.07), tarsus 1.97 (0.05). Femur and patella medium brown with black patches, tibia tan with black shading, tarsus cream. Trochanter with few dorsodistal spines; remainder of pedipalp unarmed. Patella with rounded apophysis about half length of patella body (fig. 91), tip of patellar apophysis black; medial side of patella and tibia densely setose. Microtrichia on distal two-thirds of tarsus; claw with ventral tooth row.

*Legs.* Femora 3.75 (0.19), 6.13 (0.25), 3.16 (0.20), 5.47 (0.42); patellae 1.20 (0.03), 1.37 (0.05), 0.98 (0.10), 1.22 (0.13); tibiae 3.20 (0.13), 5.75 (0.10), 2.39 (0.06), 3.81 (0.09). Trochanters I and II with dense spines on anterior faces; trochanters III and IV unarmed. Femur I orange, densely denticulate with proventral row of longer spines down entire length; patella I and tibia I mottled gold and brown with proventral spine row along entire length of patella and tibia, smaller dorsal spine row along patella and proximal half of tibia; metatarsus I and tarsus I cream with ventrodiscal black markings on metatarsus. Femur II tan with ventral and dorsal rows of small spines, dorsal row for proximal two-thirds only, ventral for proximal two-thirds or entire length, scattered extra spines on proximal half; patella II and tibia II golden-cream with brown patches, tibia not divided into pseudosegments; metatarsus II and tarsus II cream with ventrodiscal bulges on proximal pseudosegments of tarsus. Femora III and IV proximally tan, distally orange; patellae and tibiae III and IV golden-orange with brown patches; metatarsi and tarsi III and IV cream. Femur III unarmed or with sparse dorsal row of small spines, occasionally small number of small spines distally; remaining segments unarmed. Tarsi III and IV proximally inflated with double ventral rows of brush-like setae.

*Penis* (figs 92–94). Posterior bristle groups elongate. Glans may be strongly dorsoventrally flattened.

*Spiracle* (figs 36–37). Anterior spines extending only partway across spiracle. Spines reticulate laterally, becoming less so medially; terminations simple or slightly palmate.

FEMALE (N = 1). Prosoma length 1.34, width 2.13; entire body length 5.44. Articular membranes iridescent white. Background of dorsal prosomal plate iridescent white with light brown paired stripes between ocularium and anterior margin; median propeltidial area with light brown central patch behind boundary with anterior propeltidial area and light brown stripe in front of boundary with posterior propeltidial area, with posterior stripe beginning slightly laterally from

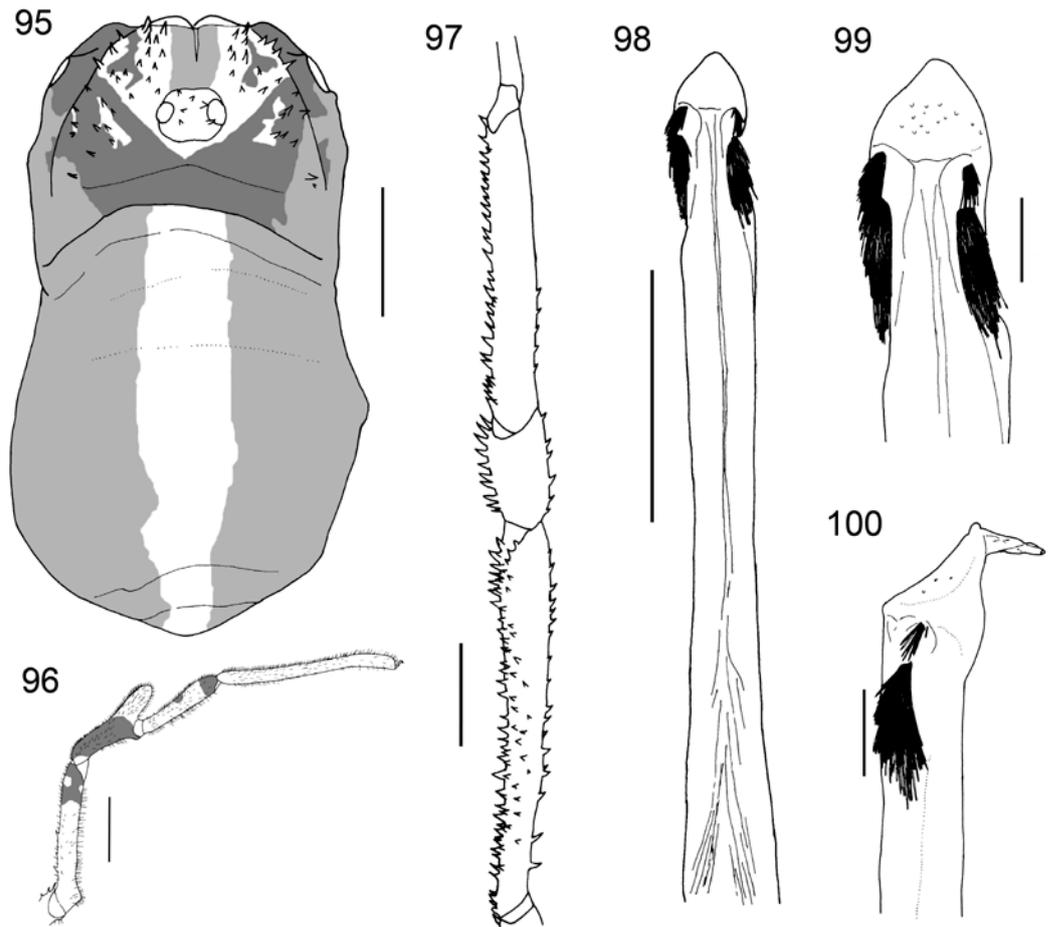
ocularium and extending two-thirds of distance to lateral edge of plate; posterior propeltidial area with dark brown patches towards lateral edge of dorsal prosomal plate, and rows of light patches in front of junction with mesopeltidium becoming progressively more elongate laterally. Ocularium white. Lateral shelves white with medium brown patches in front of, medially from and posterior to ozopore alongside junction with dorsal prosomal plate, and dark brown lateral stripe from anterior corner of prosoma to front of anterior ozopore lobe. Mesopeltidium, metapeltidium and dorsum of opisthosoma mottled light grey-brown and white with broad medial stripe of white dusted with purple. Mouthparts cream; coxae white spotted with light brown, thin medial stripe of dusted dark purple on proximal third, dusted black patch retrodistally; genital operculum cream with light brown medial stripe; venter of opisthosoma mottled white and light grey-brown with grey-brown patches darkening to light brown along midlines of segments.

*Chelicerae.* Segment I 0.95, segment II 1.82. Segment I ventrally white, dorsally white spotted with light brown distally and with dark purple lateral stripe narrowing distally; segment II cream with lateral light brown patches in herringbone pattern for proximal two-thirds; both segments unarmed.

*Pedipalps.* Femur 1.82, patella 1.04, tibia 1.14, tarsus 2.18. Basal quarter of femur white, following third light brown, distal remainder white with medium brown band starting quarter of length from distal end and dark brown retrodistal spot; patella golden-brown with cream patches distally; subcylindrical mediobasal apophysis on patella of slightly lesser length than patella body, apophysis cream with dark brown distal end; proximal part of tibia mottled golden brown and cream; distal end of tibia and tarsus cream.

*Legs.* Femora 3.04, –, 2.72, 4.85; patellae 1.13, –, 1.01, 1.17; tibiae 2.78, –, 2.13, 3.48. Femora proximally mottled white for most of length; distal end of femora to tibiae cream with mottled medium brown patches; basitarsus banded cream and light brown with dark brown band at distal end; distitarsi cream. All segments unarmed. Tibia IV without pseudosegments; tibia II not preserved.

**Comments.** The holotype of this species is very poorly preserved, and very few of its diagnostic features remain distinguishable. The specimens described herein have been assigned to this species on the basis of their distribution close to the reported type locality.



**FIGURES 95–100.** *Megalopsalis epizephyros*, male (all WAM T72092). 95. Body, dorsal view. 96. Left pedipalp, medial view. 97. Left leg I, ventrolateral view. 98. Penis, ventral view. 99. Glans, ventral view. 100. Glans, lateral view. Scale bars for figs 95–97 = 1 mm, fig. 98 = 0.5 mm, figs 99–100 = 0.1 mm.

***Megalopsalis epizephyros* new species**

(Figs 39, 41, 95–100)

**Material examined.** *Male holotype.* Stirling Range National Park, Bluff Knoll, Western Australia, 34°23'S 118°15'E, 19 June 1996, S. Barrett, wet pitfalls (WAM T72092; measured).

*Paratypes.* 154 males, 1 female, ditto (WAM T72089, T72091 [1 female measured], T72092 [8 males measured]).

**Diagnosis.** *Megalopsalis epizephyros* can be distinguished from *M. leptekes* and *M. hoggi* by the presence of ventrodistal bulges on the pseudosegments of

distitarsus II. It can be distinguished from the remaining species of *Megalopsalis* by the presence of dorsal spines on the pedipalp femur.

**Description.** MALE (figs 95–100; N = 9). Prosoma length 1.58 (0.10), width 2.30 (0.09), entire body length 3.88 (0.34). Anterior part of propeltidium medially medium brown, laterally silver with orange shading. Dark grey-brown patches along border between anterior and median parts of propeltidium; remainder of median part of propeltidium silver with orange shading. Dark grey-brown ridge between median and posterior parts of propeltidium. Posterior part of propeltidium dark grey-brown with silver patches. Propeltidium densely spinose on dorsal prosomal plate. Ocularium silver, densely spinose. Lateral shelves orange-brown, darker anteriorly. Mesopeltidium, metapeltidium and opisthosoma with broad silver median stripe, dark grey-brown immediately laterally to median stripe lightening more laterally to yellow-brown with silver-shaded tan punctures. Mouthparts cream; coxae medially purple, laterally mottled silver-orange. Venter of opisthosoma grey-cream with broken transverse white lines.

*Chelicerae.* Segment I 4.97 (0.59), segment II 6.08 (0.54). Golden-cream with dark brown markings; both segments evenly denticulate. Cheliceral fingers medium-length; mobile finger angular crescent-shaped.

*Pedipalps* (fig. 96). Femur 1.82 (0.07), patella 0.94 (0.04), tibia 1.15 (0.05), tarsus 2.08 (0.06). Trochanter with long dorsal spines. Femur golden-brown with dark brown band; patella and tibia golden-brown with darker dorsal longitudinal stripe and black shading distally; tarsus golden-cream. Femur with dorsal spine row. Patella with apophysis more than half length of patella body, apophysis silver-with black shading distally; medial side of patella and tibia densely setose. Microtrichia on distal half of tarsus; claw with ventral tooth-row.

*Legs.* Femora 3.50 (0.17), 5.50 (0.23), 3.12 (0.17), 4.96 (0.26); patellae 1.07 (0.05), 1.41 (0.07), 1.01 (0.08), 1.22 (0.10); tibiae 2.87 (0.12), 4.98 (0.14), 2.29 (0.08), 3.39 (0.13). Trochanters golden-cream; trochanters I and II with numerous spines on anterior face; trochanter III with one or a few small prodistal spines; trochanter IV unarmed. Femur I orange-brown proximally with golden band about two-thirds distalwards, dark brown distally; patella with medium-brown patches on gold background; tibia banded medium brown and gold; metatarsus banded golden-cream and purple-brown; tarsus golden-cream. Femur I (fig. 97) densely denticulate ventrally with prominent proventral spine row becoming longer distalwards, single

dorsal spine row along entire length; patella with long proventral spine row and two shorter dorsal spine rows; tibia densely spinose proximally narrowing to single spine row distally, prodorsal spine row for approximately half length proximally, retrodorsal row of only a few small spines proximally. Femur II orange-brown, mottled golden-brown distally; patella and tibia golden-cream with medium brown patches; metatarsus and tarsus as for leg I. Femur II with ventral and dorsal rows of small spines on proximal two-thirds; patella and tibia unarmed except single medial proximoventral and posterior dorsodistal spines on patella. Tibia II with three or four pseudosegments. Tarsus II with ventrodorsal bulges on proximal pseudosegments. Leg III coloration as for leg I; unarmed except few scattered small spines on femur III. Leg IV coloration as for leg II except background colour of patella and tibia golden-brown; unarmed; tibia IV undivided. Tarsi III and IV inflated proximally with two ventral rows of brush-like setae.

*Penis* (figs 98–100). Posterior bristle groups elongate; glans dorsoventrally flattened anteriorly only. Pores shallowly recessed.

*Spiracle* (fig. 39). Anterior spines slender, reticulate, extending only partway across spiracle. Terminations slightly palmate.

FEMALE (N = 1). Prosoma length 1.33, width 1.86; entire body length 4.10. Anterior part of dorsal prosomal plate in front of ocularium and ozopores iridescent white with light brown patches laterally and two light brown stripes between ocularium and anterior margin. Ocularium iridescent white. Remainder of propeltidium and mesopeltidium with light brown patches and few iridescent white spots on light tan background; lateral edges of lateral shelves iridescent white. Mesopeltidium with transverse row of iridescent white spots. Metapeltidium and opisthosoma with light tan broad median stripe; laterally mottled light brown and tan. Mouthparts and coxae cream with mediobasal purple patches on coxae; venter of opisthosoma with transverse bands of light tan and broken bands of light brown and white patches.

*Chelicerae*. Segment I 0.98, segment II 1.97. Cream with segment I dorsally broken light brown; light brown patches on segment II.

*Pedipalps*. Femur 1.90, patella 1.10, tibia 1.31, tarsus 2.23. Femur banded medium brown and cream; patella and tibia banded light brown and cream; tarsus cream. Patella with large rounded white-cream apophysis, slightly shorter than

patella body; patella and tibia densely setose on median side. Microtrichia over distal three-fifths of tarsus.

*Legs.* Femora 2.71, –, 2.44, 4.25; patellae 0.93, –, 1.02, 1.15; tibiae 2.56, –, 2.14, 3.24 (leg II not preserved). Banded medium brown and cream with silver-white patches on distalmost part of femur, patella and tibia. Tibia IV undivided.

**Etymology.** From the Greek *epizephyros*, towards the west, referring to the distribution of this species relative to the similar *Megalopsalis serritarsus* and *M. eremiotis*.

### ***Megalopsalis eremiotis* new species**

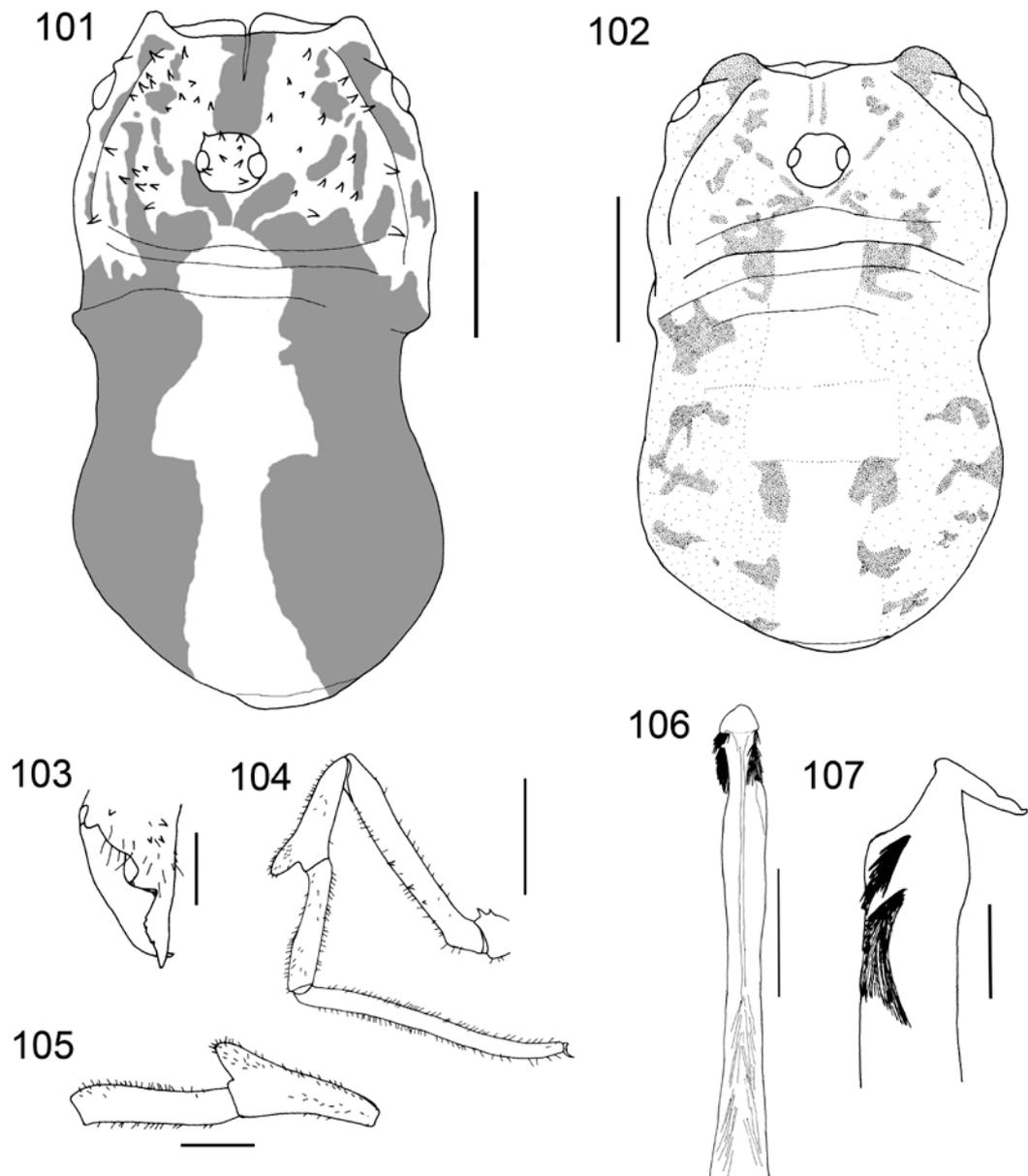
(Figs 38, 101–107)

**Material examined.** *Male holotype.* Little Desert, Victoria, 36°35'S 141°45'E, 14–20 July 1974, Biology Society Trip, pitfall trap (QM S15450; measured).

*Paratypes.* 1 male, 1 female, Lerderderg River, Victoria, 37°34'S 144°24'E, 16 July 1996, V. W. Framenau, riparian gravel bank (WAM; measured); 1 male, 1 female, Little Desert, Victoria, 36°35'S 141°45'E, 14–20 July 1974, Biology Society (V. Salantri, collector), pitfall trap (QM S15447; measured); 4 males, Second Valley, South Australia, 35°32'S 138°14'E, 1–2 August 1992, J. M. Waldock (WAM T72869; 3 measured).

**Diagnosis.** *Megalopsalis eremiotis* is most similar to *M. serritarsus*, and can only be certainly distinguished by examination of the spiracle which has more slender spines together with more elongate but less extensive lace tubercles. However, the two species can also be potentially distinguished by the presence of ventral spines on the pedipalp femur (sometimes present in *M. eremiotis*, never present in *M. serritarsus*) and their disjunct distributions. *Megalopsalis eremiotis* can be distinguished from *M. leptekes* and *M. hoggi* by the presence of dorsoventral bulges on the pseudosegments of distitarsus II, from *M. pilliga* by the distinctly denticulate femur II, and from *M. epizephyros* by the absence of dorsal spines on the pedipalp femur.

**Description.** MALE (figs 101, 103–107; N = 6). Prosoma length 1.64 (0.13), width 2.38 (0.21); entire body length 3.95 (0.16). Propeltidium orange-white with orange patches; entire propeltidium spinose. Ocularium iridescent white with numerous spines. Mesopeltidium, metapeltidium and opisthosoma with broad



**FIGURES 101–107.** *Megalopsalis eremiotis*. 101. Male, dorsal view (QM S15450). 102. Female, dorsal view (WAM, Lerderberg River). 103. Male right cheliceral fingers, anterior view (QM S15450). 104. Male left pedipalp, lateral view (QM S15450). 105. Patella and tibia of male left pedipalp, dorsal view (QM S15450). 106. Penis, ventral view (QM S15450). 107. Glans, lateral view (QM S15450). Scale bars for figs 101–102, 104 = 1 mm; figs 103, 105–106 = 0.5 mm; fig. 107 = 0.1 mm.

iridescent white to purple median stripe with or without silver border, laterally mottled iridescent orange-white and yellow-orange with yellow-orange punctures. Mouthparts cream; coxae mottled yellow and iridescent white. Venter of opisthosoma mottled iridescent white.

*Chelicerae*. Segment I 4.36 (0.60), segment II 5.62 (0.61). Long, slender; cream with light brown patches on segment II. Both segments evenly denticulate. Cheliceral fingers long; mobile finger angular crescent-shaped (fig. 103).

*Pedipalps* (figs 104–105). Femur 1.91 (0.18), patella 0.94 (0.09), tibia 1.10 (0.07), tarsus 2.26 (0.19). White with yellow patches on patella and tibia; unarmed or with few widely-spaced ventral spines on femur. Trochanter with few dorsodistal spines. Rounded apophysis on patella about third length of patella body (fig. 105). Patella and tibia densely setose on median side. Microtrichia over distal half of tarsus; claw with ventral tooth-row.

*Legs*. Femora 4.05 (0.39), 6.35 (0.66), 3.56 (0.54), 5.89 (0.67); patellae 1.19 (0.11), 1.46 (0.13), 1.07 (0.10), 1.27 (0.12); tibiae 3.34 (0.34), 5.91 (0.56), 2.61 (0.34), 3.98 (0.46). Trochanters yellow medially, white laterally; trochanters I and II with denticles on prolateral face, III and IV unarmed. Femora patched golden-white and yellow; patellae and tibiae golden-white with yellow spots; tarsi golden-white. Femur I densely spinose ventrally with slightly longer proventral spine row, additional spine row dorsally; patella with long ventral and short dorsal spine rows; tibia with ventral spine row along entire length and small dorsal spine row along proximal half. Femur II with ventral spine row along entire length and smaller dorsal spine along proximal three-quarters, extra anterior spines on proximal half. Tibia II faintly divided into four pseudosegments; tarsus II with ventrodiscal bulges on proximal segments. Femur III with widely-spaced anterior spine row for entire length, short ventral spine row for distal fifth; remaining leg segments unarmed. Tibia IV undivided; tarsi III and IV proximally broadened with double ventral rows of brush-like setae.

*Penis* (figs 106–107). Posterior bristle groups elongate; glans dorsoventrally flattened distally. Pores deeply recessed.

*Spiracle* (fig. 38). Anterior spines slender, extending only partway across spiracle; spines reticulate laterally, becoming less so medially; terminations simple or only minimally palmate; lace tubercles elongate.

FEMALE (fig. 102; N = 2). Prosoma length 1.10 (0.05), width 2.15 (0.00); entire body length 4.55 (1.17). Anterior part of propeltidium light tan shaded with silver-white with two light brown stripes between anterior margin and ocularium; remainder of propeltidium and lateral shelves light tan with light brown patches. Ocularium light tan. Mesopeltidium, metapeltidium and opisthosoma with broad

silver-white median striped shaded with purple; lateral parts yellow-tan patterned with light brown. Mouthparts white-cream; coxae white-tan with median purple patches. Genital operculum white-cream with median stripe of dusted medium brown; venter of opisthosoma light brown with transverse rows of white-cream patches across segments.

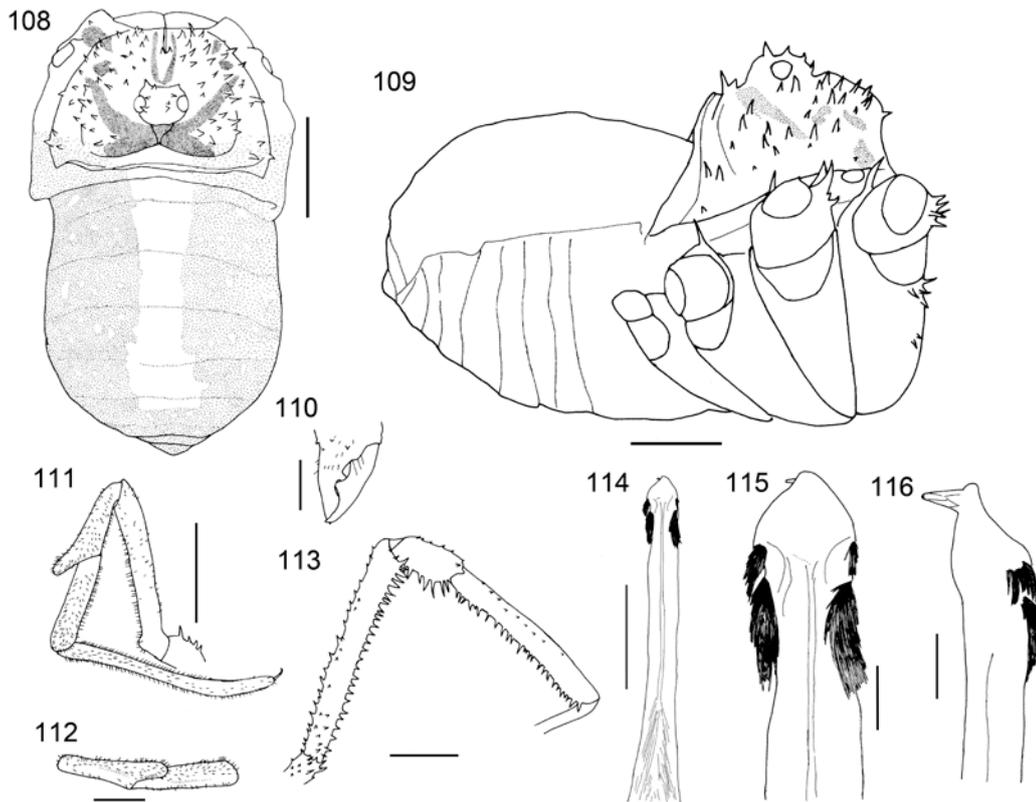
*Chelicerae*. Segment I 0.78 (0.02), segment II 1.70 (0.06). White-cream with light brown patches; unarmed.

*Pedipalps*. Femur 1.66 (0.16), patella 0.90 (0.06), tibia 1.04 (0.07), tarsus 2.02 (0.11). Femur, patella and tibia white-cream banded with medium brown and longitudinal medium brown dorsal stripe on patella and tibia; tarsus white-cream. Patella with short rounded apophysis ~ one-third length of main body of patella; apophysis cream with medium brown tip.

*Legs*. Femora 2.66 (0.24), 4.67 (0.37), 2.43 (0.22), 4.29 (0.49); patellae 0.91 (0.14), 1.16 (0.11), 0.85 (0.13), 1.02 (0.06); tibiae 2.41 (0.21), 4.40 (0.28), 1.89 (0.16), 2.97 (0.31). White-cream with light brown bands and patches; unarmed. Tibia II with four pseudosegments; tibia IV undivided.

**Variation.** Ventral spines are present on the pedipalp femur of the holotype and the male South Australian specimens (WAM T72869). Because of the geographical overlap between specimens with and without such spines, I do not regard them as distinct species. There is also variation between specimens in the colour of the median opisthosomal stripe from iridescent white in the holotype to purple with a distinct silver border to the stripe in the WAM specimen from the Lerderberg River in Victoria. This difference in coloration may be original, or it may represent post mortem bleaching.

**Etymology.** Feminine diminutive of the Greek *eremites*, “dweller of the desert”, after the name of the type locality.



**FIGURES 108–116.** *Megalopsalis hoggi*, male (all WAM T72936). 108. Body, dorsal view. 109. Body, lateral view. 110. Left cheliceral fingers, anterior view. 111. Right pedipalp, medial view. 112. Patella and tibia of right pedipalp, dorsal view. 113. Left leg I, prolateral view. 114. Penis, ventral view. 115. Glans, ventral view. 116. Glans, lateral view. Scale bars for figs 108–109, 111, 113 = 1 mm; figs 110, 112, 114 = 0.5 mm; figs 115–116 = 0.1 mm.

***Megalopsalis hoggi* (Pocock 1903a)**

(Figs 1B, 108–116)

*Macropsalis hoggi* Pocock 1903a: 398–399; Roewer 1911: 103, 1912: 280.

*Megalopsalis hoggi* (Pocock)—Roewer 1923: 867–868; Forster 1949a: 61, 63, figs 5–8 (see comments below).

**Material examined.** *Male lectotype* (designated by Forster 1949a). Macedon, Australia, H. R. Hogg (BMNH).

*Other material examined.* 1 male, Coonabaraban, near Timor Peak, New South Wales, 31°16'S 149°17'E, 9 September 1992, A. F. Longbottom, damp litter (WAM T72936; measured).

**Diagnosis.** *Megalopsalis hoggi* differs from all other *Megalopsalis* species in that the male possesses proximally inflated distitarsi III and IV, but no ventral bulges

on distitarsus II. The dorsal prosomal plate is also noticeably more densely denticulate than in other species.

**Description.** MALE (N = 1). Prosoma length 1.39, width 2.38; entire body length 3.92. Anterior and median parts of dorsal prosomal plate white with paired medium brown lines from front of ocularium to anterior margin of dorsal prosomal plate, medium brown patches subprolaterally and large medium brown area behind ocularium with radiating medium brown lines from behind ocularium to near edge of dorsal prosomal plate above ozopore. Ocularium silver with row of four spines on each side above eye. White areas of dorsal prosomal plate heavily denticulate; pair of spines at distal end of groove running from anterior margin of dorsal prosomal plate halfway to ocularium. Lateral shelves white anteriorly with dark brown patches in front of ozopore, tan posteriorly. Mesopeltidium, metapeltidium and first five segments of opisthosoma white medially, tan with white spots laterally. Mesopeltidium unarmed except for few spines laterally. Opisthosoma with lines of silver mottling along segmental boundaries. Mouthparts and coxae cream with black medial spot at distal end of coxae; venter of opisthosoma white-grey with white streaks. Coxa I with spines along ventral midline.

*Chelicerae.* Segment I 4.50, segment II 5.75. Long, slender with segment II slightly inflated distally; segment I tan with medium brown lateral margin and medium brown patches at distal end; segment II tan with longitudinal rows of medium brown patches. Both segments evenly denticulate. Cheliceral fingers short, mobile finger crescent-shaped (fig. 110).

*Pedipalps* (figs 111–112). Femur 1.53, patella 0.89, tibia 0.98, tarsus 1.98. Trochanter armed dorsally with slender spines, remainder of pedipalp unarmed; banded white and medium brown. Rounded apophysis on patella about one-third length of patella body (fig. 112); patella and tibia densely setose medially. Microtrichia over distal half of tarsus; claw with ventral tooth-comb.

*Legs.* Femora 3.42, 5.94, 2.96, 5.06; patellae 1.03, 1.31, 1.02, 1.15; tibiae 2.90, 5.06, 2.12, 3.34. Cream with purple patches at distalmost end of each segment except tarsi. Long spines on dorsodistal margins of coxae I-III. Trochanters I-III with multiple spines anteriorly, trochanter IV unarmed. Femora I-III with longitudinal rows of spines dorsally, anteriorly and ventrally (those on femur I particularly long; fig. 113); femur IV with only few denticles on proximal half. Patella I and tibia I with dorsal and ventral rows of spines; remaining segments unarmed. Tibia II with

four pseudosegments; tarsus II without ventral bulges. Tibia IV undivided; tarsi III and IV with first few pseudosegments inflated and two longitudinal ventral rows of brush-like setae.

*Penis* (figs 114–115). Posterior bristle groups elongate; glans distally dorsoventrally flattened.

*Spiracle*. Not observed.

**Comments.** The volume in which this species was published is dated ‘1902’, and has often been cited as such. However, Pocock (1903b) noted that his earlier paper (Pocock 1903a) had been published in April 1903. The title page for Pocock (1903b) gives the publication date as May, so the priority of the two papers is not affected.

As noted by Forster (1949a), the original three syntypes for this species include representatives of two species, with the so-called ‘females’ being males of *Spinicrus stewarti* (not *Neopantopsalis camelus* as suggested by Forster 1949a). Forster’s (1949a) implicit removal of those two specimens from the type series and referral to the single *Megalopsalis* specimen as ‘holotype’ can be accepted as a lectotype designation under the ICZN (International Commission on Zoological Nomenclature 1999: Article 74.5). However, his female ‘allotype’ has no type status, as it was not part of the original description. At the time Forster (1949a) allocated female specimens from Victoria and South Australia to *Megalopsalis hoggi*, it was the only *Megalopsalis* species known from Victoria. Female Enantiobuninae of closely related species are often not distinguishable (Taylor 2004) and these specimens may belong to *M. eremiotis*.

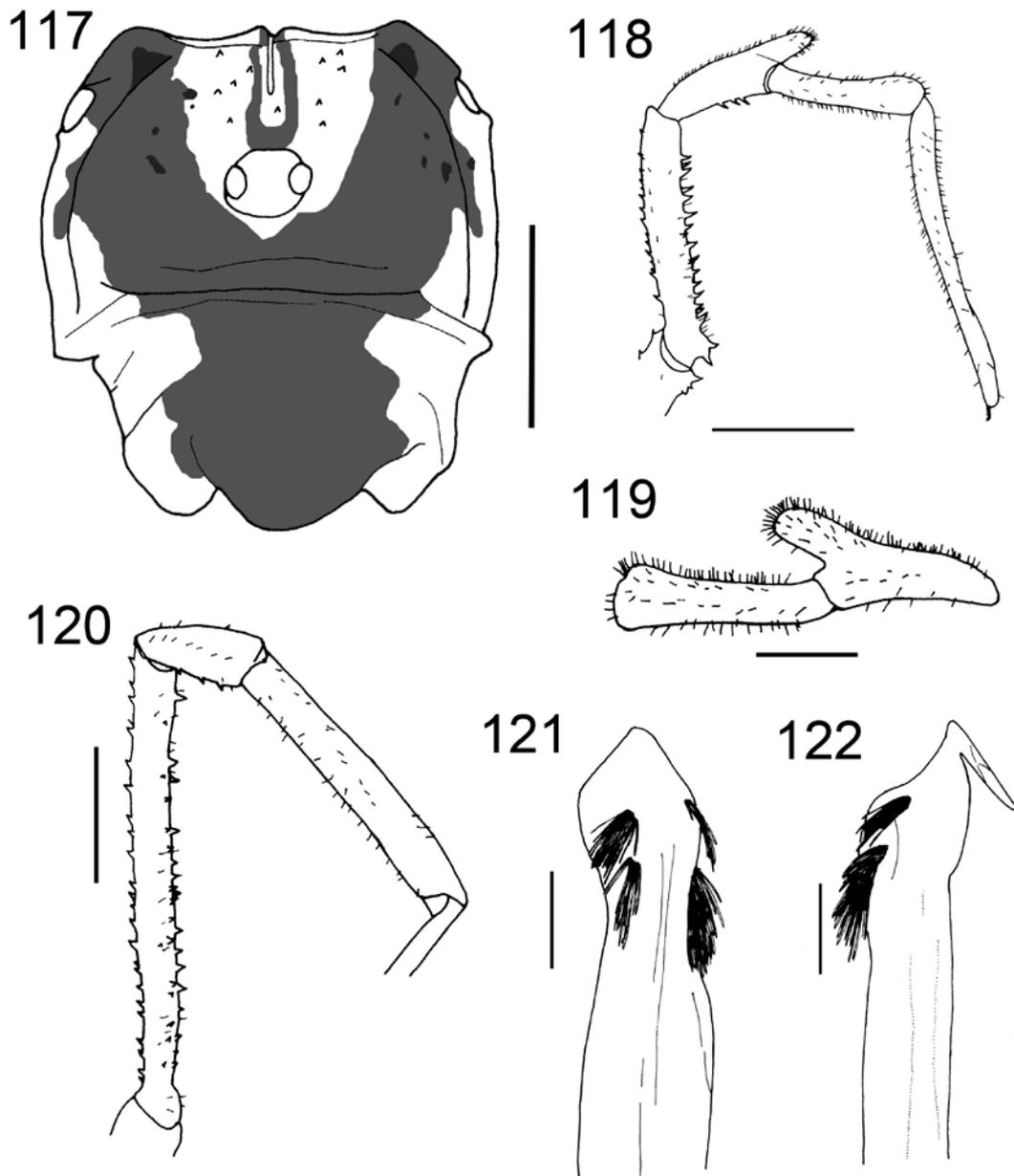
### ***Megalopsalis leptekes* new species**

(Figs 35, 117–122)

**Material examined.** *Male holotype.* Talling Station, Western Australia, 2 September 1976, R. P. McMillan (WAM 90/1313).

*Paratype.* 1 male, Mokine, Western Australia, 31°44'S 116°35'E, 15 July 1956, B. Y. Main, being carried by *Camponotus* ant (WAM T71949).

**Diagnosis.** *Megalopsalis leptekes* is readily distinguished from other *Megalopsalis* species by its slender distitarsi III and IV without ventral brush-like



**FIGURES 117–122.** *Megalopsalis leptekes*, male (all WAM 90/1313). 117. Body, dorsal view. 118. Right pedipalp, lateral view. 119. Patella and tibia of left pedipalp, dorsal view. 120. Left leg I, prolateral view. 121. Glans, ventral view. 122. Glans, lateral view. Scale bars for figs 117–118, 120 = 1 mm; fig. 119 = 0.5 mm; figs 121–122 = 0.1 mm.

setae, and also by the presence of denticulations on the anterior part of the propeltidium only.

**Description.** MALE (N = 2). Prosoma length 1.19, width 2.00. Anterior part of propeltidium dark orange-brown with dark brown stripe on either side of supracheliceral groove. Median and posterior parts of propeltidium and median part

of mesopeltidium mottled dark brown with black patches laterally. Scattered denticles on anterior part of propeltidium, remainder of dorsal prosomal plate unarmed. Ocularium dark orange-brown, unarmed. Lateral shelves and retrolateral corners of dorsal prosomal plate orange-cream with black patches on lateral shelves. Metapeltidium and opisthosoma with broad median stripe of dark green-brown with light tan spots, laterally cream. Venter cream with medium brown spots on coxae.

*Chelicerae*. Segment I 4.05 (0.21), 5.12 (0.19). Yellow-orange with dark brown patches on distal part of first segment and entire second segment; both segments evenly denticulate. Cheliceral fingers short; mobile finger angular crescent-shaped.

*Pedipalp* (figs 118–119). Femur 1.57 (0.06), 0.84 (0.01), 1.04 (0.01), 2.05 (0.08). Femur and patella orange-yellow with light brown patches, tibia cream with light brown patches, tarsus cream. Trochanter spinose dorsally and ventrally, femur with dorsal and ventral spine rows, patella with few medioventral spines. Patella with apophysis about half length of patella body (fig. 119); medial sides of patella and tibia densely setose. Microtrichia on distal half of tarsus; claw with ventral tooth-comb.

*Legs*. Femora 3.29 (0.41), 5.43 (0.42), 2.78 (0.26), 4.65; patellae 0.91 (0.03), 1.13 (0.11), 0.85 (0.03), 0.94; tibiae 2.52 (0.21), 4.35 (0.21), 2.10 (0.23), 3.03. Orange-cream. Trochanters unarmed. Femur I with dorsal and ventral spine rows, more closely spaced ventrally; patella with ventral spine row; tibia unarmed (fig. 120). Femur II with dorsal and ventral rows of small, relatively widely-spaced spines for proximal half. Remaining segments unarmed except for few dorsal spines on proximal half of femur. Tibiae undivided; tarsi unspecialised.

*Penis* (figs 121–122). Bristle groups of medium length; glans distally dorsoventrally flattened. Pores shallowly recessed.

*Spiracle* (fig. 35). Anterior spines thick, slightly flattened, mostly lacking reticulations except cornermost spines, extending across entire spiracle; terminations broadly palmate.

**Variation.** The colour pattern described above refers to the holotype. The paratype has a more evenly orange-brown dorsal prosomal plate with brown patches, but this is possibly due to post-mortem bleaching.

**Etymology.** From the Greek *leptekes*, fine-pointed and delicate, referring to the animal's appearance.

**Comments.** The presence of lace tubercles on the lateral corner of the spiracle could not be confirmed for *M. leptekes* due to obscuring grit on the specimen observed.

***Megalopsalis pilliga* new species**

(Figs 123–128)

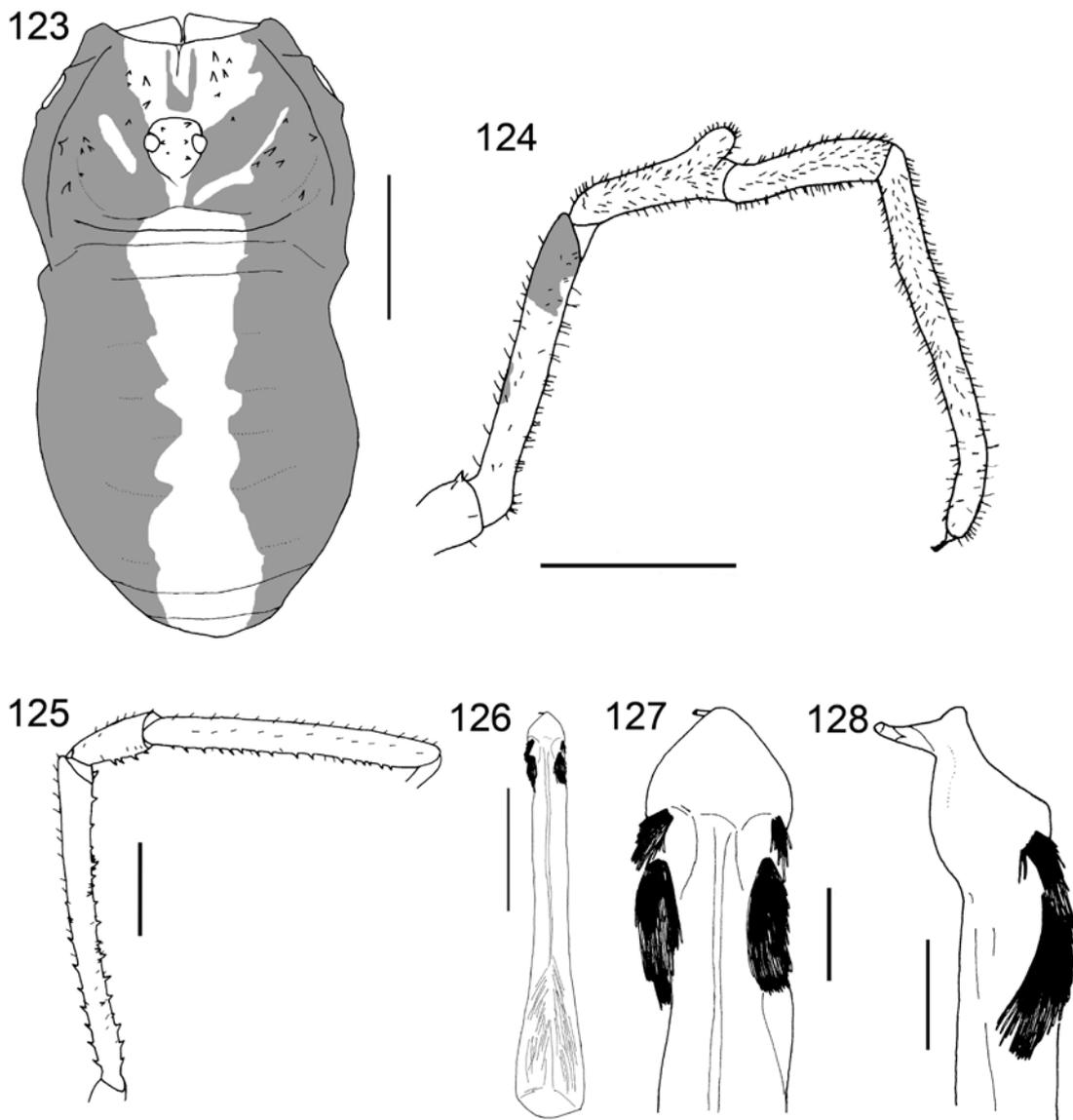
**Material examined.** *Male holotype.* Pilliga East State Forest, Bohera Bore, Forest Way Road, New South Wales, 10 July 1991, H. Parnaby (AMS KS30695).

*Paratype.* 1 male, ditto (AMS KS30695).

**Diagnosis.** *Megalopsalis pilliga* can be distinguished from all other *Megalopsalis* species by the lack of prominent denticulation on femur II.

**Description.** MALE (N = 2). Prosoma length 1.34 (0.14), width 1.70 (0.17); entire body length 3.50 (0.37). Anterior part of propeltidium light yellow-tan with light brown stripe along either side of supracheliceral groove. Remainder of propeltidium mottled light brown with light yellow-tan line between median and posterior parts of propeltidium. Ocularium light yellow-tan with row of three small sharp spines on each side. Scattered spines on dorsal prosomal plate, particularly on anterior and posterior parts of propeltidium. Postocularium directed downwards posteriad, dorsal prosomal plate raised slightly on either side of ocularium. Lateral shelves light yellow-tan with medium brown patches; lateral margins black. Mesopeltidium, metapeltidium and first six segments of opisthosoma with median stripe of cream dusted with purple. Mesopeltidium laterally medium brown with single spine towards each side of dorsal prosomal plate. Metapeltidium and opisthosoma laterally yellow grey-brown with medium brown patches along margins of median stripe and darker mottled lines along segment boundaries on either side of median stripe. Transverse lines of black setae across midlines of opisthosomal segments. Posterior part of opisthosoma laterally dark brown with yellow-tan spots, becoming lighter medially. Venter of prosoma orange-cream with dark brown distal margins on coxae. Venter of opisthosoma yellow grey-brown with broken dark-brown transverse stripes laterally.

*Chelicerae.* Segment I 2.84 (0.17), segment II 4.00 (0.14). Cream with dark brown patches on segment II and distal part of segment I; dorsolateral black patch at very base of segment I; both segments densely denticulate, segment I more so on



**FIGURES 123–128.** *Megalopsalis pilliga*, male (all AMS KS30695). 123. Body, dorsal view. 124. Left pedipalp, medial view. 125. Right leg I, retrolateral view. 126. Penis, ventral view. 127. Glans, ventral view. 128. Glans, lateral view. Scale bars for figs 123–125 = 1 mm; fig. 126 = 0.5 mm; figs 127–128 = 0.1 mm.

medial side; black tips on spines. Cheliceral fingers short; mobile finger crescent-shaped.

*Pedipalps* (fig. 124). Femur 1.59 (0.06), patella 0.77 (0.10), tibia 0.91 (0.04), tarsus 1.86 (0.05). Femur banded dark brown and cream; patella and tibia banded light brown and cream; tarsus and patella apophysis cream. Unarmed. Short rounded apophysis on patella about one-quarter length of main body of patella. Microtrichia on distal half of tarsus; claw with ventral tooth-comb.

*Legs.* Femora 3.67 (0.13), 6.16 (0.05), 3.41 (0.13), 5.43 (0.02); patellae 1.05 (0.03), 1.42 (0.06), 0.92 (0.01), 1.10 (0.10); tibiae 2.95 (0.10), 5.24 (0.02), 2.27 (0.21), 3.52 (0.14). Trochanters cream with light brown mottling. Trochanters I and II with spines on anterior face; III and IV unarmed. Legs banded medium brown and cream. Femur I spinose on ventral, prolateral and dorsal sides, but no distinct hypertrophied ventral spine row (fig. 125). Patella I with small ventral spine row, dorsally unarmed. Tibia I with small ventral spine row along entire length, few small prodorsal spines in proximalmost part only. Femur II mostly unarmed except few small dorsal spines proximally. Remaining segments unarmed. Distitarsus II with ventrodistal bulges on pseudosegments, distitarsi III and IV inflated proximally with double ventral rows of brush-like setae. Tibia II with three or four pseudosegments; tibia IV undivided.

*Penis* (figs 126–128). Posterior bristle groups elongate; glans distally dorsoventrally flattened. Pores shallowly recessed.

*Spiracle.* Not observed.

**Etymology.** Named after the type locality.

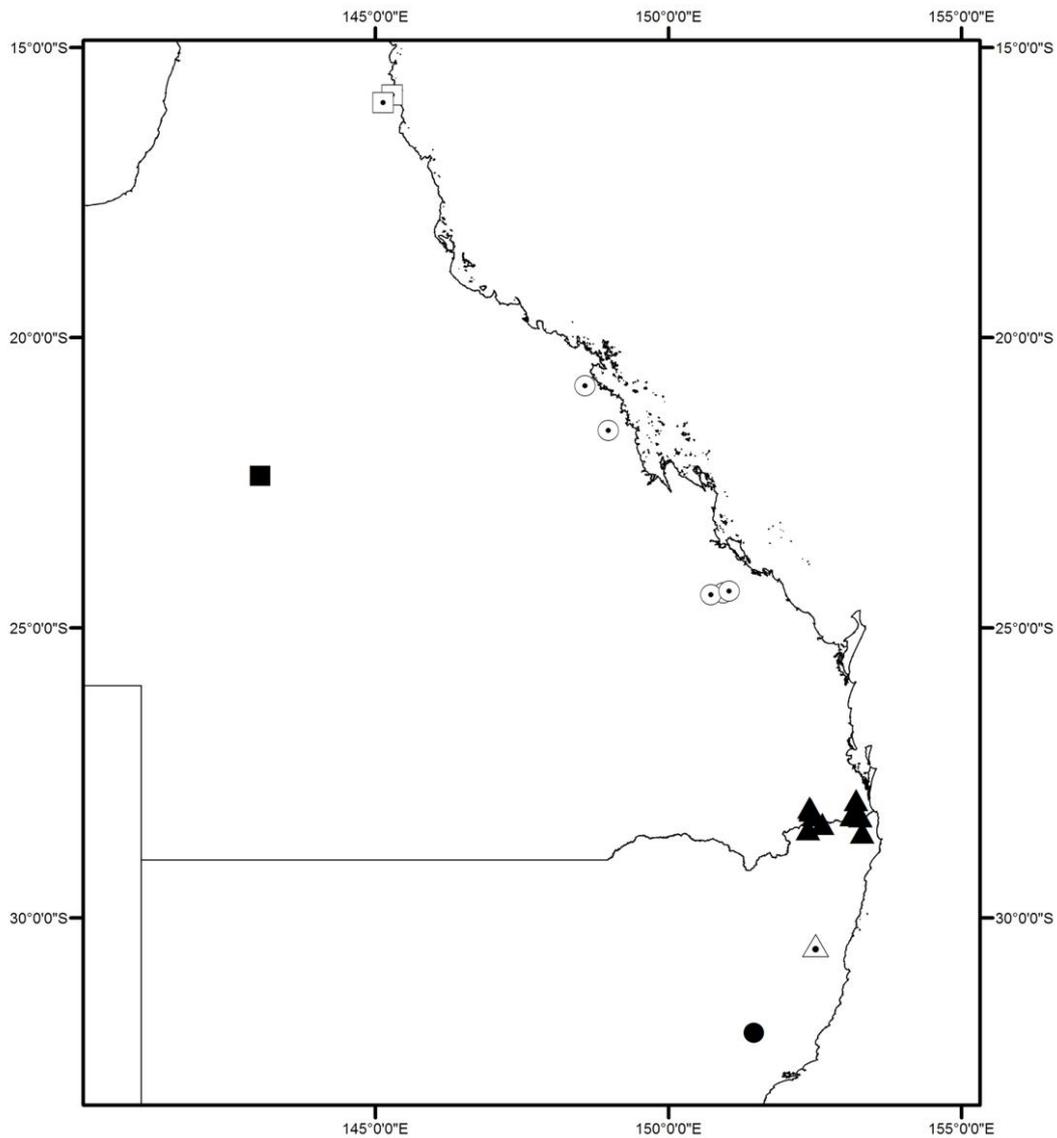
### ***Monoscutum* Forster 1948a**

*Monoscutum* Forster 1948a: 314; Crawford 1992: 32; Taylor 2008: 177, 179.

**Type (and only) species.** *Monoscutum titirangiense* Forster 1948a by original designation.

**Diagnosis.** *Monoscutum* can be distinguished from other Enantiobuninae except *Acihasta* and *Templar* by the heavily sclerotised dorsum of the opisthosoma. It can be distinguished from the latter two genera by the complex divided tubercles on the opisthosoma (Taylor 2008), from *Acihasta* by the absence of large lateral spines on the opisthosoma and from *Templar* by the presence of a large multifurcate promedial tubercle on the ocularium.

**Distribution.** North Island, New Zealand.



**FIGURE 129.** Records of distribution for *Neopantopsalis* in north-eastern Australia: square with dot = *N. quasimodo*; solid square = *N. continentalis*; circle with dot = *N. psile*; solid triangle = *N. pentheter*; triangle with dot = *N. thaumatopios*; solid circle = *N. camelus*.

***Neopantopsalis* new genus**

*Neopantopsalis* Taylor & Hunt 2009: 45–46.

**Type species.** *Neopantopsalis quasimodo* new species by present designation.

**Diagnosis.** Major males of *Neopantopsalis* are distinguished from those of all other genera of Monoscutidae by the raised humps on the dorsal prosomal plate and the proventral row of greatly hypertrophied spines on leg I. Both major and minor

males can be distinguished from representatives of other genera by the long, oblong, dorsoventrally flattened glans of the penis. *Neopantopsalis* is distinguishable from Monoscutinae by the unsclerotised and unornamented opisthosoma, and from *Megalopsalis* by the absence of a pedipalp patellar apophysis. *Spinicrus* has the dorsal margin of the prosoma in front of the ocularium horizontal rather than sloping downwards and the glans of its penis is short and triangular (Hickman 1957). Species of *Pantopsalis* have the medial side of the pedipalp patella and tibia more densely setose, and the glans of the penis is not dorsoventrally flattened (Taylor 2004).

**Description.** MALE. Dorsal prosomal plate of major males with humps on either side and behind the ocularium at the boundary of the median and posterior propeltidial areas. Postocularium and mesopeltidium raised in major males to form third hump directly behind ocularium. Metapeltidium sclerotised medially to form round sclerotised area with dorsal prosomal plate. Chelicerae long and slender, with both segments evenly denticulate. Cheliceral fingers sinuous. Pedipalps without apophyses or heavily setose areas. Legs very long; leg I with longitudinal row of hypertrophied spines on proventral margin of femur; row of shorter stouter spines on dorsal margin, dwindling distad. Glans of penis long, dorsoventrally flattened. Bristle groups on the penis significantly reduced, particularly on left side.

**Etymology.** The name *Neopantopsalis* had been given to this genus by Glenn Hunt. Doubtless it was derived from the Greek prefix *neo-*, meaning new, and *Pantopsalis*, another genus of the Monoscutidae found in New Zealand (Taylor 2004). The gender is feminine.

**Distribution** (fig. 129). Queensland, northeast New South Wales.

**Comments.** The late Glenn Hunt was the most recent significant worker on Australian Opiliones, and described and revised a number of species of Laniatores (Hunt 1971, 1972, 1985, 1990a, 1992, 1993, 1995; Hunt & Hickman 1993). Hunt also worked on Australian Eupnoi, and was one of the original describers of the neopilionid subfamily Ballarrinae (Hunt & Cokendolpher 1991). However, only preliminary work (Hunt 1990b) was published on Australian long-legged harvestmen (Eupnoi) before his untimely death in 1999. Gray (2001) gives a complete bibliography of Hunt's publications.

While sorting through the collection of Monoscutidae held by the Queensland Museum in Brisbane, I (C. Taylor) found a specimen that had been designated by Glenn Hunt as holotype of a new genus and species. Illustrations of this species were

also found among Glenn's unpublished notes held in the archives of the Australian Museum in Sydney. Further studies established that the new species was part of a noteworthy radiation of species in Queensland and New South Wales. Two of these species, *Pantopsalis continentalis* Roewer 1923 and *Spinicrus camelus* Forster 1949a, had been described previously whereas the remaining species were new. Glenn's new species is therefore presented herein, along with descriptions and redescriptions of further species of his new genus.

Despite the fact that only eight species have been assigned to it, *Spinicrus* as previously described includes a wide range of morphologies, and may not represent a coherent group. The only two defining characters established for this genus by Forster (1949a) are absence of a pedipalp patellar apophysis and presence of a ventral tooth-row on the claw of the pedipalp. The type species, *S. tasmanicum*, is very different from the taxa here placed in *Neopantopsalis* (see Hickman 1957), and it is felt that recognising the *Neopantopsalis* species as a separate genus better reflects their identity as a distinguishable group that is widespread in eastern Australia.

The species assigned to *Neopantopsalis* herein can be divided into three phenetically distinct groups, with the exception of *Neopantopsalis continentalis* whose identity is currently uncertain. *Neopantopsalis camelus* and *N. thaumatopios* are most similar to one another, with femur II pseudoarticulated and numerous small denticles on the propeltidium. *Neopantopsalis quasimodo* is currently distinct from the other described species, with no pseudoarticulations in femur II, fewer and larger denticles on the propeltidium, and a more elongate glans than other species, but as yet undescribed species similar to *N. quasimodo* may also be present (see comments after the description for *N. quasimodo*). *Neopantopsalis pentheter* and *N. psile* form a third group, also with no pseudoarticulations in femur II but with the propeltidium entirely or almost entirely unarmed. As well as the morphological distinction between these groups, there is also a clear geographical distinction (Fig. 129). *Neopantopsalis quasimodo* is the northernmost species, and is found well north of the Tropic of Capricorn. *Neopantopsalis pentheter* and *N. psile* have a more southerly distribution, with that of *N. psile* near the coast of Queensland straddling the Tropic of Capricorn, and *N. pentheter* on the Queensland to New South Wales border. *Neopantopsalis camelus* and *N. thaumatopios* are the southernmost species, being known from localities in northern New South Wales.

### Key to species of *Neopantopsalis*

Because of its uncertain status (see below) *Neopantopsalis continentalis* (Roewer 1923) is omitted from the following key.

1. Propeltidium unarmed or with very few denticles on apices of lateral mounds only...2  
Propeltidium with numerous denticles...3
2. Median propeltidial area of dorsal prosomal plate with broad white 'mask' ...*N. pentheter*  
Only ocularium white, remainder of dorsal prosomal plate dark brown...*N. psile*
3. Propeltidium with few, large denticles (fig. 131); femur II not pseudoarticulated...*N. quasimodo* (complex).  
Propeltidium with numerous small denticles (fig. 160); femur II pseudoarticulated...4
4. Ocularium slightly rugose; lateral mounds on dorsal prosomal plate rounded in lateral view; proventral spines on femur I short...*N. camelus* (Forster 1949a).  
Ocularium strongly rugose; lateral mounds on dorsal prosomal plate angular in lateral view; proventral spines on femur I long...*N. thaumatopios*

***Neopantopsalis quasimodo* new species**

(Figs 1A, 29, 130–139)

*Neopantopsalis quasimodo* Taylor & Hunt 2009: 47–50, figs 1a, 3–12.

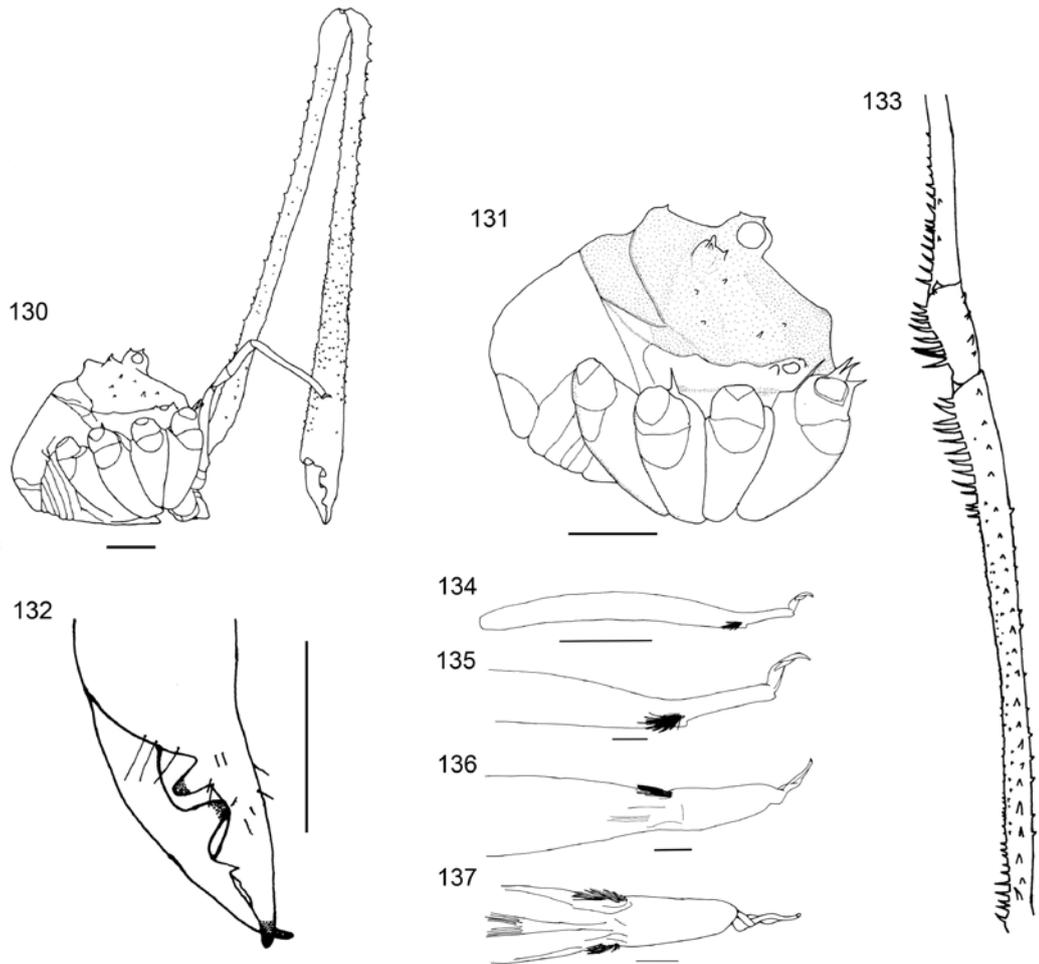
**Material examined.** *Male holotype.* Mt. Finnigan, 850–1100 m, 37 km S. of Cooktown, N. Queensland, 15°49'S 145°17'E, 19–22 April 1982, rainforest; Monteith, Yeates & Cook (QM S2481, QM S39684, this specimen has two accession numbers; measured).

*Paratypes.* 1 male, as above (QM S2488); 1 male, Mt. Finnigan summit, 1100m, via Helenville, N. Queensland, 28 November 1985, G. Monteith & D. Cook, pyrethrum knockdown/RF (QM S2491); 1 male, Mt. Finnigan, ~950–1050 m (QM S2833); 6 males (including 1 juvenile male), Mt. Finnigan summit, via Helenville, 28–30 November 1985, Monteith, Cook & Roberts (QM S3415; 5 males measured); 2 males, ditto, 1050 m, 3–5 December 1990, Monteith, Thompson, Cook, Sheridan & Roberts (QM S35968); 1 male, ditto, Monteith, Sheridan, Roberts & Thompson, pyrethrum (QM S74269; measured), 1 minor male, ditto, 850–950 m, Monteith, Thompson, Cook, Sheridan & Roberts (QM S74300), 5 males (including 2 minor males), ditto, 1050 m (QM S74301; minor males measured).

*Other material examined.* 5 males, Mt. Boolbun Sth. (Camp), 850 m, NE Queensland, 15°57'S 145°08'E, 5 November 1995–11 January 1996, Monteith, Cook & Roberts, intercept trap (QM S41346; 1 measured); 2 males, Mt. Hartley, SW slope, 750 m, 8 November 1995–16 January 1996, Monteith, Cook & Roberts, intercept trap (QM S41376; measured).

**Diagnosis.** *Neopantopsalis quasimodo* is distinguished from *N. psile* and *N. pentheter* by the presence of armature on the dorsal prosomal plate and ocularium. It is distinguished from *N. camelus* and *N. thaumatopios* by having larger, fewer denticles on the dorsal prosomal plate and lacking pseudoarticulations in femur II.

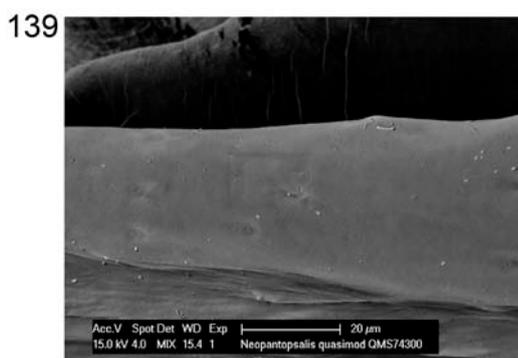
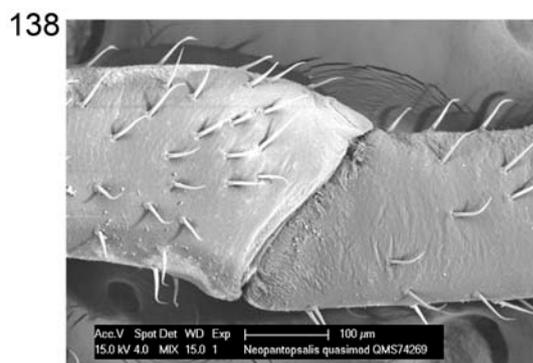
**Description.** MAJOR MALE (N = 10). Prosoma length 2.76 (0.27), width 2.82 (0.34). Dorsal prosomal plate uniformly orange-brown, with bases of denticles silver. Anterior propeltidial area unarmed. Median propeltidial area denticulate, with pair of large denticles at apex of lateral mounds and further denticles anterior and lateral to mounds. Posterior propeltidial area mostly unarmed except for few small denticles lateral to lateral humps. Ocularium with row of few large denticles on each



**FIGURES 130–137.** *Neopantopsalis quasimodo*, male. 130. Lateral view of body showing chelicerae and pedipalps (QM S2481, holotype). 131. Lateral view of body with appendages removed (QM S2481, holotype). 132. Cheliceral fingers, frontal view (QM S74301). 133. Femur to tibia of right leg I, dorsal view (QM S2481, holotype). 134. Total penis, right lateral view (QM S2488). 135. Glans, right lateral view (QM S2488). 136. Glans of same male, ventral view (QM S2488). 137. Glans of different male, ventral view (QM S74301). Scale bars for figs 130–133 = 1 mm; fig. 134 = 0.5 mm; figs. 135–137 = 0.1 mm.

side. Lateral shelves mottled purple-brown, ozopore lobes white. Metapeltidium sclerotised medially to form distinctly round sclerotised area with dorsal prosomal plate. Dorsum of opisthosoma purple-brown, with large white spots, tan transverse stripes at segmental boundaries. Anal operculum white. Venter of opisthosoma tan, with some purple-brown areas laterally.

*Chelicerae.* Segment I 10.74 (1.34), segment II 12.20 (1.44). Very long and slender; purple-brown, with both segments white distally. Both segments evenly denticulate; segment I with larger denticles dorsally than ventrally. Cheliceral fingers sinuous (fig. 132).



**FIGURES 138–139.** *Neopantopsalis quasimodo*, male. 138. Pedipalp, patella/tibia junction, proteral view (QM S74269). 139. Close-up of glans to show sensory pore morphology (QM S74300).

*Pedipalps.* Femur 1.56 (0.17), patella 0.63 (0.04), tibia 0.92 (0.06), tarsus 1.99 (0.16). Unarmed; white with purple-brown bands. No apophyses or hypersertose areas. No plumose setae (fig. 138). Claw with many ventral teeth.

*Legs.* Femora 7.02 (0.66), 11.86 (0.82), 5.96 (0.31), 7.95 (0.52); patellae 1.25 (0.07), 1.37 (0.08), 1.28 (0.06), 1.37 (0.10); tibiae 6.27 (0.47), 12.58 (1.05), 5.82 (0.43), 7.99 (0.63). All segments light tan, with purple-brown bands except tan distitarsi. Coxae I–III with long spines on dorsal distal margins. Trochanter I with three long spines on dorsal proteral margin, other trochanters unarmed. Femur I with proventral longitudinal row of long thin spines, longest at proximal and distal ends, dwindling to small denticles medially, turning along proventral margin at distal end (fig. 133). Dorsal longitudinal row of stouter large denticles, dwindling distally. Small scattered denticles on remainder of femur I. Patella I and tibia I with continuations of both longitudinal rows. Proventral spines long on patella I, turning along distal proventral margin; dwindling distally on tibia, ending ~1/3 of length from proximal end. Dorsal spines short on patella I, reduced to very few at proximal end of tibia. Remaining legs with small scattered denticles on femora, remaining segments unarmed except for distally-directed spines on dorsodistal edges of patellae. Tibia II with eight to eleven pseudosegments; tibia IV with three pseudosegments; femur II without pseudosegments.

*Penis* (figs 134–137, 139). Bristle groups on left side of junction between shaft and glans absent or reduced; anterior right group also greatly reduced. Glans at low angle to shaft; long and dorsoventrally flattened; rectangular in profile. Pores on glans shallowly recessed, not raised on papillae (fig. 139). Stylus directed dorsad from glans.

MINOR MALE (N = 3). Prosoma length 1.37 (0.23), width 2.13 (0.09). Considerably smaller than major male, with lateral mounds not as raised and no postocularial hump. Armature on dorsal prosomal plate not as prominent.

*Chelicerae*. Segment I 4.23 (1.48), segment II 5.36 (1.47).

*Pedipalps*. Femur 1.29 (0.06), patella 0.55 (0.03), tibia 0.77 (0.05), tarsus 1.66 (0.08).

*Legs*. Femora 5.90 (0.23), 10.19 (0.21), 5.23 (0.39), 7.03 (0.31); patellae 1.16 (0.04), 1.25 (0.04), 1.15 (0.12), 1.20 (0.07); tibiae 5.78 (0.36), 10.87 (0.52), 5.36 (0.55), 6.07 (0.34). Spine row on leg I not as developed.

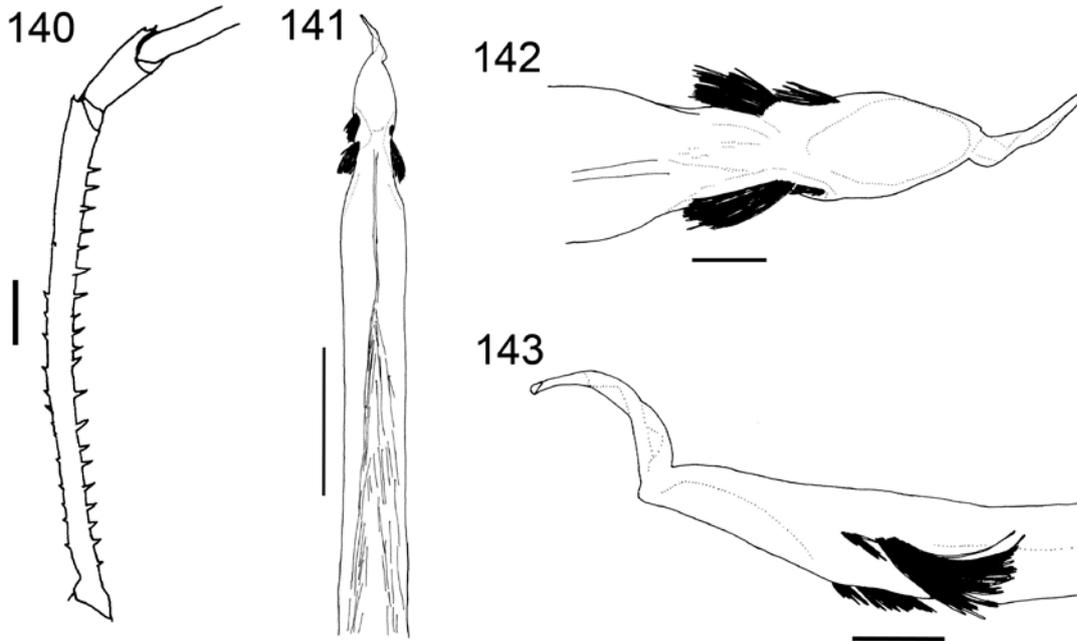
**Variation.** Some specimens differ from the holotype in that the mesopeltidium is not sclerotised. This probably indicates a younger age for these specimens, with less cuticular hardening. Cuticular hardening over time after the last moult can result in significant differences in appearance of individuals of *Eupnoi* at different ages (Shultz 2008). Some individual variation occurs in the amount of denticulation present on the dorsal prosomal plate. In particular, two specimens of QM S3415 show more denticles on the lateral humps, as well as denticles on the posterior hump.

The most significant variation from a taxonomic point of view is that relating to the length of the left bristle groups on the penis. In some specimens (including the holotype) the left bristle groups are entirely absent (fig. 136) whereas in others small but distinct bristle groups are still present (fig. 137). However, no external characters can be identified distinguishing specimens differing in this way. Genitalic polymorphism has been described only occasionally in arachnids, but cannot be ruled out *a priori* (Jocqué 2002). Until the *Neopantopsalis quasimodo* species complex can be properly analysed (see comments below), I provisionally recognise only one species at the type locality.

**Etymology.** The name of this species was given by G. Hunt, and doubtlessly refers to the hunchbacked character from Victor Hugo's novel *Notre-Dame de Paris*.

**Comments.** Specimens comparable to *N. quasimodo* from many localities in north-eastern Queensland are held in the collection at QM. However, a wide range of variation can be seen within and between localities in size, development of the bristle groups on the penis and extent of the proventral spine row on leg I, and it seems likely that a complex of closely related species is involved rather than a single taxon. Unfortunately, establishing species boundaries within the group has proven difficult,

and will require no small amount of study. Matters are complicated further by the uncertain nature of *N. continentalis*, as described below. Until such a study can be conducted, I recommend that specimens similar to *N. quasimodo* be referred to as the ‘*N. quasimodo* complex’.



**FIGURES 140–143.** *Neopantopsalis camelus* (all MV K-8902). 140. Femur to tibia of right leg I, retrolateral view. 141. Total penis, ventral view. 142. Glans, ventral view. 143. Glans, lateral view. Scale bars for fig. 140 = 1 mm; fig. 141 = 0.5 mm; figs 142–143 = 0.1 mm.

***Neopantopsalis camelus* (Forster 1949a) new combination**

(Figs. 140–143)

*Spinicrus camelus* Forster, 1949a: 64–66, figs 1–4, 9–10.

*Neopantopsalis camelus* (Forster)—Taylor & Hunt 2009: 50–51, figs 13–16.

**Material examined.** *Paratypes.* 2 males, 1 juvenile, Tubrabucca, New South Wales, 31°59’S 151°27’E, 19 January 1948, R. T. M. P[escott] & A. N. B[urns] (MV K-8902).

**Diagnosis.** *Neopantopsalis camelus* is distinguished from all other species of *Neopantopsalis* except *N. thaumatopoioides* by the small, granular armature on the dorsal prosomal plate and the presence of pseudoarticulations in femur II. It is distinguished from *N. thaumatopoioides* by having a less rugose ocularium, lateral humps less angular in profile, and shorter, more widely spaced spines on femur I.

**Description.** MALE. A full description of this species is given in Forster (1949a), except for the following: Femur II with five pseudosegments. Penis with left anterior bristle group greatly reduced; stylus directed dorsad from glans (figs 141–143).

**Comments.** Despite being included by Forster (1949a) in his genus *Spinicrus*, there can be no doubting the distinction of *Neopantopsalis camelus* from other species assigned to that genus, particularly the type species *S. tasmanicum*. Together with the closely related *N. thaumatopoios*, *N. camelus* has a more southerly distribution than other species of *Neopantopsalis*.

The leg II used to ascertain the presence of pseudoarticulations in the femur was found detached in the paratype vial.

***Neopantopsalis continentalis* (Roewer 1923) new combination**

*Pantopsalis continentalis* Roewer 1923: 866, fig. 1032; Forster 1949a: 63.

*Spinicrus continentale* (Roewer)—Hickman 1957: 73.

*Neopantopsalis continentalis* (Roewer)—Taylor & Hunt, 2009: 51.

**Type locality.** Winton, Queensland, 22°23'S 143°02'E (Roewer 1923). No material examined.

**Comments.** The original description of *N. continentalis* by Roewer (1923) is unfortunately brief, and inadequate to identify the species involved. In establishing his new genus *Spinicrus* and transferring *Pantopsalis tasmanica* to it, Forster (1949a) mused that it was ‘highly probable that on examination of the type specimen... [*P. continentalis*] will also be placed in *Spinicrus*’, but did not personally do so. Hickman (1957) included this species under the name *Spinicrus continentale* in his key to the genus, but did not discuss it further, and it is unclear whether he did so due to examination of specimens or by inference from Forster (1949a).

The holotype specimen at the Senckenberg Museum, Germany, was not available for direct study due to transport restrictions, but Peter Jäger kindly supplied photos of the holotype and a sketch of its genitalia. The holotype is a minor male of uncertain affinities. The absence of armature on the dorsal prosomal plate or ocularium in Roewer’s (1923) illustration (unfortunately not clearly visible in the photos supplied) originally suggested a relationship with *Neopantopsalis psile*, but the glans of the penis is proportionately longer than in that species and resembles that

of *N. quasimodo*. Though probably a member of the *N. quasimodo* complex, *N. continentalis* is distinguishable from that species in the strict sense by the lack of armature on the dorsal prosomal plate and by having proportionately longer bristle groups on both sides of the penis. Until the identity of *N. continentalis* can be more clearly established, it is omitted from further consideration. Minor males of *Neopantopsalis* generally show a reduction in secondary sexual characteristics, and even with a complete investigation into the *N. quasimodo* complex it may be difficult to conclusively identify *N. continentalis*.

### ***Neopantopsalis pentheter* new species**

(Figs 28, 144–150)

*Neopantopsalis pentheter* Taylor & Hunt, 2009: 51–54, figs 17–23.

**Material examined.** *Male holotype.* Springbrook Repeater, 1000 m, south-east Queensland, 28°15'S 153°16'E, 14 March–15 May 1997, G. Monteith, rainforest intercept (QM S74246; measured).

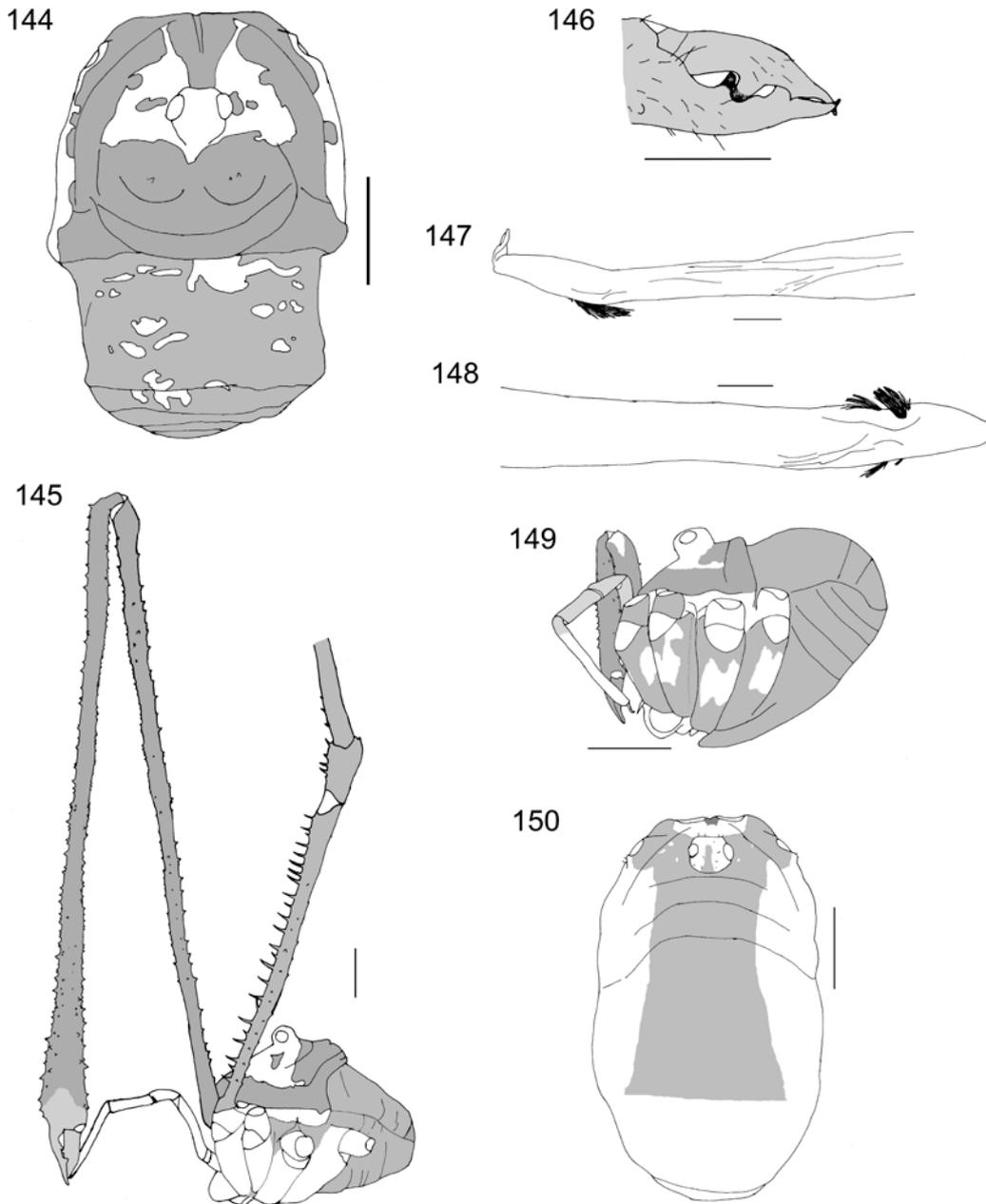
*Paratypes.* 2 males, ditto, 29 February–11 April 1992, D. J. Cook, rainforest intercept (QM S25056; measured); 3 males, ditto, 15 May–30 August 1997, G. B. Monteith, rainforest intercept (QM S35852); 1 male, ditto, 19 February–6 April 1995, G. B. Monteith, intercept trap (QM S38908; measured); 1 male, 2 females, ditto, 31 October–31 December 1997, G. Monteith, rainforest, intercept (QM S56748; females measured); 4 males (including 2 minor males), 1 female, ditto, 14 March–15 May 1997, G. Monteith, rainforest intercept (QM S74246; measured); 5 males (including 2 minor males), ditto, 21 December 1996, G. B. Monteith, pyrethrum, dead trees (QM S74260; minor males measured).

*Other material examined.* 1 male, Binna Burra, Lamington National Park, 28°11'S 153°11'E, 11 February 1981, Y. Lub[in?], RR, VED (QM S2844); 10 males (including 1 minor male), Binna Burra, 28°11'S 153°11'E, 27 March 1976, RR, VED (QM S2835); 1 male, Lamington National Park, south-east Queensland, 28°13'S 153°08'E, 24 March 1973, J. Wessels, Plant Path D.P.I., on road at night (QM S2821; measured); 2 males, Tullawallal, Binna Burra, 950 m, south-east Queensland, 28°12'S 153°12'E, 9 January–6 April 1995, G. B. Monteith, intercept trap (QM S74334); 5 males (including 4 minor males), 1 female, Nagaragoon, Lamington National Park, 28°12'S 153°12'E, 8 April 1976, Queensland Museum

Party (QM S2864; 3 minor males, 1 female measured); 1 male, Wishing Tree Circuit, O'Reillys, Lamington National Park, 28°14'S 153°08'E, 16 January 1990, T. Churchill, night collection (QM S16527); 2 males (including 1 minor male), Lower Ballunju Falls, 500 m, south-east Queensland, 28°12'S 153°12'E, 3 December 1995, G. B. Monteith, pyrethrum, trees (QM S74242; minor male measured); 2 males, 4 females, Mt. Asplenium, 1290m, south Queensland, 28°09'S 152°26'E, 20 December 1992–March 1993, G. Monteith, intercept & pitfall (QM S27468; 2 males, 3 females measured); 1 male, ditto, 30 January 1993, G. B. Monteith, pyrethrum, trees & logs (QM S74239); 1 male, Mt Chingbee, 720 m, 12km SE Rathdowney, south-east Queensland, 17 December 1982, Monteith, Yeates & Thompson, pyrethrum in rainforest (QM S2867); 1 male, Mt Huntley, 1250 m, Queensland, 28°08'S 152°26'E, 29–30 January 1993, G. B. Monteith (QM S49375); 1 male, Mt Matheson, Nightcap Ra., 800 m, New South Wales, 28°32'S 153°18'E, 23 April 2002, G. B. Monteith, pyrethrum, tree trunks (QM S74335); 1 male, Mt. Superbus, Teviot Brook track, 825 m, south-east Queensland, 28°14'S 152°29'E, 8 March 1990, T. Churchill, night (QM S15903; measured); 1 male, Mt Superbus, 8 February 1990, T. Churchill, night collecting, raining, rainforest, active on foliage etc. (QM S16522); 12 males (including 6 minor males), 1 female, Mt. Superbus summit, 1300 m, 8–9 February 1990, Monteith, Thompson & Janetski (QM S35943; 2 minor males measured); 1 male, Mt. Tamborine, Curtis Falls, south-east Queensland, 27°58'S 153°12'E, 27 April 1988, J. Gallon (QM S15434); 1 male, 2 females, Nothofagus Mtn., 1100–1280 m, via Woodenbong, New South Wales, 28°23'E 152°37'E, 4–6 February 1982, G. Monteith & D. Yeates (QM S2877; measured); 1 male, Spicer's Peak summit, 1200 m, south-east Queensland, 28°06'S 152°24'E, 30–31 December 1993, G. B. Monteith (QM S73816); 1 male, Tooloom Scrub, Tucker Box Rd., 28°28'S 152°23'E, 3 February 1983, D. Clyne (QM S2849).

**Diagnosis.** The white 'face' of *Neopantopsalis pentheter* is unmistakable, and allows it to be easily distinguished from all other *Neopantopsalis* species. It is also distinguishable from all other species except *N. psile* by the absence of denticles on the dorsal prosomal plate except for some small armature at the apex of the lateral mounds.

**Description.** MAJOR MALE (figs 144–148; N = 10). Prosoma length 2.22 (0.35), width 2.45 (0.20). Anterior propeltidial area dark brown; ocularium and medial part of median propeltidial area white; lateral part of median propeltidial area



**FIGURES 144–150.** *Neopantopsalis pentheter*. 144. Major male, dorsal view of body (QM S74246). 145. Major male, lateral view of body and anterior limbs (QM S74246). 146. Cheliceral fingers, frontal view (QM S74260). 147. Tip of penis, lateral view (QM S74246). 148. Tip of penis, ventral view (QM S74246). 149. Minor male, lateral view (QM S74260). 150. Female, dorsal view of body (QM S74246). Scale bars for figs 144–146, 149–150 = 1 mm; figs 147–148 = 0.1 mm.

and posterior propeltidial area dark brown. Ocularium and dorsal prosomal plate unarmed except for denticles at apex of lateral mound. Lateral shelves white. Metapeltidium sclerotised except for lateral corners, forming a round sclerotised area

with dorsal prosomal plate. Dorsum of abdomen lighter brown. Venter purple-brown, with white spots.

*Chelicerae*. Segment I 11.46 (2.04), segment II 12.98 (2.17). Proximal half of first segment gold, distal half and second segment chestnut. Both segments evenly covered with denticles. Cheliceral fingers sinuous (fig. 146).

*Pedipalps*. Femur 1.33 (0.09), patella 0.57 (0.05), tibia 0.83 (0.07), tarsus 1.74 (0.15). White with black setae; unarmed. No apophysis or hypersertose areas. Claw with small ventral spines.

*Legs*. Femora 5.87 (0.24), 11.30 (1.07), 5.56 (0.30), 7.07 (0.73); patellae 1.18 (0.09), 1.36 (0.11), 1.12 (0.09), 1.31 (0.09); tibiae 5.94 (0.33), 11.78 (0.98), 5.81 (0.37), 8.08 (0.61). Coxae with chestnut and white patches. Trochanters and bases of femora white, remainder of legs chestnut. Longitudinal row of long spines on proventral side of leg I femur, patella and proximal third of tibia. Longitudinal rows of shorter, stouter spines on retrolateral and dorsal sides. Other legs with longitudinal rows of spines on femora; remaining segments smooth except dorsal distal denticles on patella. Femur II not pseudosegmented; tibia II with 12 pseudosegments; tibia IV with four pseudosegments.

*Penis* (figs 147–148). Both left bristle groups reduced. Stylus directed dorsad.

MINOR MALE (fig. 149; N = 8). Prosoma length 1.25 (0.20), width 1.95 (0.12). As for major form, but smaller, with humps less raised on dorsal prosomal plate.

*Chelicerae*. Segment I 1.96 (0.78), segment II 3.03 (0.82).

*Pedipalps*. Femur 1.10 (0.10), patella 0.47 (0.04), tibia 0.68 (0.05), tarsus 1.37 (0.09).

*Legs*. Femora 5.30 (0.48), 9.18 (1.11), 4.83 (0.44), 6.32 (0.49); patellae 1.06 (0.09), 1.21 (0.07), 1.04 (0.06), 1.08 (0.08); tibiae 5.31 (0.55), 9.66 (1.26), 5.06 (0.55), 6.67 (0.76). Spine row on leg I much reduced. Tibia II with 12 or 13 pseudosegments; tibia IV with 4 or 5 pseudosegments.

FEMALE (fig. 150; N = 9). Prosoma length 1.42 (0.10), width 2.28 (0.10). Dorsum of prosoma anterior to ocularium cream with black medial point on anterior margin, remainder of propeltidium mottled grey-brown with silver patches. Ocularium grey-white, darker along medial groove. Ozopore with silver margins. Mesopeltidium, metapeltidium and anterior part of opisthosoma with silver darkening posterior to light grey-brown band across opisthosoma, or else medially

medium brown and laterally silver. Posterior part of opisthosoma cream. Venter of prosoma white medially, with coxae dark brown distally; genital operculum light brown with dark brown margins; opisthosoma cream medially, medium brown, with cream patches laterally.

*Chelicerae*. Segment I 0.72 (0.08), segment II 1.34 (0.04). Segment I cream with silver reticulation, segment II brown. Both segments unarmed.

*Pedipalps*. Femur 1.13 (0.02), patella 0.55 (0.02), tibia 0.71 (0.02), tarsus 1.41 (0.06). Banded cream and dark brown. Patella triangular distomedially, no distinct apophysis.

*Legs*. Femora 3.32 (0.31), 6.16 (0.45), 3.20 (0.33), 4.78 (0.43); patellae 0.97 (0.09), 1.16 (0.03), 0.93 (0.06), 1.10 (0.04); tibiae 3.19 (0.35), 6.50 (0.61), 3.00 (0.28), 4.55 (0.49). Banded cream and dark brown. Femora with dorsal longitudinal rows of small denticles; remaining segments unarmed.

**Etymology.** From Greek *pentheter*, a mourner, referring to the white ‘face’ of this species.

**Comments.** The majority of female specimens available for this species are poorly preserved, and the variation in colour pattern described for the opisthosoma may represent variation in preservation rather than original differences in live coloration.

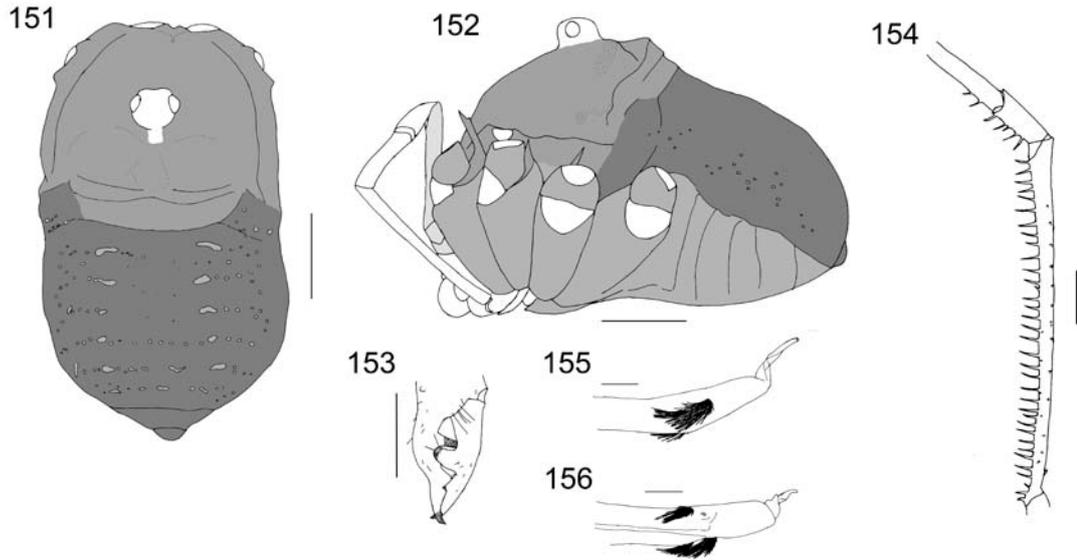
### ***Neopantopsalis psile* new species**

(Figs 4, 151–159)

*Neopantopsalis psile* Taylor & Hunt, 2009: 54–57, figs 24–32.

**Material examined.** *Male holotype*. Kroombit Tops (Calliope Range), 45 km SSW Calliope, Queensland, 24°24’S 150°56’E, 9–19 December 1983, G. Monteith & G. Thompson, open forest (QM S2865; measured).

*Paratypes*. 1 male, Kroombit Tops (Beauty Spot 98), 24°26’S 150°43’S, 9–19 December 1983, G. Monteith & G. Thompson, rainforest (QM S2582; measured); 1 male, Kroombit Tops (Northern Escarpment), 9–19 December 1983, V. E. Davies & J. Gallon, open forest (QM S2588; measured), 1 male, Kroombit Tops (Upper Kroombit Ck.), 24°22’S 151°02’E, 9–19 December 1983, G. Monteith & G. Thompson, open forest (QM S2818; measured).



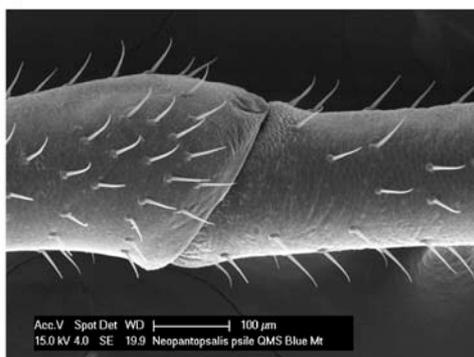
**FIGURES 151–156.** *Neopantopsalis psile*, male. 151. Major male, dorsal view of body (QM S2865). 152. Major male, lateral view of body and pedipalp (QM S2818). 153. Cheliceral fingers, frontal view (QM S2818). 154. Femur to tibia of left leg I, retrolateral view (QM S2818). 155. Glans of penis, lateral view (QM S2865). 156. Glans of penis, ventral view (QM S2865). Scale bars for figs 151–154 = 1 mm; figs 155–156 = 0.1 mm.

*Other material examined.* 8 males, 2 females, 0.6 km SE Blue Mt., 930 m, 21°36'S 148°58'E, 4 October 1999, G. B. Monteith, rainforest, pyrethrum, trees and logs (QM S52050); 5 males (including 1 minor male), 6 females, ditto, 4 October–17 December 1999, D. & I. Cook, rainforest, intercept trap (QM, unnumbered; minor male, females measured); 1 male, ditto, pitfall (QM S74321); 2 males (including 1 minor male), 1 female, ditto, 17 December 1999 – 23 March 2000, Monteith, intercept trap (QM S74266; males measured); 3 males, 7 females, ditto, rainforest, pitfall (QM S57792; 3 males, 2 females measured); 3 males, 3 females, ditto, 23 March 2000, G. Monteith, rainforest, pyrethrum, trees (QM, unnumbered; 2 females measured); 2 males, Mt. Macartney, 900 m, 20°50'S 148°34'E, 19 November 1992, Monteith, Thompson & Janetzki, pyrethrum (QM S74276; measured).

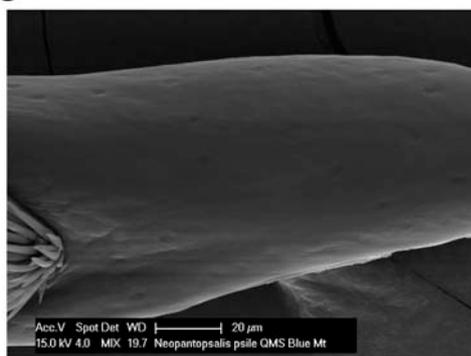
**Diagnosis.** This species is readily distinguished from all species except *N. pentheter* by the absence of armature on the dorsal prosomal plate, and from *N. pentheter* by the absence of white markings on the dorsal prosomal plate.

**Description.** MAJOR MALE (figs 151–158; N = 10). Prosoma length 2.21 (0.40), width 2.54 (0.29). Dorsal prosomal plate orange-brown; lateral margins around and posterior to ozopore iridescent white. Dorsal prosomal plate unarmed. Ocularium iridescent white, unarmed. Metapeltidium and dorsum of opisthosoma

157



158



**FIGURES 157–158.** *Neopantopsalis psile*, major male (QM, Blue Mt., 4 Oct – 17 Dec 1999, intercept trap). 157. Pedipalp, patella/tibia junction, prolateral view. 158. Glans of penis, lateral view; close-up to show sensory pore morphology.

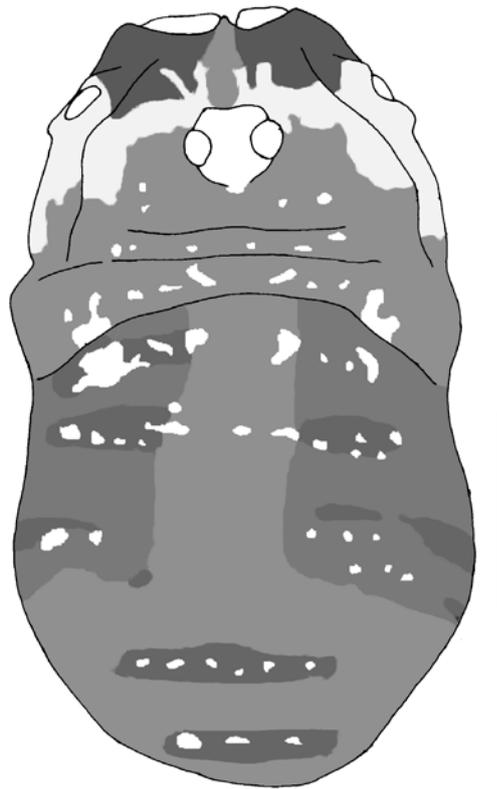
purple-brown, with tan punctures laterally. Venter of prosoma cream medially; coxae dark brown prodistally. Venter of opisthosoma light chocolate.

*Chelicerae.* Segment I 9.47 (1.14), 10.70 (1.29). Segment I golden-orange, darkening to orange-brown distally; segment II orange-brown, fingers golden-yellow. Both segments evenly denticulate, segment I with distinctly larger denticles dorsally than ventrally. Fingers bowed, long (fig. 153).

*Pedipalps.* Femur 1.36 (0.11), patella 0.56 (0.06), tibia 0.86 (0.07), tarsus 1.84 (0.15). White, femur with purple blush. No armature or apophysis. No plumose setae (fig. 157). Aciculate ornamentation over almost entire tarsus. Claw with ventral tooth-row.

*Legs.* Femora 5.98 (0.55), 11.17 (0.91), 5.12 (0.44), 7.20 (0.58); patellae 1.20 (0.07), 1.32 (0.07), 1.08 (0.11), 1.21 (0.09); tibiae 6.10 (0.61), 11.86 (1.21), 5.41 (0.58), 7.61 (0.79). Retrolateral distal ends of coxae, trochanters and proximal ends of femora iridescent white; remainder of legs banded golden yellow and darker brown. Leg I with proventral longitudinal row of hypertrophied spines from femur to proximal end of tibia, not dwindling medially on femur (fig. 154). Dorsal row of shorter stouter spines on proximal half of femur I. All femora with small scattered denticles; remaining segments unarmed except few dorsal denticles on patella I.

*Penis* (figs 4, 155–156, 158). Anterior left bristle group significantly reduced, remaining bristle groups well developed. Glans at low angle to shaft, subrectangular in lateral and ventral view. Pores on glans shallowly recessed, not raised on papillae (fig. 158). Stylus directed dorsad from glans.



**FIGURE 159.** *Neopantopsalis psile*, body of female, dorsal view (QM, Blue Mt., 23 Mar 2000, pyrethrum). Scale bar = 1 mm.

MINOR MALE (N = 2). Prosoma length 1.23 (0.14), width 1.87 (0.13). As above, except considerably smaller size.

*Chelicerae.* Segment I 2.10 (0.01), segment II 3.01 (0.01).

*Pedipalps.* Femur 1.09 (0.01), patella 0.48 (0.03), tibia 0.70, tarsus 1.42.

*Legs.* Femora 4.85, 7.92, 4.27 (0.05), 6.04 (0.22); patellae 0.95, 1.19, 0.95 (0.08), 1.10 (0.01); tibiae 4.65, 8.77, 4.32 (0.19), 5.93 (0.42). No enlarged spine row on femur I. [NB. Those measurements for which no range is given refer to segments that were only preserved in one of the two specimens available. Leg I was only preserved in the QM S74266 minor male whereas the distal half of the pedipalp and leg II were only preserved in the other minor male specimen.]

FEMALE (fig. 159; N = 10). Prosoma length 1.43 (0.24), width 2.19 (0.13). Dorsum of prosoma anterior to ocularium dark brown; remainder of prosoma densely patched with iridescent silver on grey background, lateral shelves almost entirely silver. Dorsal prosomal plate unarmed. Ocularium cream, with darker shading along median groove, unarmed. Mesopeltidium, metapeltidium and opisthosoma with

transverse rows of silver patches. Opisthosoma with grey background, lighter medially and posteriorly than prolaterally, and dark brown patches laterally across segments. Venter of prosoma cream, with coxae dark brown distally; opisthosoma grey, with silver patches laterally.

*Chelicerae*. Segment I 0.76 (0.09), segment II 1.67 (0.11). Segment I dark brown dorsally, cream ventrally; segment II dark brown dorsoproximolaterally, remainder cream; both segments unarmed.

*Pedipalps*. Femur 1.23 (0.07), patella 0.53 (0.02), tibia 0.77 (0.07), tarsus 1.56 (0.09). Banded cream and dark brown. Patella triangular distomedially, no distinct apophysis.

*Legs*. Femora 4.28 (0.32), 7.68 (0.54), 4.02 (0.30), 5.73 (0.39); patellae 1.07 (0.10), 1.27 (0.08), 1.03 (0.09), 1.12 (0.09); tibiae 4.30 (0.26), 8.29 (0.67), 4.23 (0.29), 5.95 (0.39). Femora with longitudinal rows of small denticles dorsally, remaining segments unarmed; legs banded cream and dark brown.

**Etymology.** From the Greek *psilos*, bare or smooth, referring to the absence of armature on the dorsal prosomal plate.

### ***Neopantopsalis thaumatopios* new species**

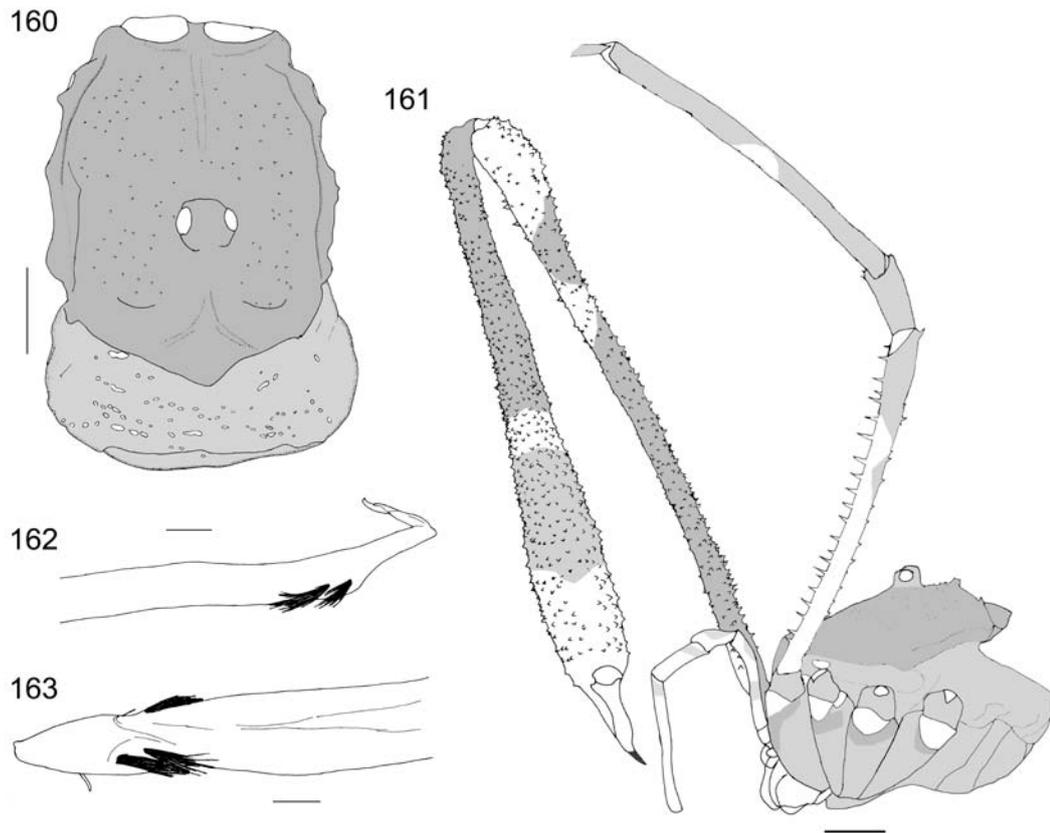
(Figs 160–163)

*Neopantopsalis thaumatopios* Taylor & Hunt, 2009: 57–58, figs 33–36.

**Material examined.** *Male holotype*. New England National Park, New South Wales, 30°28'S 152°29'E, 13 December 1973, R. Raven, under rock (QM S2850).

**Diagnosis.** *Neopantopsalis thaumatopios* is distinguished from *N. camelus* by having a more rugose ocularium, longer proventral spines on femur I, and lateral humps more angular in profile. It is distinguished from all other species by the presence of pseudoarticulations in femur II.

**Description.** MALE. Prosoma length 3.72, width 3.16. Dorsal prosomal plate medium brown, sloped upwards towards posterior, with lateral humps angular in profile with posterior shelf. Postocularial hump directed posteriad. Anterior and median propeltidial areas uniformly covered with small denticles, posterior propeltidial area mostly unarmed. Ocularium lighter than surrounds, rugose. Metapeltidium and dorsum of opisthosoma lighter than pro- and mesopeltidium, with tan punctures. Venter yellow-tan.



**FIGURES 160–163.** *Neopantopsalis thaumatopios*, male (QM S2850). 160. Dorsal view of body. 161. Lateral view of body with anterior limbs. 162. Tip of penis, lateral view. 163. Tip of penis, ventral view. Scale bars for figs 160–161 = 1 mm; figs 162–163 = 0.1 mm.

*Chelicerae.* Segment I 9.88, segment II 11.75. Both segments medium brown proximad, with yellow areas distad; very long and slender, with second segment broader distad and anteroposteriorly flattened; uniformly denticulate. Cheliceral fingers sinuous.

*Pedipalps.* Femur 1.71, patella 0.75, tibia 0.98, tarsus 2.21. White with purple bands; all segments smooth. No apophysis or hypersertose areas. Claw with ventral tooth-comb.

*Legs.* Femora 6.07, 11.00, 5.00, ?; patellae 1.36, 1.56, 1.25, ?; tibiae 5.47, 11.75, 4.80, ? (legs IV not preserved). Banded yellow and brown. Leg I with longitudinal row of elongated spines on proventral side of femur, with longest spines at about two-thirds of the way distad. Longitudinal rows of shorter spines on dorsal and retrolateral sides. Patella and tibia smooth except for spines on dorsodistal margin of patella, and few scattered spines along longitudinal rows of setae in line with rows of spines on femur. Other legs with dorsal and retrolateral rows of spines,

no proventral rows. Femur II with five pseudosegments, tibia II with eleven pseudosegments.

*Penis* (figs 162–163). Left anterior bristle group reduced. Stylus recurved posteriad from glans.

**Etymology.** From Greek *thaumatopoiios*, a performer, puppeteer or acrobat, referring to the resemblance of the relatively large second segment of the chelicera at the end of the narrow first segment to a bowling pin being held by a juggler.

### ***Scissorestis* new genus**

**Type species.** *Spinicrus nigricans* Hickman 1957 by present designation.

**Diagnosis.** *Scissorestis* is distinguishable from *Monoscutum*, *Acihasta*, *Templar* and *Australiscutum* by its proportionately long and slender legs and unornamented opisthosoma, and from all other genera of Enantiobuninae by its small round ozopore without flanking lobes.

**Description.** As for type and only species (see Hickman 1957).

**Etymology.** From the Latin *scissus*, torn, and *restis*, a cord or rope, after the distinctive ‘frayed’ appearance of the ends of the bristles on the penis. Gender feminine.

**Distribution.** Tasmania.

### ***Scissorestis nigricans* (Hickman, 1957) new combination**

(Figs 2–3, 9, 26)

*Spinicrus nigricans* Hickman 1957: 77, figs 34–40.

**Material examined.** 1 major male, Tasmania, V. V. Hickman (AMS KS23737); 1 female, SW Tasmania, 12 February 1977, C. Howard, C. Johnson (AMS KS24747); 2 males, NE Tasmania, August 1993 (QMS C3.2, C5.1); 1 minor male, 1 female, SW Tasmania, Mount Rufus track, 42°07’S 146°07’E, 29 April 1987, R. Raven, T. Churchill, open forest, pyrethrum knockdown (QM S1707).

**Description.** MALE. As for Hickman (1957), except for minor male: As for male, except chelicerae not enlarged relative to female. Armature of chelicerae reduced: segment I mostly unarmed with ventral spur, segment II with dorsal longitudinal row of denticles only, with long black seta on each denticle.

*Penis*. Bristle groups fused basally; terminations of bristles multifurcate. Pores with surrounding rim, not raised.

*Spiracle* (fig. 26). Curtain of partially reticulate spines (reticulation reduced basally) extending partway across spiracle; spines broad, terminations palmate; dense patch of lace tubercles at lateral corner, outer lace tubercles terminally anastomosing.

**Comments.** ‘*Spinicrus*’ *nigricans* is a very distinctive species that has previously been suggested to be misplaced by Hunt (1990). The phylogenetic analysis conducted herein confirms the absence of a close relationship between *S. nigricans* and *S. tasmanicum*, the type species of *Spinicrus*, and hence supports the removal of *S. nigricans* from *Spinicrus*. Indeed, *S. nigricans* may be the basalmost known species of Enantiobuninae (fig. 42). It is therefore intriguing that *S. nigricans* exhibits a number of similarities with species of the subfamily Ballarrinae – ozopores not raised and without flanking lobes, pedipalp patella longer than tibia, and multifurcate lateral processes on the penis. Whether the significance of these features requires further investigation.

### ***Spinibunus* new genus**

**Type species.** *Spinibunus atrocidiana* new species by present designation.

**Diagnosis.** *Spinibunus* is readily distinguished from all other Enantiobuninae by the combination of proportionately long and slender legs and transverse rows of spines on the opisthosoma.

**Description.** As for type and only species.

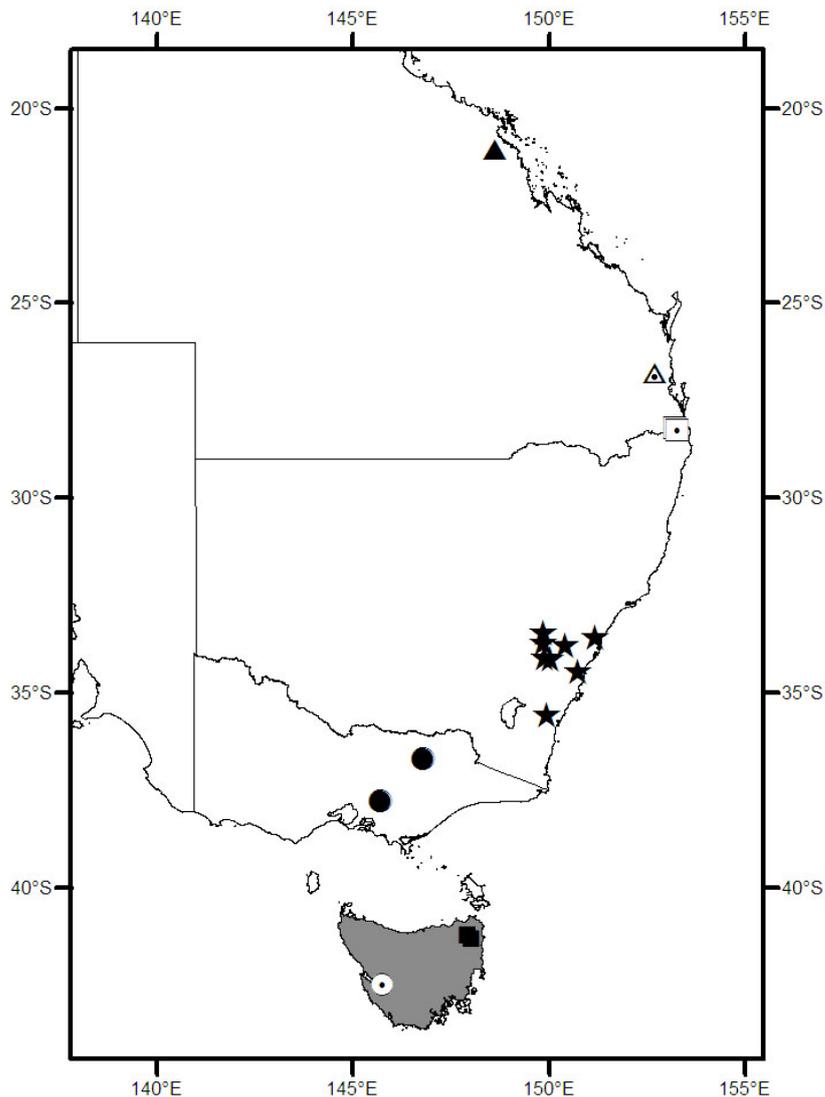
**Etymology.** From the Latin *spina*, spine, as used in *Spinicrus*, combined with the Greek *bounos*, mound, used in the names of numerous phalangioid genera.

**Distribution** (fig. 164). Central eastern Queensland.

### ***Spinibunus atrocidiana* new species**

(Figs 165–172)

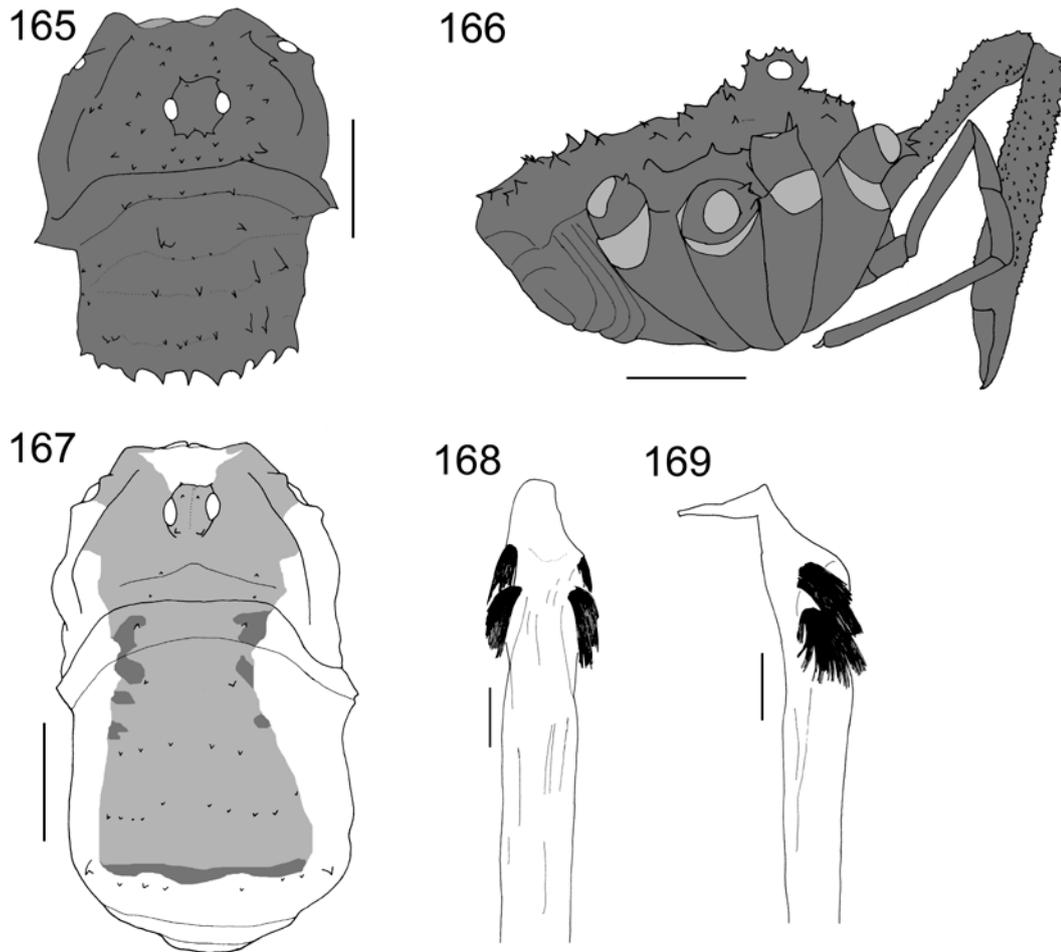
**Material examined.** *Male holotype*. Central Queensland, Mt Dalrymple, 21°03’S 148°38’E, 1200 m, 21 December 1992–10 January 1993, ANZSES Expedition, flight intercept trap (QM S35935).



**FIGURE 164.** Records of distribution for *Spinicrus* and other Enantiobuninae in eastern Australia: grey shading = *Spinicrus tasmanicum*; circle with dot = *Spinicrus sublucens*; solid square = *Spinicrus thrypticum*; solid circle = *Spinicrus stewarti*; solid star = *Spinicruroides caeruleomontium*; square with dot = *Spinicrurellum coronatum*, triangle with dot = *Spinicrurellum puerile*, solid triangle = *Spinibunus atrocidiana*.

*Paratype.* 1 female, ditto (QM S35935).

**Description.** MALE (figs 165–166, 168–169; N = 1). Prosoma length 2.18, width 1.26; total body length 2.66. Body medium brown; darker mottling on prosoma. Dorsal prosomal plate sharply denticulate; denticles along posterior margins of prosomal segments. Lateral spines on each side of metapeltidium.



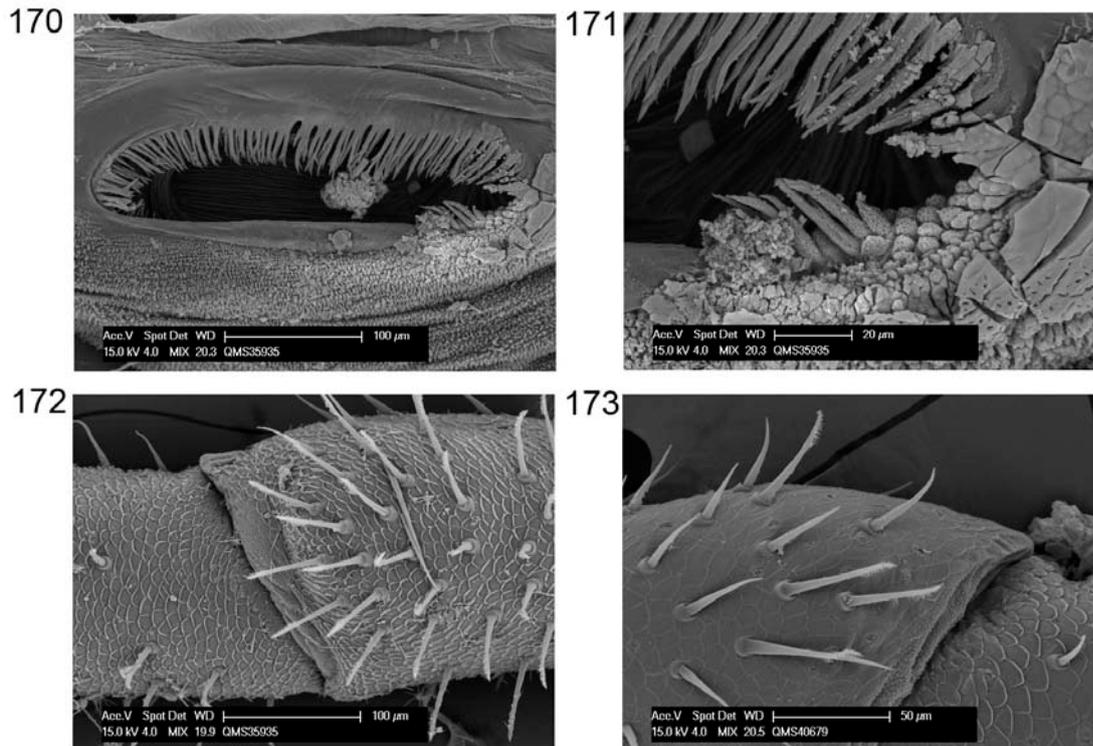
**FIGURES 165–169.** *Spinibunus atrocidiana* (all QM S35935). 165. Body of male, dorsal view. 166. Body of male, lateral view, showing chelicera and pedipalp. 167. Body of female, dorsal view. 168. Penis, ventral view. 169. Penis, lateral view. Scale bars for figs 165–167 = 1 mm; figs 168–169 = 0.1 mm.

Ocularium with high spines. Ozopore large. Abdomen with transverse rows of spines on raised mounds along midlines of first four segments. Coxae golden brown with dark brown patches distally; venter of opisthosoma light grey-brown.

*Chelicerae.* Segment I 1.40, segment II 2.53. Segment II darker than segment I; distal end of segment I white. Both segments evenly denticulate. Cheliceral fingers long, mobile finger angular crescent-shaped.

*Pedipalps.* Femur 1.15, patella 0.53, tibia 0.63, tarsus 1.42. Proximal half of femur brown, distal half of femur to tibia white, tarsus tan. Unarmed; no apophysis on patella. Plumose setae present medially (fig. 172). Microtrichia on distal three-quarters of tarsus; claw with ventral tooth-row.

*Legs.* Femora –, 6.77, 3.48, 5.41; patellae –, 1.19, 1.01, 1.11; tibiae –, 7.89, 3.24, 5.03. Golden brown. Trochanters with robust spines on prolateral face. Leg I



**FIGURES 170–173.** *Spinibunus atrocidiana* and *Spinicrurellum coronatum*, SEM images. 170. *Spinibunus atrocidiana*, spiracle. 171. Same, close-up of lateral corner. 172. *Spinibunus atrocidiana*, right pedipalp, medial view of patella and tibia, showing plumose setae. 173. *Spinicrurellum coronatum*, left pedipalp, medial view of distal end of patella, showing mixture of plumose and non-plumose setae.

not preserved. Femora of remaining legs denticulate; patellae with longitudinal rows of small denticles; remaining segments unarmed. Tibia II with seven or eight pseudosegments; tibia IV undivided.

*Penis* (figs 168–169). Left anterior bristle group slightly reduced, remaining bristle groups well developed. Glans of medium length, edges converging in ventral view.

*Spiracle* (figs 170–171). Dense curtain of robust reticulate spines extending partway across spiracle; terminations of spines multifurcate but not palmate; lace tubercles in lateral corner, with small number of reticulate spines at lateral end of posterior margin.

**FEMALE** (fig. 167; N = 1). Prosoma length 1.5, width 2.3; total body length 3.48. Anterior propeltidial area tan, remainder of propeltidium mottled medium brown. Ocularium with row of denticles on each side. Mesopeltidium medially medium brown, laterally tan with black mottling; small denticles medially. Metapeltidium and first three segments of opisthosoma medially medium brown with

black patches on edge of medial area, laterally tan mottled with black. Metapeltidium and first four segments of opisthosoma with transverse rows of small denticles. Posterior part of opisthosoma tan mottled with black. Coxae patched tan and dark brown; venter of opisthosoma grey with longitudinal rows of dark brown patches.

*Chelicerae*. Segment I 0.77, segment II 1.65. Segment I tan with dark brown lateral patches proximodorsally; segment II golden brown with tan fingers. Unarmed.

*Pedipalps*. Femur 1.28; patella 0.59; tibia 0.72; tarsus 1.60. Femur dark brown on proximal half, tan on distal half with golden brown patch on distalmost end; patella and tibia each golden brown proximally, tan distally; tarsus tan. Unarmed; no apophysis on patella.

*Legs*: Femora 3.56, 6.77, 3.40, –; patellae 1.17, 1.23, 1.11, –; tibiae 3.84, 7.69, 3.24, –. Banded tan and medium brown; longitudinal dorsal rows of denticles on femora and patellae. Tibia II with eight pseudosegments; leg IV not preserved.

**Etymology.** From the Latin *atrox*, cruel, and the goddess Diana. The transverse rows of mounds on the opisthosoma are reminiscent of the figure known as Diana of Ephesus and the epithet ‘cruel’ refers to the addition of a spine on each of the mounds.

### ***Spinicrurellum* new genus**

**Type species.** *Spinicrurellum coronatum* new species by present designation.

**Diagnosis.** *Spinicrurellum* is distinguished from *Megalopsalis*, *Hypomegalopsalis*, *Tercentenarium* and *Forsteropsalis* by the absence of an apophysis on the pedipalp patella. It is distinguished from *Scissorestis* by the presence of ozopore lobes and the simple, pointed terminations to the bristles on the penis. It differs from *Pantopsalis* and *Spinicruroides* in the lack of setae on the mobile cheliceral finger. It differs from *Neopantopsalis*, *Spinicrus* and *Intutoportula* in the shape of the glans, shorter than that of *Neopantopsalis*, but with the sides in ventral view subparallel rather than converging as in *Spinicrus* and *Intutoportula*.

**Description.** Prosoma and dorsum of opisthosoma unarmed. Ozopores large, oblong. Chelicerae unarmed; fingers long, mobile finger closing tightly against finger of segment II. Pedipalps unarmed; patella shorter than tibia; no apophysis on patella; claw with ventral tooth-row. Femora only of legs denticulate; distitarsus II without ventrodiscal bulges on pseudosegments; distitarsi III and IV not swollen

proximally, without ventral brush-like bristles. Sides of glans subparallel in ventral view. Reticulate spines extending partway across spiracle; terminations of spines multifurcate; lace tubercles in lateral corner.

**Etymology.** Diminutive form of genus name *Spinicrus*. Gender neuter.

**Distribution** (fig. 164). Southeast Queensland.

### Key to Species of *Spinicrurellum*

1. Ocularium with double row of denticles...*Spinicrurellum coronatum*  
Ocularium unarmed...*Spinicrurellum puerile*

### *Spinicrurellum coronatum* new species

(Figs 173–180)

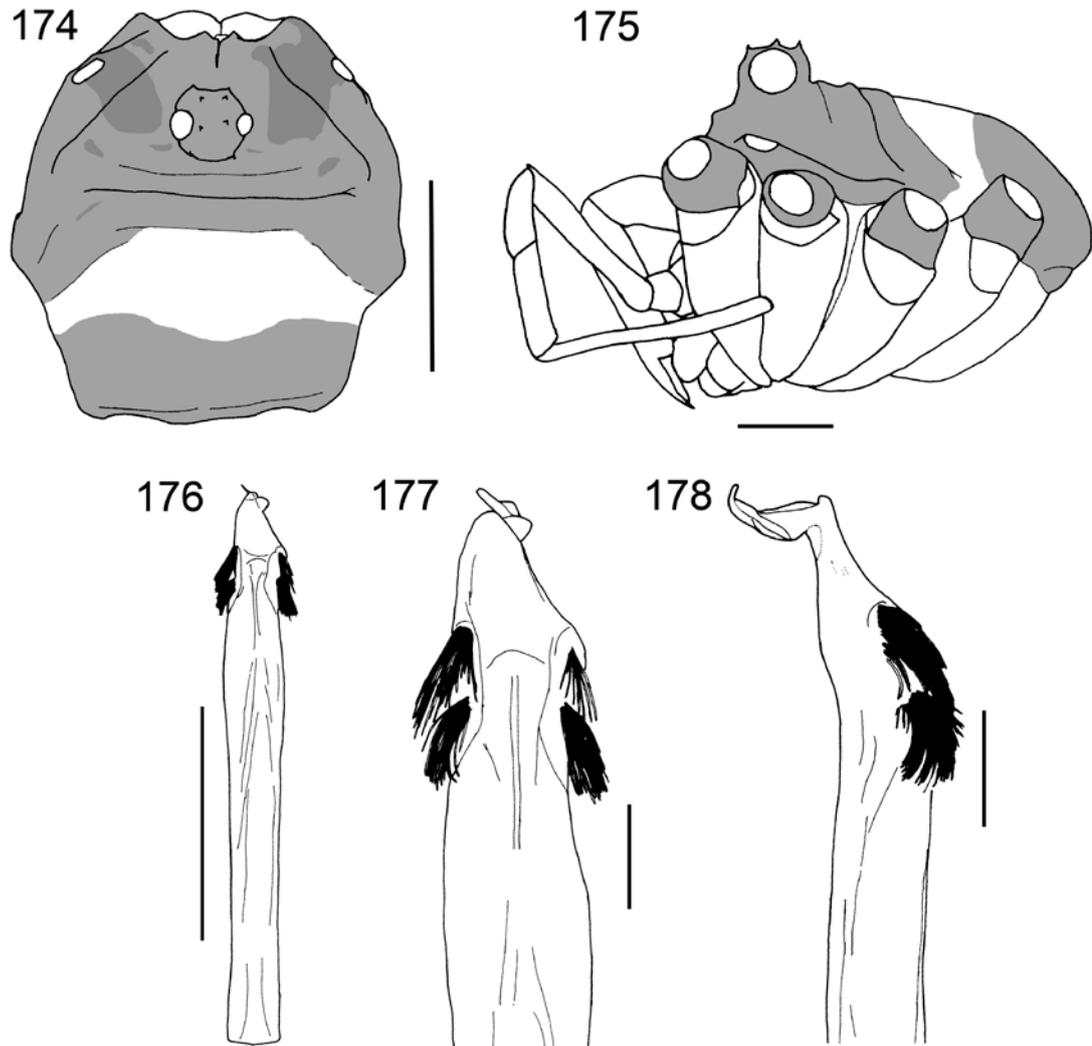
**Material examined.** *Male holotype.* Queensland, Sunday Creek, 18 December 1996–20 January 1997, G. Monteith, rainforest intercept (QM S40679).

*Paratypes.* 1 male, ditto (QM S40679); 1 male, ditto, Conondale Range, 900 m, 2 March – 12 April 1992, D. J. Cook, rainforest pitfall (QM S74237).

**Diagnosis.** *Spinicrurellum coronatum* is distinguished from *S. puerile* by the presence of denticles on the ocularium.

**Description.** MALE (N = 3). Prosoma length 0.97 (0.06), width 1.79 (0.06); total body length 1.94 (0.18). Propeltidium golden-brown reticulated with iridescent white, anterior propeltidial area mottled with black; prosoma unarmed. Lateral shelves mostly iridescent white. Mesopeltidium and metapeltidium medially light golden-brown with transverse rows of iridescent white spots, laterally iridescent gold-white. First three segments of opisthosoma medially yellow-brown with iridescent white spots, median area broadening posteriorly; laterally solid gold-white, fading posteriorly, with medium brown edges medially and along boundary of segments I and II. Posterior part of opisthosoma patched white and mottled purple. Coxae I-III yellow-cream; coxae IV and venter of opisthosoma orange.

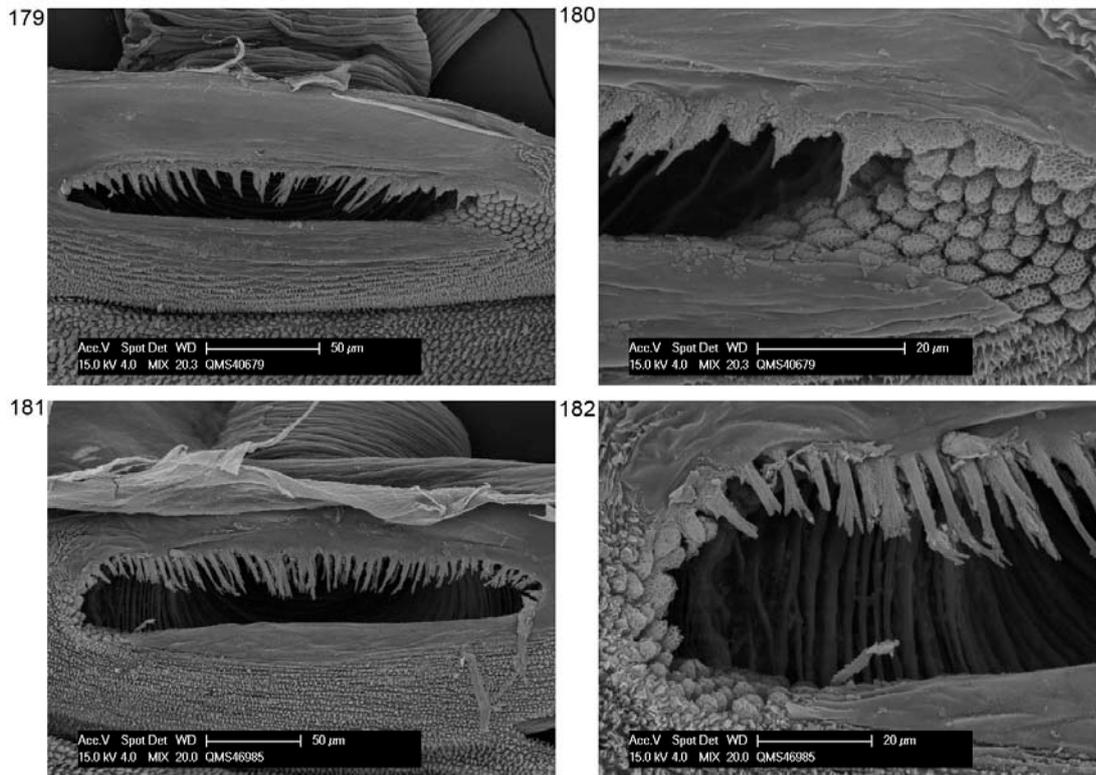
*Chelicerae.* Segment I 0.48 (0.11), segment II 1.09 (0.03). Iridescent white articular membranes between prosoma and chelicerae. Chelicerae white-cream reticulated with iridescent white; unarmed. Fingers long, closing tightly against each other.



**FIGURES 174-178.** *Spinicrurellum coronatum*, male (all QM S74237). 174. Body, dorsal view. 175. Body, lateral view, showing chelicera and pedipalp. 176. Penis, ventral view. 177. Glans, ventral view. 178. Glans, lateral view. Scale bar for fig. 174 = 1 mm; figs 175-176 = 0.5 mm; figs 177-178 = 0.1 mm.

*Pedipalps.* Femur 0.89 (0.01), patella 0.44 (0.02), tibia 0.53 (0.02), tarsus 1.09 (0.04). White-cream, unarmed. Patella with angular mediodistal bulge, but no apophysis; medial side not hypersetose. Small number of plumose setae on mediodistal end of patella only (fig. 173). Microtrichia along most of tarsus; claw with ventral tooth row.

*Legs.* Femora 3.60, 6.70 (0.33), 3.48 (0.19), 5.45 (0.43); patellae 0.88, 0.97 (0.02), 0.80 (0.05), 0.93 (0.04); tibiae 3.36, 7.40 (0.03), 3.06 (0.27), 4.91 (0.31). Trochanters medium-brown, unarmed. Legs banded medium-brown and golden-brown; legs I and III predominantly medium-brown, legs II and IV predominantly golden-brown. Femora with scattered denticles, remaining segments unarmed.



**FIGURES 179-182.** Spiracles of *Spinicrurellum* species. 179. *Spinicrurellum coronatum*, spiracle. 180. Same, close-up of lateral corner. 181. *Spinicrurellum puerile*, spiracle. 182. Same, close-up of lateral corner.

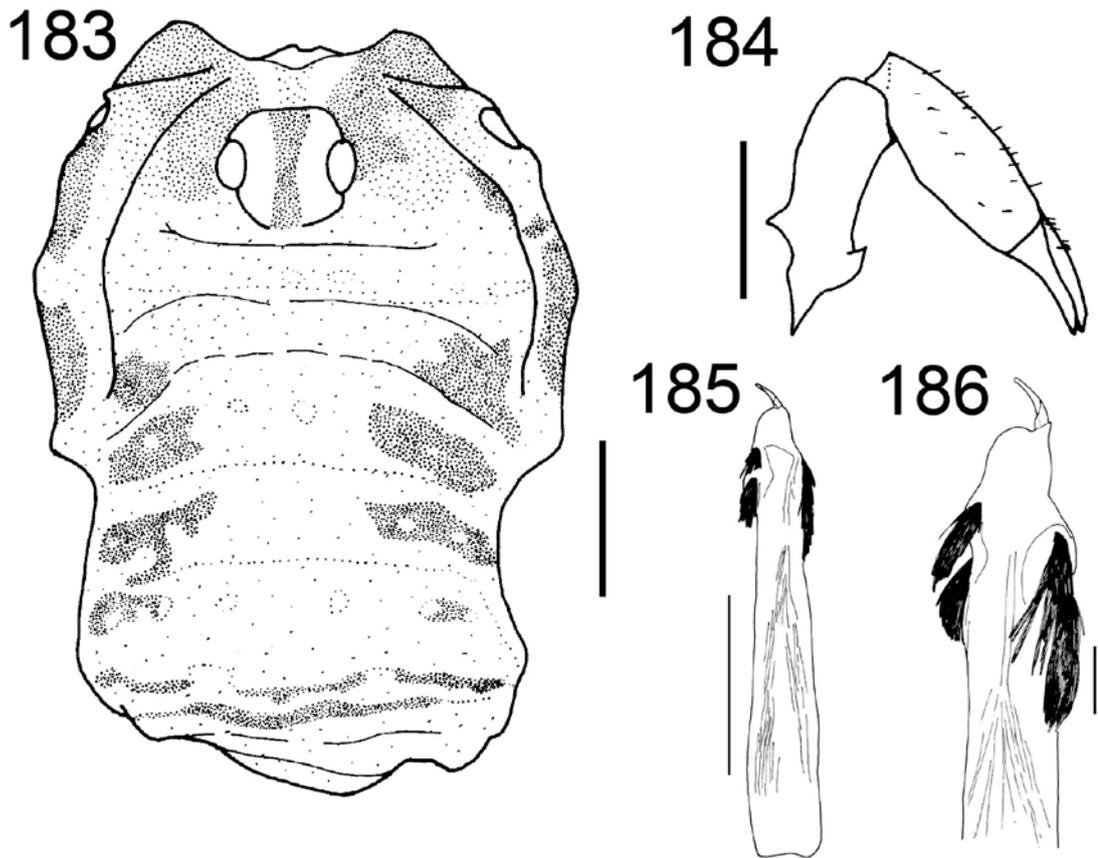
*Penis* (figs 176–178). Tendon relatively short; bristle groups well-developed. Glans of medium length; sides in ventral view subparallel, converging only slightly; dorsal side angled only slightly dorsad from shaft. Pores with surrounding rim, not raised.

*Spiracle* (figs 179–180). Sparse curtain of reticulate spines extending partway across spiracle; spines basally much broader than terminally; terminations of spines simple, pointed, some larger central spines multifurcate; dense patch of lace tubercles at lateral corner.

**Variation.** The paratype specimens differ in coloration from the holotype – this may be due to preservation. QM S74237 has the prosoma golden-brown mottled with orange-brown patches whereas both QM S74237 and the paratype QM S40679 have a brown transverse band, cream in the former and iridescent white in the latter, across the anterior part of the opisthosoma.

**Etymology.** From the Latin *coronatus*, crowned, referring to the denticulate ocularium.

**Comments.** Leg I was only preserved in the holotype.



**FIGURES 183-186.** *Spinicrurellum puerile*, male (all QM S2835). 183. Body, dorsal view. 184. Right chelicera, lateral view. 185. Penis, ventral view. 186. Glans, ventral view. Scale bars for figs 183-185 = 0.5 mm; fig. 186 = 0.1 mm.

***Spinicrurellum puerile* new species**

(Figs 181–186)

**Material examined.** *Male holotype.* SE Queensland, Binna Burra, 27 March 1976, R. Raven, VED, night collection (QM S2835).

*Paratype.* 1 male, Springbrook Repeater, SE Queensland, 1000 m, 28°15'S 153°16'E, 9 January–19 February 1995, G. B. Monteith, intercept traps (QM S46985).

**Diagnosis.** *Spinicrurellum puerile* is distinguished from *S. coronatum* by its unarmed ocularium.

**Description.** MALE (N = 2). Prosoma length 0.89 (0.08), width 1.72 (0.23); total body length 2.37 (0.02). Dorsum entirely unarmed. Anterior propeltidial area with central stripe of light orange-brown between ocularium and anterior margin of prosoma, flanked by two yellow stripes; remainder of anterior and median

propeltidial areas mottled black and dark orange-brown with broad iridescent dark silver patches between ocularium and ozopores. Ocularium iridescent white with dark grey stripe down central groove. Mesopeltidium, metapeltidium and first four segments of opisthosoma orange-yellow medially and along segment boundaries with blackish brown patches laterally; fifth opisthosomal segment with transverse iridescent white stripe bordered by mottled black; remaining segments mottled black with yellow segment boundaries. Mouthparts brown-cream. Coxae dull orange proximally, mottled black distally; venter of opisthosoma iridescent white.

*Chelicerae* (fig. 184). Segment I 0.53 (0.01), segment II 1.07 (0.10). Cream; segment I with iridescent white reticulation dorsally. Both segments unarmed. Fingers long; mobile finger closes tightly with segment II.

*Pedipalps*. Femur 0.94 (0.05), patella 0.45 (0.01), tibia 0.58 (0.01), tarsus 1.15 (0.01). Cream; unarmed. Patella with distomedial bulge, but no true apophysis. Microtrichia on distal three-quarters of tarsus; claw with ventral tooth-comb. *Legs*: Femora 4.16 (0.42), 7.20 (1.58), 4.00 (0.33), 5.65 (0.77); patellae 0.91 (0.05), 1.13 (0.00), 0.87 (0.04), 1.00 (0.03); tibiae 4.10 (0.64), 7.50 (1.47), 3.74 (0.40), 5.46 (0.68). Trochanters mottled black on orange, remaining segments orange-yellow, with widely-spaced mottled black transverse stripes. Femora with scattered denticles, mostly dorsal; other segments unarmed.

*Penis* (figs 185-186). Bristle groups well-developed on both sides, left groups set slightly back and longer than right groups. Glans short, sides in ventral view subparallel, dorsoventrally flattened distally, dorsal surface in plane with shaft. Deep pores.

*Spiracle* (figs 181–182). Curtain of robust reticulate spines extending only partway across spiracle; terminations of spines multifurcate but not palmate; lace tubercles on margin of lateral corner only.

**Etymology.** From the Latin *puerilis*, childish, referring to the lack of ornamentation or significant secondary sexual characteristics in the adult male.

### ***Spinicruroides* new genus**

**Type species.** *Spinicruroides caeruleomontium* new species by present designation.

**Diagnosis.** *Spinicruroides* is distinguished from other genera of Enantiobuninae except *Pantopsalis*, *Forsteropsalis* and *Neopantopsalis* by the

presence of setae on the mobile cheliceral finger. It is distinguished from the remaining genera by the shape of the glans which is short rather than elongate.

**Description.** As for the type and only species.

**Etymology.** From the genus name *Spinicrus* plus the suffix *-oides*, resembling. Gender masculine.

**Distribution** (fig. 164). Central eastern New South Wales.

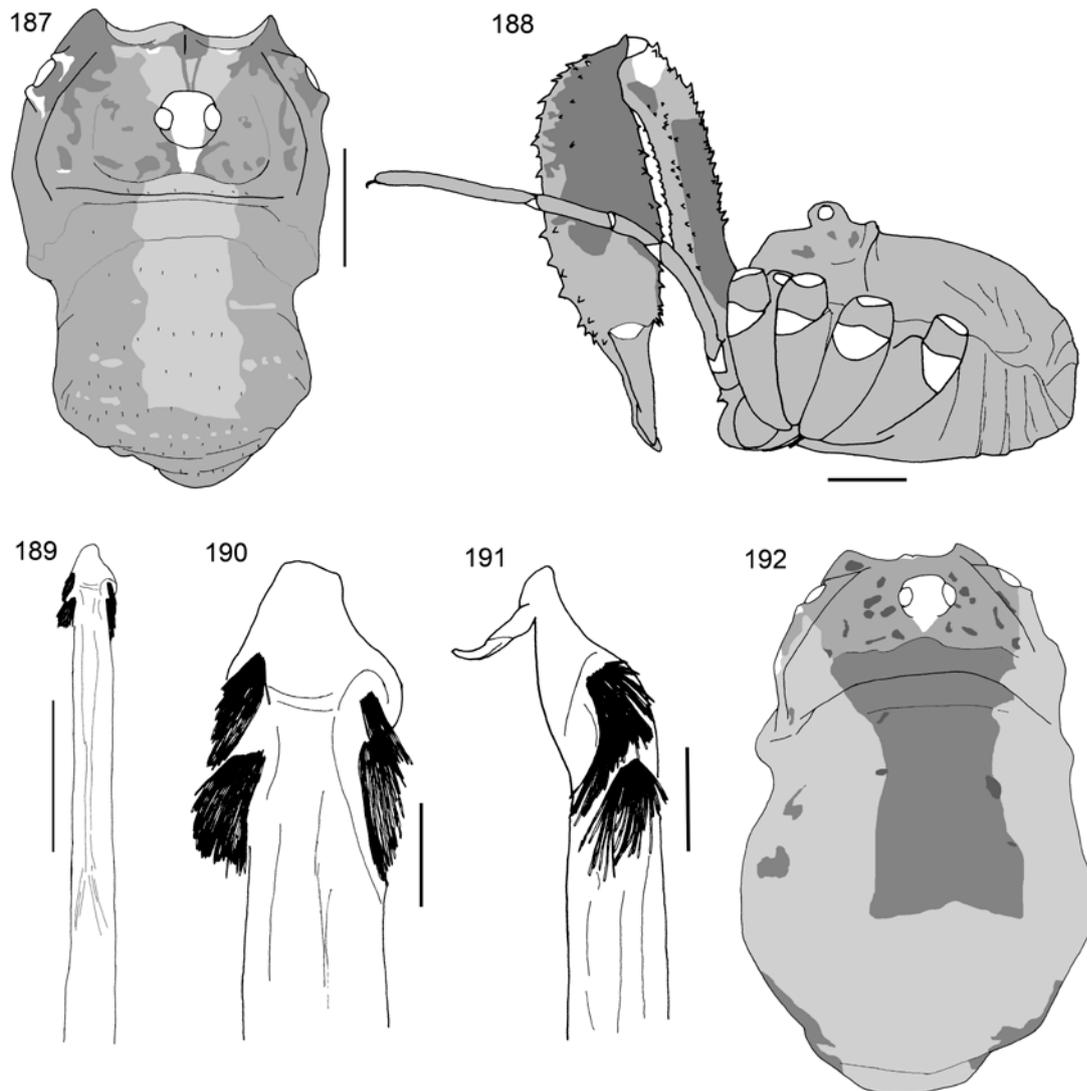
### ***Spinicruroides caeruleomontium* new species**

(Figs 187–194)

**Material examined.** *Male holotype.* Mt Kembla, Sydney Catchment Authority Reserve, New South Wales, 34°26'33"S 150°44'24"E, 11–15 December 1998, L. Gibson, pitfall traps (AMS KS63019; measured).

*Paratypes.* 2 males, 1 female, Blue Mountains road to Ingar picnic area, New South Wales, 33°46'03"S 150°24'30"E, 3 October 1996, pitfall trap (AMS KS57166, KS57168; all measured); 3 males, Clyde Mountain, 35°33'S 149°57'E, 24 October 1968, G. B. Milledge (AMS KS65018; measured); 3 males, 2 females, Kirkconnell, 28 May 1972, G. S. Hunt (AMS KS21480; 2 females measured); 1 male, Mt Shivering (near pluviometer), E of Oberon, New South Wales, 23 September 1972, G. S. Hunt (AMS KS21484; measured); 4 males, 6 females, Mt Werong (near pluviometer), New South Wales, 3 July 1972, G. S. Hunt (AMS KS23117; 2 males, 5 females measured); 4 males, 3 females, Muogamarra Nature Reserve, Pacific Highway, 0.7 km SE of Bird Gully Swamp, New South Wales, 33°33'42"S 151°11'15"E, 2–16 December 1999, M. Gray, G. Milledge, H. Smith, pitfall traps (AMS KS62256; 2 females measured); 1 male, hill NE of Oberon, 10 June 1972, G. S. Hunt (AMS KS21483; measured).

**Description.** MALE (figs 187–191; N = 10). Prosoma length 1.18 (0.16), width 2.37 (0.10); total body length 3.28 (0.34). Propeltidium light orange-brown spotted with white and dark brown patches. Anterior propeltidial area pinkish-brown, with diverging dark-brown lines from ocularium to anterior margin, and dark-brown area around short supracheliceral groove on sharply downturned face. Prosoma unarmed. Ocularium bright white with light orange-brown base and behind eyes; postocularium bright white. Mesopeltidium, metapeltidium and first four segments of opisthosoma grey-brown with slightly lighter median band and distinctive transverse



**FIGURES 187–192.** *Spinicruroides caeruleomontium*. 187. Body of male, dorsal view (AMS KS63019). 188. Body of male, lateral view, showing chelicera and pedipalp (AMS KS63019). 189. Penis, ventral view (AMS KS63019). 190. Glans, ventral view (AMS KS63019). 191. Glans, lateral view (AMS KS63019). 192. Body of female, dorsal view (AMS KS57168). Scale bars for figs 187–188, 192 = 1 mm; fig. 189 = 0.5 mm; figs 190–191 = 0.1 mm.

row of black setae in lighter spots across each segment. Posterior part of opisthosoma yellow-brown dusted with dark-brown; anal operculum silver. Coxae pinkish-brown with median white areas proximally; venter of opisthosoma grey-brown.

*Chelicerae*. Segment I 2.43 (0.53), segment II 3.57 (0.65). Segment I medium-brown dorsally and on proximal two-thirds laterally, peach-coloured ventrally and distolaterally, white patch at distolateralmost end with ventrolateral medium-brown patch directly underneath it; denticulate dorsally and on ventrolateral and ventromedial edges. Segment II inflated, proximally mottled medium-brown and

pink dorsally, medium-brown laterally, peach ventrally; distally pink-cream, fingers yellow-cream; denticulate dorsally and ventrolaterally.

*Pedipalps.* Femur 1.33 (0.11), patella 0.57 (0.04), tibia 0.81 (0.07), tarsus 1.69 (0.13). Trochanter and proximalmost part of femur cream; proximal two-thirds of femur medium-brown, then peach band, then light-brown band; patella pink-brown; tibia pink-brown proximally, cream distally; tarsus pink-brown at proximalmost end, remainder cream. No patellar apophysis. Microtrichia on tarsus and distal third of tibia; tooth-comb on claw.

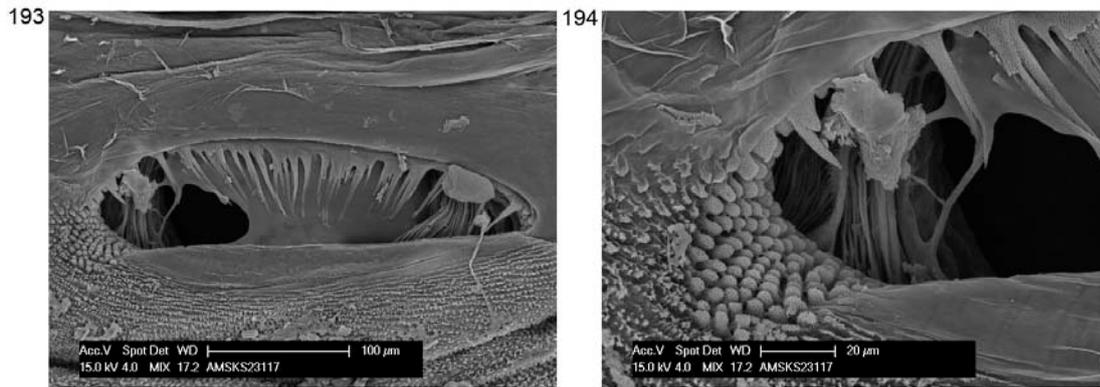
*Legs.* Femora 4.32 (0.28), 7.33 (0.61), 4.01 (0.22), 5.96 (0.30); patellae 1.13 (0.08), 1.29 (0.11), 1.11 (0.11), 1.26 (0.06); tibiae 4.03 (0.28), 7.42 (0.61), 3.88 (0.25), 5.57 (0.32). Trochanters pinkish-cream, unarmed. Legs I and III medium-brown with cream bands, legs II and IV yellow-brown. Femora denticulate, with larger denticles dorsally than ventrally; fewer denticles dorsally on patellae, remaining segments unarmed.

*Penis* (fig. 189–191). Tendon long; bristle groups well-developed. Glans in line with shaft; dorsoventrally flattened for entire length with bases of bristle groups (especially left) consequently more ventral than lateral; glans short, sides converging in ventral view. Deep pores.

*Spiracle* (figs 193-194). Sparse curtain of slender reticulate spines extending only partway across spiracle; terminations of spines multifurcate; dense patch of lace tubercles at lateral corner.

FEMALE (fig. 192; N = 10). Prosoma length 1.30 (0.22), width 2.29 (0.18); total body length 4.60 (0.64). Propeltidium medium-grey-brown with dark-brown patches; prosoma unarmed. Ocularium grey-brown, unarmed. Mesopeltidium, metapeltidium and first three segments of opisthosoma medially dark-grey-brown, laterally whitish-grey with dark-brown patches on lateral margins. Posterior part of opisthosoma whitish-grey with mottled dark-brown patches laterally. Coxae light-brown mottled with white proximally followed by central cream band, medium-brown distally darkening to dark-brown pro- and retrolaterally. Mouthparts and genital operculum light tan. Venter of opisthosoma medium-orange-brown densely mottled with silver-white.

*Chelicerae.* Segment I 0.84 (0.07), segment II 1.66 (0.11). Dark orange-brown reticulated with silver dorsally and large silver-white patch distolaterally on first segment; unarmed.



**FIGURES 193-194.** *Spinicruroides caeruleomontium*. 193. Spiracle. 194. Same, close-up of lateral corner.

*Pedipalps.* Femur 1.21 (0.07), patella 0.55 (0.02), tibia 0.78 (0.04), tarsus 1.55 (0.09). Femur light tan at proximalmost end, remainder medium brown; patella medium brown with small silver patches distolaterally; tibia and tarsus each proximally medium brown, distally light tan silvered dorsally. No apophysis or hypersertose areas; microtrichia over entire length of tibia and tarsus.

*Legs.* Femora 3.57 (0.15), 6.30 (0.36), 3.37 (0.19), 5.20 (0.23); patellae 1.10 (0.05), 1.22 (0.06), 1.06 (0.06), 1.18 (0.09); tibiae 3.40 (0.15), 6.31 (0.24), 3.26 (0.16), 4.84 (0.17). Trochanters grey-tan mottled with white, unarmed. Legs banded medium brown and light tan, with tan bands overlain by silver from distalmost end of femur to tibia. Femora and patellae with longitudinal rows of small denticles.

**Etymology.** From the Latin words *caeruleus*, blue, and *mons*, mountain—“of the Blue Mountains”, in reference to the distribution of this species.

### ***Spinicrus* Forster, 1949a**

*Spinicrus* Forster, 1949a: 63; Hickman, 1957: 73; Crawford, 1992: 43.

**Type species.** *Pantopsalis tasmanica* Hogg 1910 by original designation.

**Included species.** *Spinicrus stewarti* Forster 1949a; *S. sublucens* new species; *S. thrypticum* Hickman 1957.

**Diagnosis.** *Spinicrus* is distinguished from *Megalopsalis*, *Hypomegalopsalis*, *Tercentenarium* and *Forsteropsalis* by the absence of an apophysis on the pedipalp patella. It is distinguished from *Scissorestis* by the presence of ozopore lobes and the simple, pointed terminations to the bristles on the penis. It is distinguished from

*Pantopsalis*, *Neopantopsalis* and *Spinicrurellum* by its short and broad triangular glans. It differs from *Spinicruroides* in lacking setae on the mobile cheliceral finger.

**Description.** Ozopores large, oblong. Dorsum of opisthosoma unarmed. Chelicera segment II at least denticulate; mobile finger closing tightly against finger of segment II. Pedipalp unarmed; patella shorter than tibia; no apophysis on patella; claw with ventral tooth-row. Distitarsus II without distoventral bulges on pseudosegments; distitarsi III and IV not swollen proximally, with double rows of brush-like bristles ventrally. Glans short, triangular in ventral view, distal end dorsoventrally flattened. Spiracle with reticulate or partially reticulate covering spines; lace tubercles present or absent.

**Distribution** (fig. 164). Victoria, Tasmania.

**Comments.** As noted in the discussion of the phylogenetic analysis, the validity of this genus as circumscribed herein is poorly supported and future analyses may lead to its further subdivision. *Spinicrus thrypticum*, not included in the phylogenetic analysis, remains assigned to *Spinicrus* on the basis of its similarity to *S. stewarti*. Despite its doubtful monophyly, *Spinicrus* is biogeographically distinct from most other Enantiobuninae. Three of the four species are found in Tasmania whereas *S. stewarti* is found on the other side of the Bass Strait in Victoria.

*Spinicrus tasmanicum* and *S. thrypticum* were described in detail by Hickman (1957), and so are not redescribed here. Both sexes of *Spinicrus tasmanicum* can be distinguished from other Neopilionidae by their distinctive elongate opisthosoma as illustrated by Hickman (1957: fig. 23); this distinction is even more pronounced in the female. *Spinicrus thrypticum* can be distinguished from other Neopilionidae except *S. stewarti* and some *Megalopsalis* and *Neopantopsalis* species by the dense armature of spines on the prolateral face of each trochanter; it differs from *Megalopsalis* in the lack of an apophysis on the patella, from *Neopantopsalis* in the absence of raised humps on the dorsal prosomal plate and from *S. stewarti* in the lack of denticles on basitarsus I (but see comments for *S. stewarti* below).

#### **Key to Species of *Spinicrus***

1. Opisthosoma elongate; penis without left lateral protrusion (Tasmania)...*Spinicrus tasmanicum*

Opisthosoma not elongate; left lateral protrusion on penis at shaft-glans junction above bristle groups...2

2. Dorsum of prosoma unarmed (Tasmania)...*Spinicrus sublucens*

Dorsum of prosoma strongly denticulate...3

3. Basitarsus I often denticulate (Victoria)...*Spinicrus stewarti* (see comments below)

Basitarsus I unarmed (Tasmania)...*Spinicrus thrypticum*

### ***Spinicrus stewarti* Forster, 1949a**

(Figs 195–198)

*Spinicrus stewarti* Forster, 1949a: 68–70, figs 11–16.

**Material examined.** *Paratypes.* 1 female, Victoria, Mount Buffalo, 30–31 December 1947, ex bole of snow gum (*Eucalyptus pauciflora*) (NMV K-8910); 8 males, ditto (NMV K-8911-8919).

*Other material examined.* 1 male, Victoria, Lala Falls, near Warburton, 37°46'S 145°42'E, 22 December 2002, M. S. Harvey, M. E. Blosfelds, under bark of *Eucalyptus regnans* (WAM T72315).

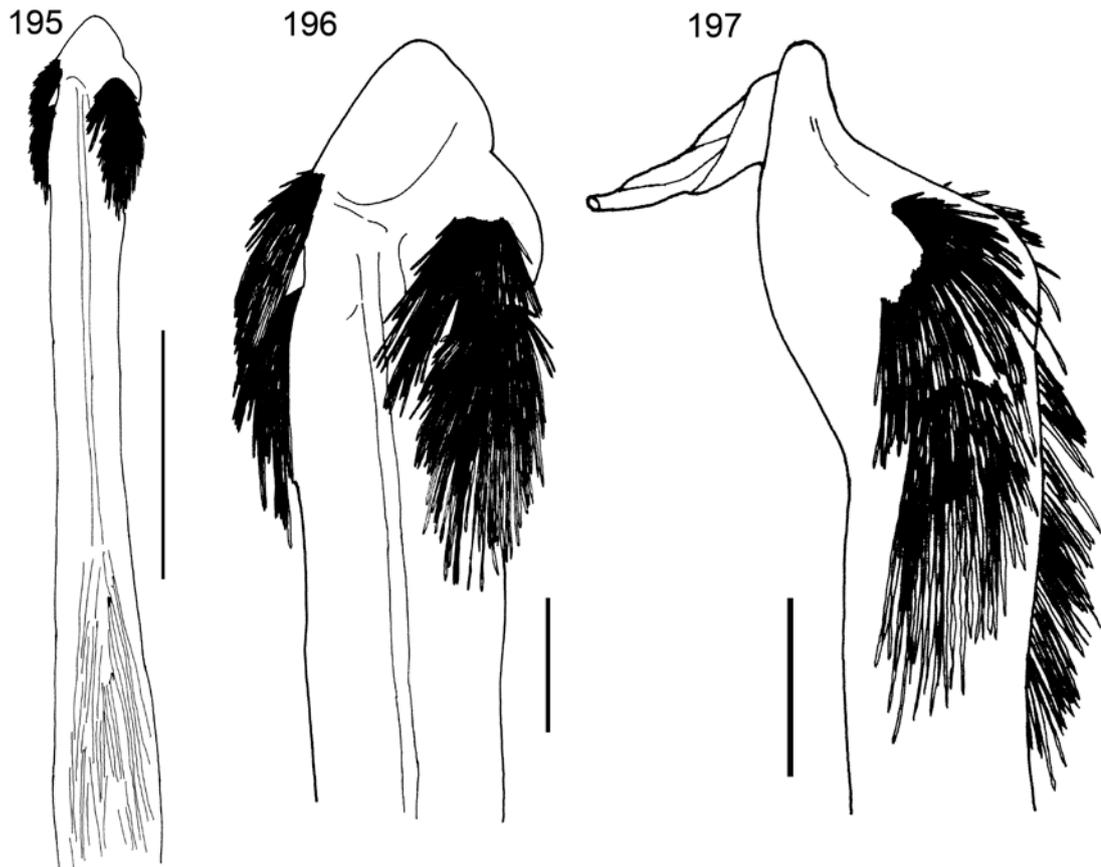
**Diagnosis.** *Spinicrus stewarti* is readily distinguished from *S. sublucens* and *S. tasmanicum* by the high level of denticulation over the entire prosoma; *S. sublucens* has an unarmed prosoma whereas *S. tasmanicum* has denticles restricted to the anterior propeltidial area. Larger specimens of *S. stewarti* are potentially distinguished from *S. thrypticum* by the presence of denticles on basitarsus I (see comments below).

**Description.** MALE. Description as in Forster (1949a), except following.

*Chelicerae.* Length of chelicerae variable.

*Legs.* Leg I with anterior longitudinal row of enlarged denticles from proximal end of femur to distal end of tibia (males with smaller chelicerae with reduced denticle row on femur only), scattered denticles on basitarsus I; smaller row on femora and patellae of other legs.

*Penis* (figs 195-197). Shaft and tendon elongate; all four bristle-groups well-developed. Distinct lateral protrusion of glans above left anterior bristle group. Glans short, broad, triangular in dorsal view, dorsoventrally flattened at distal end. Pores shallowly recessed.



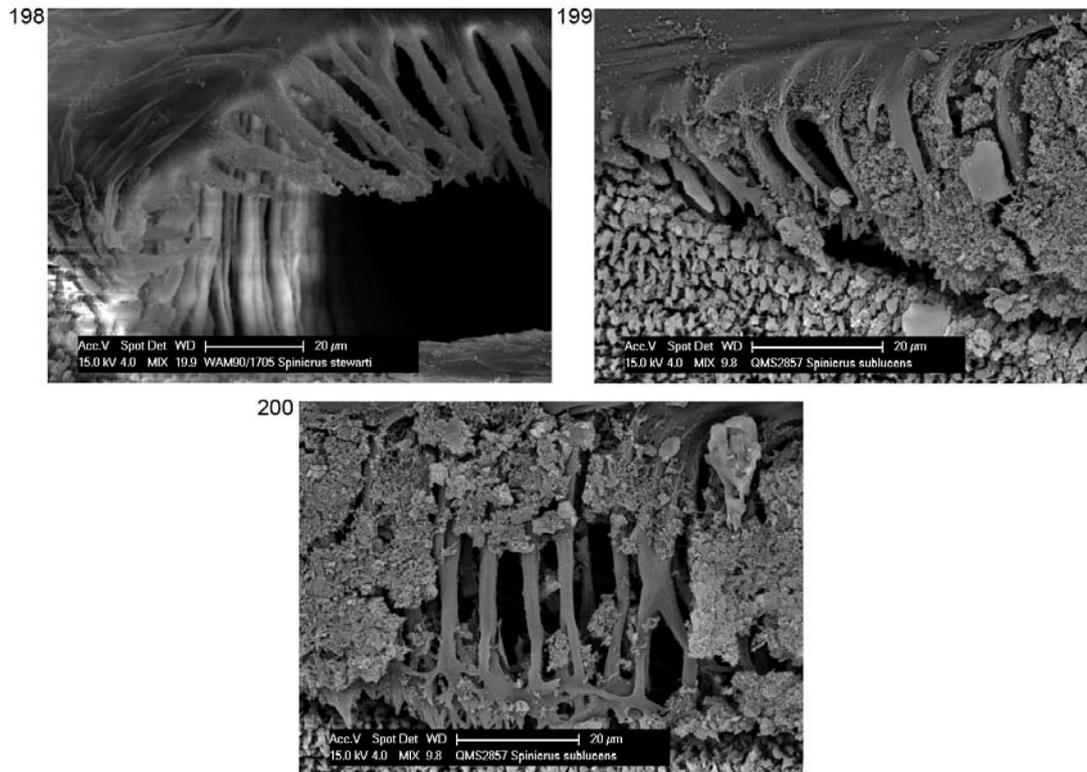
**FIGURES 195–197.** *Spinicrus stewarti*, male (all WAM T72315). 195. Penis, ventral view. 196. Glans, ventral view. 197. Glans, ventrolateral view. Scale bar for fig. 195 = 0.5 mm; figs 196–197 = 0.1 mm.

*Spiracle* (fig. 198). Reticulate spines extending only partway across spiracle; terminations of spines palmate; small group of lace tubercles in lateral corner.

**FEMALE.** Description as in Forster (1949a), except all legs with dorsal longitudinal row of small denticles along femora.

**Comments.** Forster (1949a) stated that the holotype and female paratype had been deposited in NMV and the remaining male paratypes (of unspecified number) had been deposited in the Canterbury Museum, Christchurch, New Zealand (CMNZ). However, as indicated above, NMV holds eight male specimens of this species labelled as paratypes. Because these specimens share the same collection data as the female paratype, it seems likely that these correspond to the specimens that Forster (1949a) intended to place in CMNZ.

The distinction between *Spinicrus stewarti* and *S. thrypticum* requires confirmation. Hickman (1957) distinguished the two by the presence of denticles on tibia I in *S. thrypticum*, compared to their supposed absence in *S. stewarti* as



**FIGURES 198–200.** Spiracles of *Spinicrus* species. 198. *Spinicrus stewarti*, lateral corner. 199. *Spinicrus sublucens*, lateral corner. 200. Same, showing anastomosing ends of median spines.

described by Forster (1949a). However, specimens of *S. stewarti* with longer chelicerae also have more extensive denticulation on leg I, extending as far as the basitarsus. There is insufficient data as yet to determine whether this indicates a division between major and minor males or whether variation is continuous. Hickman's (1957) description of *S. thrypticum* (still known only from the male holotype and female paratype) suggests that it may have longer chelicerae than specimens of *S. stewarti* with comparable denticulation.

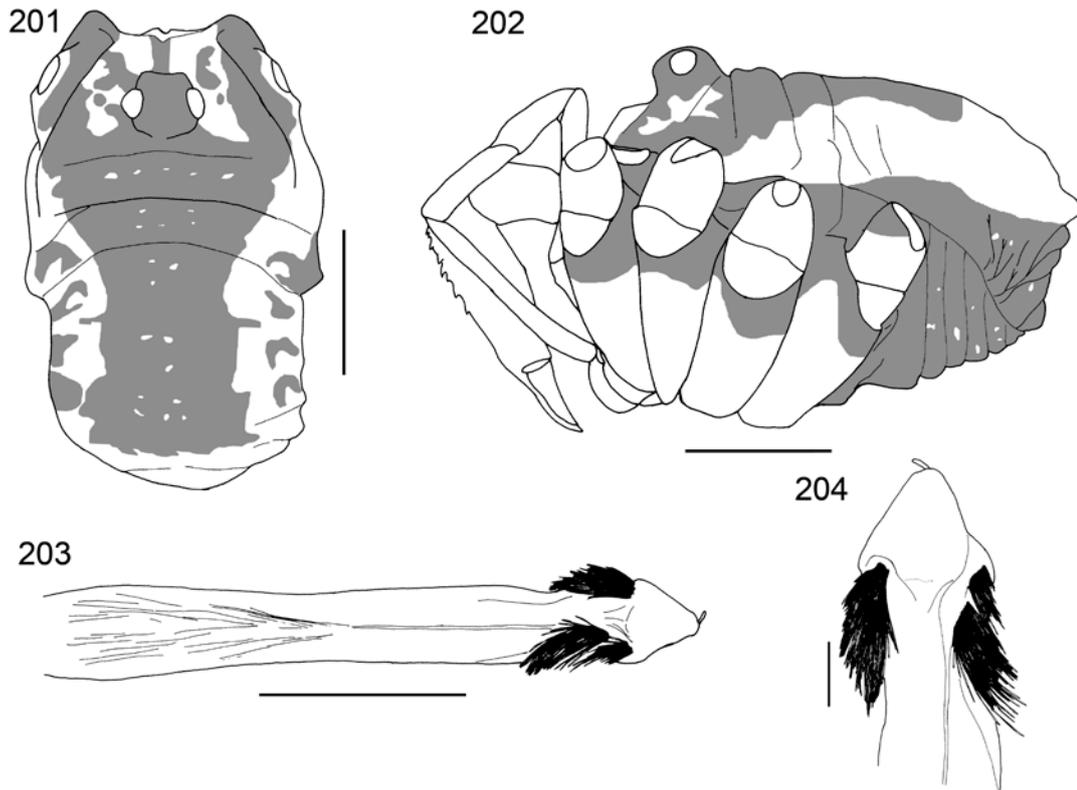
### ***Spinicrus sublucens* new species**

(Figs 199–204)

**Material examined.** *Male holotype.* SW Tasmania, Franklin River, below Goodwin's Peak, January 1983, ANZSES Expedition (QM S2857).

*Paratypes.* 1 male, 1 female, as above (QM S2857).

**Diagnosis.** *Spinicrus sublucens* can be readily distinguished from other *Spinicrus* species by the absence of enlarged chelicerae. It can be distinguished from



**FIGURES 201–204.** *Spinicrus sublucens*, male (all QM S2857). 201. Body, dorsal view. 202. Body, lateral view, showing chelicera and pedipalp. 203. Penis, ventral view. 204. Glans, ventral view. Scale bars for figs 201–202 = 1 mm; fig. 203 = 0.5 mm; fig. 204 = 0.1 mm.

*Scissorestis nigricans* by its larger oblong ozopore, from *Spinicrurellum* by the converging edges in dorsal view of the shorter glans, and from *Intutoportula* by the left lateral protrusion at the junction of shaft and glans.

**Description.** MALE (N = 2). Prosoma length 1.34 (0.01), width 1.99 (0.01); total body length 2.66 (0.09). Dorsum entirely unarmed. Dark tan stripes from ocularium to anterior margin, remainder of anterior iridescent white. Median propeltidial area white with dark brown patches. Posterior propeltidial area mottled dark brown. Lateral shelves dark brown anteriorly, iridescent white around and posterior to ozopores. Ocularium golden-brown with anterior face silver. Mesopeltidium, metapeltidium and first four segments of opisthosoma medially yellow-brown edged with dark brown with medial iridescent white spots; laterally iridescent white with dark purple mottling. Posterior of opisthosoma white with purple mottling. Venter of prosoma cream, coxae mottled black distally; opisthosoma purple-brown with transverse rows of iridescent white spots.

*Chelicerae*. Segment I 0.68 (0.00), segment II 1.65 (0.11). Yellow-cream with tan mottling; not particularly enlarged compared to female. Segment I unarmed, segment II with proximodorsal denticles only. Fingers long, mobile finger closely opposed to finger of segment II.

*Pedipalp*. Femur 1.13 (0.03), patella 0.54 (0.06), tibia 0.70 (0.00), tarsus 1.35 (0.04). Banded dark brown and yellow-brown; unarmed; no apophyses. Ventral tooth-comb on claw.

*Legs*. Femora 3.50 (0.11), 6.26 (0.18), 3.28, 5.44 (0.35); patellae 1.17 (0.05), 1.27, 1.02, 1.13 (0.10); tibiae 3.15 (0.11), 5.48, 3.08, 4.70 (0.28). Banded dark brown and yellow-brown, with prominent iridescent white spots around accessory spiracles on tibiae. No denticles, but robust spinose setae on all legs to tibiae. Brush-like bristles intermittently present on ventral side of distitarsi III and IV. Femur II not pseudosegmented, tibia II with six pseudosegments, tibia IV with two pseudosegments.

*Penis* (figs 203–204). Left anterior bristle group reduced, but left posterior group well-developed. Glans short, triangular in dorsal view, dorsoventrally flattened, dorsal edge in plane with shaft.

*Spiracle* (figs 199–200). Sparse spines, reticulate basally with reticulations fading terminally, extending across spiracle; terminations of spines palmate, anastomosing; no lateral lace tubercles.

FEMALE (N = 1). Prosoma length 1.40, width 2.03; total body length 4.45. As for male except for following. Ocularium iridescent white. Venter of opisthosoma duller.

*Chelicerae*. Segment I 0.75, segment II 1.32. Unarmed.

*Pedipalps*. Femur 1.01, patella 0.50, tibia 0.64, tarsus 1.27.

*Legs*. Femora 2.32, 4.45, 2.28, 3.56; patellae 0.82, 1.01, 0.93, 0.95; tibiae 2.43, 4.30, 2.35, 3.44. Tibia IV undivided.

**Etymology.** From the Latin *sublucens*, gleaming faintly, in reference to the iridescent patches covering part of the dorsum.

**Comments.** Those segments in the male description for which a standard deviation is not given were only preserved in the holotype.

Whereas *Spinicrus sublucens* possesses brush-like bristles on distitarsi III and IV as found in *S. stewarti* and *S. tasmanicum*, the number of bristles is reduced and

they are proportionately more widely spaced and less regular. This may be related to *S. sublucens*' smaller size.

### ***Templar* new genus**

**Type species.** *Templar incongruens* new species by present designation.

**Diagnosis.** Distinguished from *Acihasta* by absence of flanking spines on the dorsum of the opisthosoma and from *Monoscutum* by denticles on dorsum of body being simple and rounded, not complex, without large denticle on ocularium. Pedipalp patellar apophysis short, rounded. Legs short (e.g., femur II ca. one-third length of body versus three-quarters in *Monoscutum*).

**Description.** As for type and only known species.

**Etymology.** Name given in recognition of the appearance of the female of the type species – heavily armoured, and with a Cross marking.

**Distribution.** Canterbury, New Zealand.

### ***Templar incongruens* new species**

(Figs 205–212)

*Templar incongruens* Taylor 2008a: 176–177, figs 1–8.

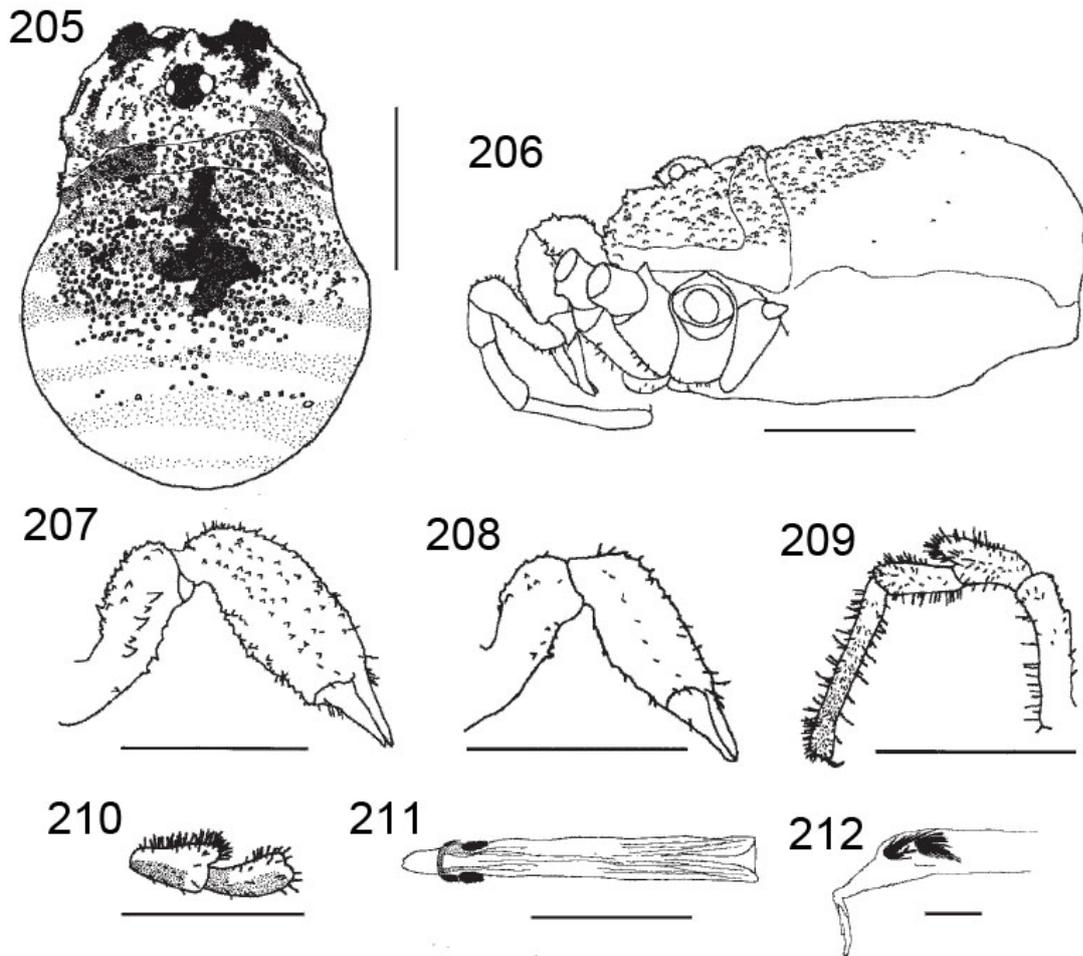
**Material examined.** *Male holotype.* Ahuriri Reserve, mid Canterbury, South Island, New Zealand, 43°41'S 172°38'E, 22 January 2000, M.S. Harvey (CMNZ).

*Paratype.* 1 female, collected with holotype (CMNZ).

**Description.** MALE (figs 205, 207, 210–212; N = 1). Prosoma length 0.76, width 1.52; total body length 2.3. Mottled medium and dark brown; dorsal prosomal plate with lighter longitudinal stripes on either side of ocularium. Dorsum of prosoma and first five segments of opisthosoma except for lateral margins densely and evenly covered with simple, rounded denticles. Ocularium rugose. Ozopores small, not visible from above.

*Chelicerae* (fig. 207). Segment I 0.72, segment II 1.42. Both segments heavily denticulate. Segment I with ventral row of large denticles. Segment II enlarged relative to segment I. Outside of fingers smoothly convex.

*Pedipalps.* Femur 0.57, patella 0.29, tibia 0.35, tarsus 0.71. Femur without spines; setae in rows on sides and centreline of femur, with concentration of setae at



**FIGURES 205–212.** *Templar incongruens*. 205. Body, dorsal view (female paratype). 206. Body, lateral view, showing chelicera and pedipalp (female paratype). 207. Right male chelicera, retrolateral view (holotype). 208. Right female chelicera, retrolateral view (paratype). 209. Right female pedipalp, medial view (paratype). 210. Patella and tibia of male pedipalp, dorsal view (holotype). 211. Penis, ventral view (holotype). 212. Glans, lateral view (holotype). Scale bars for figs 205–210 = 1 mm; fig. 211 = 0.05 mm; fig. 212 = 0.01 mm.

inner distal end. Patella with rows of setae on sides and centreline. Patella apophysis rounded, not extending far past patella-tibia junction, with scattered large setae (fig. 210). Tibia with rows of setae on sides, otherwise glabrous, and concentration of setae at inner distal end. Tarsus uniformly covered with small setae, with interspersed large setae.

*Legs.* Femora 0.88, 1.81, 0.86, 1.32; patellae 0.40, 0.70, 0.35, 0.53; tibiae 0.83, 1.68, 0.81, 1.09. Legs noticeably shorter than in other Monoscutidae. Femora, patellae and tibiae of all legs denticulate except leg II, which has only femur denticulate. Tibia II not divided into pseudosegments.

*Penis* (figs 211-212). Glans bent dorsad to shaft, stylus slightly anterior from vertical. Bristle groups on left smaller than right, with left anterior group very reduced.

FEMALE (figs 206, 209; N = 1). Prosoma length 1.0, width 1.84; total body length 2.94. Features as for male except for following. Mottled medium- and yellow-brown with darker median crucifix-shaped marking on opisthosoma from first to fourth segments, with “cross-bar” on third segment.

*Chelicerae*. Segment I 0.43, segment II 0.96. Chelicerae smaller than in male; no row of enlarged denticles on segment I.

*Pedipalps* (fig. 209). Femur 0.74, patella 0.33, tibia 0.40, tarsus 0.95.

*Legs*. Femora 0.95, 1.87, 0.84, 1.34; patellae 0.45, 0.76, 0.41, 0.54; tibiae 0.68, 1.97, 0.86, 1.18.

**Etymology.** Latin for “incongruent,” to reflect the presence in this species of enlarged chelicerae in the male, a feature previously associated with the subfamily Megalopsalidinae, not Monoscutinae.

**Comments.** Due to insufficient specimens, it cannot be established at present whether the differences in colour pattern described for the male and female represent differences between the sexes or simply differences between individuals. Unfortunately, the male genitalia were lost after examination.

### ***Tercentenarium* new genus**

**Type species:** *Tercentenarium linnaei* new species (= *Megalopsalis linnaei* Taylor 2008a) by present designation.

**Description.** As for type and only known species.

**Etymology.** From the Latin *tercentenarium*, three-hundredth anniversary, as the type species was given the species name ‘*linnaei*’ to mark the three-hundredth anniversary of the birth of Carl Linnaeus. Gender neuter.

**Distribution.** Southwest Western Australia.

**Comments.** The type species of this genus was provisionally placed in the genus *Megalopsalis* by Taylor (2008a); however, it differs significantly from other *Megalopsalis* species in a number of features, including genital and cheliceral morphology. Phylogenetic analysis did not support an association of *M. linnaei* with other *Megalopsalis* species; instead, a sister relationship between *M. linnaei* and the

'Monoscutinae' was suggested, and *M. linnaei* has consequently been removed from *Megalopsalis*. The phylogenetic association of Western Australian (*Tercentenarium linnaei*) and New Zealand ('Monoscutinae') species with no known geographic intermediates is unusual, but no suitable explanation is currently forthcoming. In light of the significant age suggested for many generic divisions in Enantiobuninae (see discussion of phylogenetic analysis above), it seems likely that this represents a relictual distribution following the extinction of interlinking members of this clade.

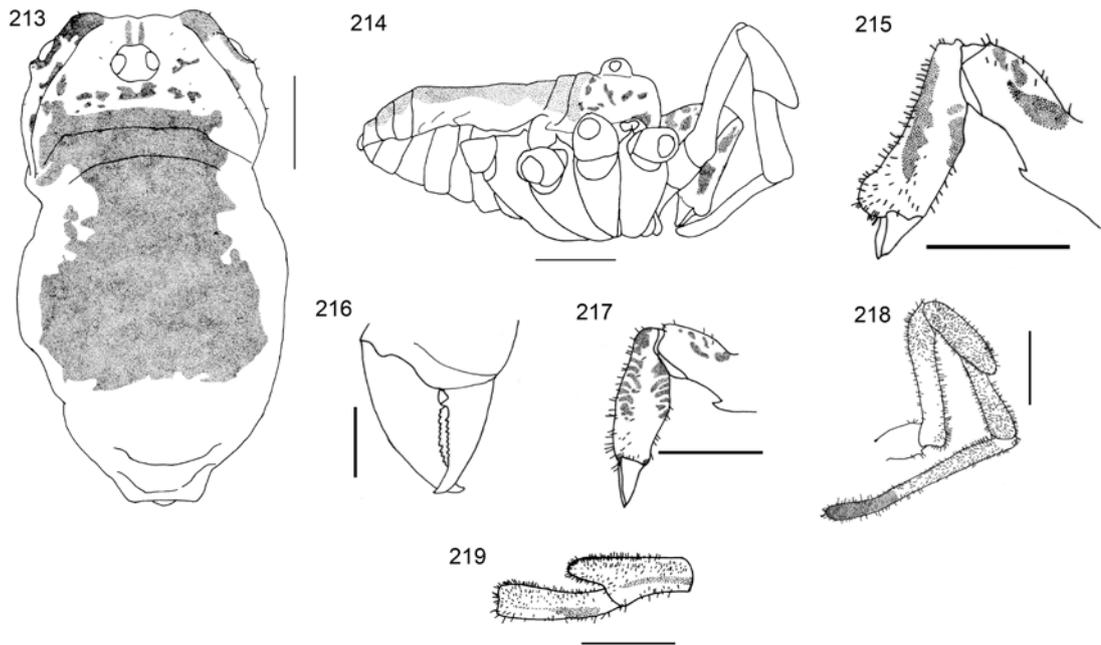
### ***Tercentenarium linnaei* new species**

(Figs 32, 213–226)

*Megalopsalis linnaei* Taylor, 2008b: 376–378, figs 1–14.

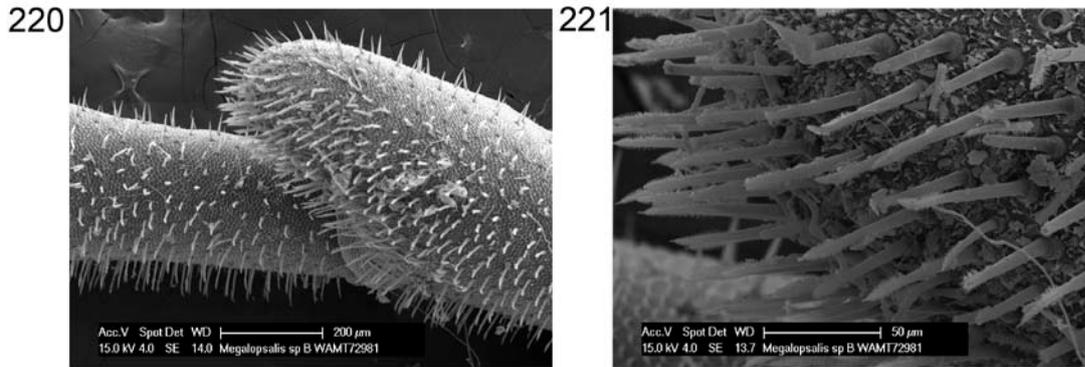
**Material examined.** *Male holotype.* Lake Gounter Nature Reserve, Western Australia, 32°23'48"S 118°49'06"E, 19 May–22 September 1998, wet pitfalls, P. Van Heurck, CALM Survey (WAM T72981).

*Paratypes.* 2 males, 3 females, Bruce Rock–Doodlakine Road, 31°51'26"S 118°06'14"E, 22 May–22 September 1998, wet pitfalls, N. Guthrie, CALM Survey (WAM T73006; 2 males, 1 female measured); 1 male, Comitun Dam Nature Reserve, 31°45'38"S 118°03'47"E, 22 May–29 September 1998, wet pitfalls, L. King, CALM Survey (WAM T73034); 1 male, 5 female, Lake Mollerin, west, 30°31'41"S 117°33'54"E, 15 September 1998–25 October 1999, wet pitfalls, P. Van Heurck, CALM Survey (WAM T73036; 1 female measured); 19 males, 12 females, Long Muir Rd, granite rock, S of Mollerin Lake, 30°32'50"S 117°33'56"E, 16 September 1998–25 October 1999, wet pitfalls, P. Van Heurck, CALM Survey (WAM T73000; 6 males, 7 females measured); 11 males, 7 females, Mungarri Nature Reserve, north, 30°19'51"S 117°45'12"E, 15 September 1998–25 October 1999, wet pitfalls, P. Van Heurck, CALM Survey (WAM T73041; 3 males measured); 4 males, 1 female, Noorajin Soak Nature Reserve, 30°45'17"S 117°14'30"E, 15 September 1998–18 October 1999, N. A. Guthrie, CALM Survey (WAM T73060; 2 males measured); 1 male, Pinjarrega Nature Reserve, 30°03'42"S 115°55'17"E, 15 October 1999–1 November 2000, wet pitfalls, P. Van Heurck *et al.*, CALM Survey (WAM T73082); 8 males, 3 females, Vermin Proof Fence, east, E of Beacon, 30°14'17"S 118°20'09"E, 15 September 1998–25 October 1999, wet pitfalls, P. Van Heurck, CALM Survey (WAM T73002; 2 males measured).



**FIGURES 213–219.** *Tercentenarium linnaei*. 213. Body of female, dorsal view (WAM T73000). 214. Body of male, lateral view, showing chelicerae and pedipalp (holotype). 215. Left male chelicera, retrolateral view (WAM T73000). 216. Right male chelicera, frontal view (WAM T73000). 217. Left female chelicera, retrolateral view (WAM T73000). 218. Left female pedipalp, medial view (WAM T73000). 219. Left female pedipalp, dorsal view (WAM T73000). Scale bars for figs 213–215, 217–219 = 1 mm; fig. 216 = 0.2 mm.

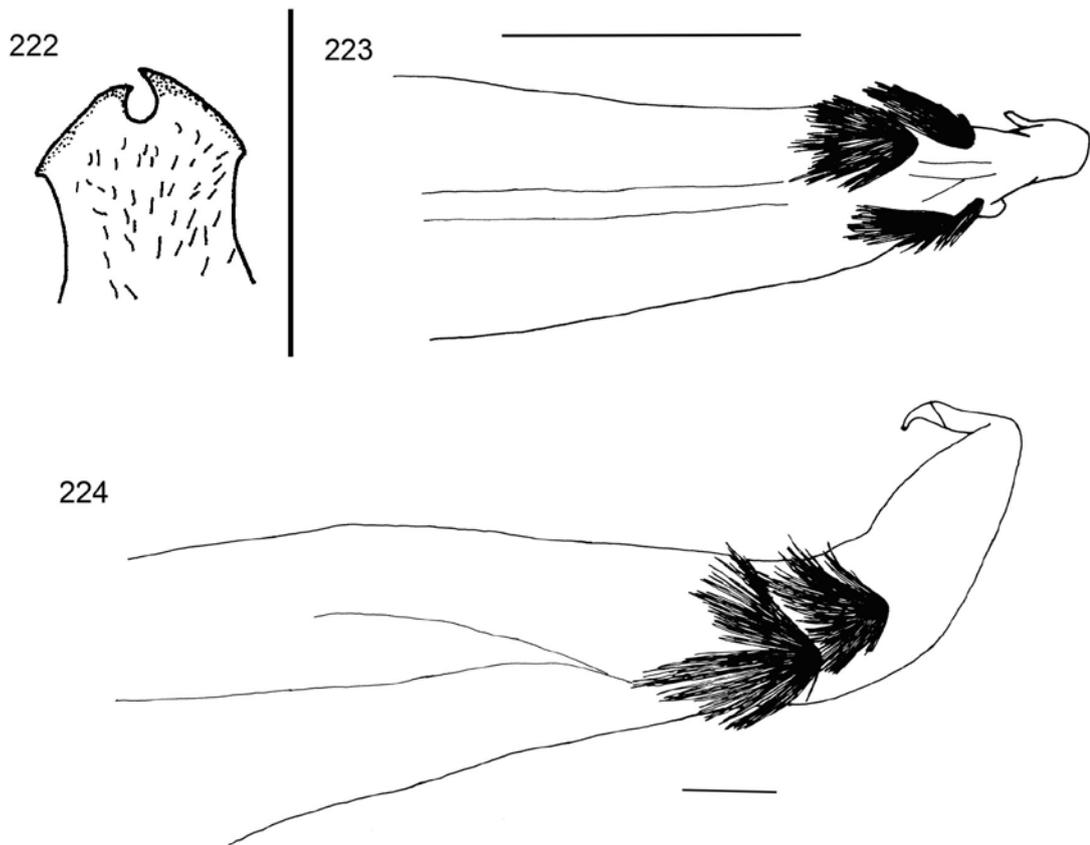
*Other specimens examined.* 1 female, Badjaling Siding, 31°59'10"S 117°29'53"E, 27 May–5 October 1998, wet pitfalls, P. Van Heurck, CALM Survey (WAM T73008); 3 males, 2 females, Bending Reserve Road, 32°21'27"S 118°29'46"E, 19 May–22 September 1998, wet pitfalls, N. Guthrie, CALM Survey; 1 male, 1 female, Buntine Nature Reserve, west, 29°58'29"S 116°34'59"E, 15 September 1998–25 October 1999, wet pitfalls, L. King, CALM Survey (WAM T72990); 1 female, Dragon Rocks Nature Reserve, northern end, 32°41'27"S 118°58'30"E, 20 May–22 September 1998, wet pitfalls, N. A. Guthrie, CALM Survey (WAM T73019); 1 female, Durokoppin Nature Reserve, south, 31°24'46"S 117°45'16"E, 22 May–22 September 1998, wet pitfalls, L. King, CALM Survey (WAM T72983); 7 females, Erikin Road, W of Bruce Rock, 31°57'51"S 117°56'05"E, 22 May–29 September 1998, wet pitfalls, L. King, CALM Survey (WAM T72957); 2 males, Koorda Rd, Nature Reserve 22363, 30°45'25"S 117°05'26"E, 15 September 1998–25 October 1999, wet pitfalls, B. Durrant, CALM Survey (WAM T73012); 1 male, Kulja-Mollerin Rock Road, 30°31'50"S



**FIGURES 220–221.** *Tercentenarium linnaei*, right male pedipalp. 220. Medial view of patella apophysis, showing laterodorsal non-plumose and medioventral plumose setae. 221. Same, close-up of plumose setae.

117°33'49"E, 15 September 1998–25 October 1999, L. King, CALM Survey (WAM T73046); 1 male, Lochada Road Nature Reserve, south-east, 29°15'34"S 116°23'08"E, 15 September 1998–18 October 1999, wet pitfalls, L. King, CALM Survey (WAM T73011); 1 female, Mt Hampton Nature Reserve, dam, 31°45'40"S 119°04'21"E, 29 April–22 September 1998, wet pitfalls, N. A. Guthrie, CALM Survey (WAM T73003); 1 female, Mt Hampton Nature Reserve, north, 31°44'26"S 119°05'02"E, 29 April–22 September 1998, P. Van Heurck, CALM Survey (WAM T73017); 4 females, Mt Moore Nature Reserve, 31°12'45"S 118°18'15"E, 21 May–22 September 1998, wet pitfalls, N. A. Guthrie, CALM Survey (WAM T73007); 1 male, 1 female, Mungarri Nature Reserve, south, 30°20'55"S 117°45'29"E, 15 September 1998–25 October 1999, wet pitfalls, L. King, CALM Survey (WAM T73091); 1 female, Talgomine Reserve, north, N of Merredin, 31°14'40"S 118°24'25"E, 28 April–22 September 1998, wet pitfalls, N. A. Guthrie, CALM Survey (WAM T73009); 1 male, Tambellup water supply reserve, 34°02'20"S 117°33'30"E, 15 October 1999–1 November 2000, P. Van Heurck *et al.*, CALM Survey (WAM T73088); 2 females, Wamenusking Nature Reserve, 32°07'34"S 117°30'31"E, 26 May–5 October 1998, wet pitfalls, N. A. Guthrie, CALM Survey (WAM T72968); 1 male, Yarding Nature Reserve, 31°55'02"S 117°58'49"E, 22 May–29 September 1998, wet pitfalls, L. King, CALM Survey (WAM T72979).

**Diagnosis.** *Tercentenarium linnaei* differs from all other Monoscutidae in its lack of both heavy sclerotisation and enlarged chelicerae in the male. The male is also distinguished from all other monoscutid species by its frontal cheliceral

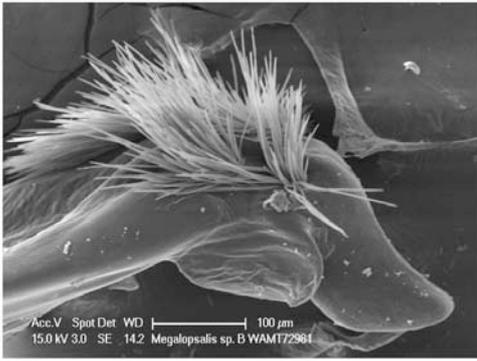


**FIGURES 222–224.** *Tercentenarium linnaei*, genitalia. 222. Anterior portion of female genital operculum (WAM T73000). 223. Penis, ventral view (holotype). 224. Penis, right lateral view (holotype). Scale bars for fig. 222 = 1 mm; fig. 223 = 0.05 mm; fig. 224 = 0.01 mm.

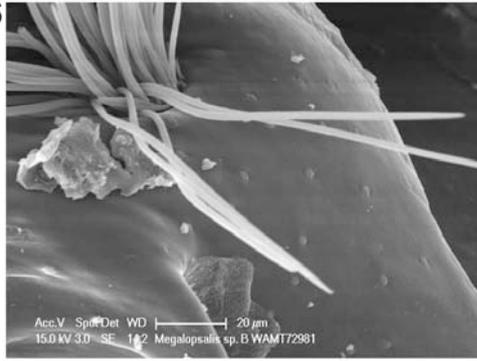
apophysis. The female is distinguished from all other Monoscutidae by the round opening at the anterior of the genital operculum.

**Description.** MALE (figs 214–216, 220–221, 223–226; N = 17). Prosoma length 1.24 (0.12), width 2.15 (0.16). Dorsal prosomal plate white with brown ticking and scattered darker brown patches; smooth. Ocularium white with brown ticking, unarmed. Ozopore large, easily visible from above, with flanking lobes. Bright white lateral areas on prosoma and dorsum of first two opisthosomal segments. Medial zone of first two segments, and all of third and fourth segments of dorsum of opisthosoma dark brown. Posterior of opisthosoma white ticked with brown medially and bright white laterally. Spiracle with branched covering spines arising from anterior margin. Genital operculum without circular opening on anterior margin. Interior of genital operculum with sclerotised recess for penis.

225



226



**FIGURES 225-226.** *Tercentenarium linnaei*, penis. 225. Glans, left lateral view (holotype). 226. Same, close-up showing raised pores.

*Chelicerae.* Segment I 0.83 (0.10), segment II 1.56 (0.09). White with brown patches; unarmed; large frontal apophysis on prodistal face of segment II (fig. 215). Outer edge of fingers smoothly convex (fig. 216).

*Pedipalps.* Femur 1.77 (0.10), patella 0.92 (0.06), tibia 1.17 (0.05), tarsus 2.04 (0.12). Femur, patella and tibia white with tan patches; tarsus tan. All segments unarmed. Femur to tibia with dense plumose setae medially, fewer non-plumose setae laterally (figs 220–221). Tarsus with plumose setae over proximal two-thirds, non-plumose setae and aciculate ornamentation over distal third. Large rounded distal apophysis on patella and distal medial bulge on femur and tibia (figs 218–219). Claw without ventral tooth-comb.

*Legs.* Femora 2.95 (0.23), 5.90 (0.39), 2.97 (0.29), 4.44 (0.22); patellae 1.12 (0.08), 1.46 (0.11), 0.99 (0.05), 1.01 (0.07); tibiae 2.77 (0.25), 5.32 (0.38), 2.45 (0.20), 3.18 (0.15). Femora unarmed; femora and patellae with longitudinal rows of setae. Tibiae with longitudinal rows of setae and densely covered with microtrichia. Tibia I with increased density of setae ventrally. Tibiae not pseudosegmented.

*Penis* (figs 223–226). Heavily sclerotised; shaft flattened dorsoventrally. Glans at  $\sim 90^\circ$  from shaft; all four bristle groups well developed, with right bristle groups significantly larger than left-hand groups. Left side of glans-shaft junction with plate-like dorsolateral process (fig. 225). Glans laterally compressed, subrectangular in left lateral view to triangular in right lateral view, torted anti-clockwise in distal view. Pores on glans on raised papillae (fig. 226). Stylus attached at right distal end of glans, strongly recurved back onto glans.

FEMALE (fig. 213). Prosoma length 1.33 (0.17), width 2.40 (0.15). As for male except for following: Genital operculum with circular medial opening on anterior margin (fig. 222).

*Chelicerae* (fig. 217). Segment I 0.72 (0.07), segment II 1.62 (0.06). No frontal apophysis on second segment.

*Pedipalps*. Femur 1.71 (0.07), patella 0.89 (0.09), 1.26 (0.06), tarsus 2.29 (0.12).

*Legs*. Femora 2.06 (0.10), 4.08 (0.18), 1.91 (0.10), 3.12 (0.16); patellae 0.96 (0.08), 1.31 (0.06), 0.90 (0.05), 0.99 (0.03); tibiae 2.12 (0.12), 4.15 (0.10), 1.84 (0.10), 2.44 (0.09).

**Etymology.** Named after Carl Linnaeus to commemorate the 250th anniversary of the publication of the 10th edition of *Systema Naturae* (Linnaeus, 1758), regarded as the initial publication for binomial nomenclature in animals (International Commission on Zoological Nomenclature 1999).

#### ***Thrasychiroides* Soares & Soares 1947**

*Thrasychiroides* Soares & Soares 1947: 82; Cokendolpher 1984a: 472; Crawford, 1992: 45.

**Type (and only) species.** *Thrasychiroides brasilius* Soares & Soares 1947 by original designation.

**Diagnosis.** *Thrasychiroides* is distinguished from *Thrasychirus* by the absence of an apophysis on the pedipalp patella. Distinguishing characters from other Enantiobuninae have not yet been established but *Thrasychiroides* is the only genus other than *Thrasychirus* described to date from South America. *Thrasychiroides* and *Thrasychirus* can be distinguished from South American Gagrellinae (which include all other South American representatives of Phalangioidea) by the absence of a sclerotised scute on the dorsum of the opisthosoma.

**Distribution.** Paraná, Brazil (Soares & Soares 1947).

**Comments.** *Thrasychiroides brasilius* has not been redescribed since its original description and features such as genitalia have not yet been described; its position among Enantiobuninae therefore requires confirmation.

*Thrasychiroides tuberculatus* Schenkel 1963 (from Vietnam) was not included in this genus but a new junior homonymous genus, renamed *Schenkeliobunum* by Starega (1964).

#### ***Thrasychirus* Simon 1884**

*Thrasychirus* Simon 1884: 142, 1887: 38, 1902: 45, 46; Roewer 1923: 921.

*Enantiobunus* Mello-Leitão 1931: 92.

*Thrasychirus* Simon—Ringuelet 1959: 212, 216; Šilhavý 1970: 175; Cokendolpher 1984a: 472, 1984b: 396, 399–400; Cokendolpher & Lanfranco 1985: 312; Hunt & Cokendolpher 1991: 134–135; Crawford 1992: 18.

**Type species.** *Thrasychirus dentichelis* Simon 1884 by subsequent designation of Ringuelet 1959.

**Included species.** *Thrasychirus gulosus* Simon 1884; *T. modestus* Simon 1902.

**Diagnosis.** *Thrasychirus* can be distinguished from *Thrasychiroides* by the presence of a distomedial apophysis on the pedipalp patella. It can be distinguished from all Australasian genera of Enantiobuninae by the presence of single bristles only instead of bristle groups as lateral processes at the shaft-glans junction (Hunt & Cokendolpher, 1991).

**Comments.** *Thrasychirus* is a senior synonym of *Enantiobunus* Mello-Leitão 1931, type genus of the subfamily Enantiobuninae (Ringuelet 1959; Crawford 1992). The type species of *Enantiobunus*, *E. spinulosus* Mello-Leitão 1931, is a junior synonym of *Thrasychirus gulosus* Simon 1884. See the discussion of the phylogenetic analysis for discussion of the significance of *Thrasychirus*' phylogenetic position within Enantiobuninae.

## Appendix I

### Revision of the Australian Gagrellinae (Arachnida: Opiliones: Sclerosomatidae), with a description of a new species

#### Abstract

A new species of the Indo-Australian Gagrellinae (Arachnida: Opiliones: Sclerosomatidae), *Gagrella cauricrepa*, is described from the Iron Range, Cape York Peninsula, Queensland, Australia. This represents the first definite indigenous Australian record of Sclerosomatidae, though the family has previously been known from Papua New Guinea and the Solomon Islands. The previous record of *Zaleptus marmoratus* Roewer 1910 from the Australian fauna is regarded as currently unconfirmable.

#### Introduction

The subfamily Gagrellinae represents the greater part of the tropical and subtropical fauna of Eupnoi (long-legged harvestmen) for Indo-Malaya and the Neotropics (Giribet & Kury 2007). Over 800 species are currently recognised in 127 genera, though many remain poorly known. Whereas Gagrellinae have been well documented from New Guinea and the Solomon Islands (Forster 1949b; Roewer 1954a,b, 1955a), their presence in Australia has been more uncertain. The only species previously attributed to Australia, *Zaleptus marmoratus* Roewer 1910, is of doubtful provenance (Roewer 1955b). A new species described in this paper from northernmost Queensland confirms the presence of Gagrellinae in Australia. It is also the first definite indigenous Australian record for the family Sclerosomatidae, as the supposed Australian leiobunine *Nelima dumni* Forster 1947 has been synonymised with the introduced European species *N. doriae* (Canestrini 1871; Gruber & Hunt 1973).

Gagrellinae was included by Crawford (1992) in Sclerosomatidae along with the subfamilies Sclerosomatinae, Gyinae and Leiobuninae. Starega (1976a,b) suggested that Gagrellinae and Leiobuninae were closely related and separated them as the family Gagrellidae, but this does not seem justified as the boundaries between all four subfamilies remain unclear (Martens 1973, 1982; Tourinho 2007). The phylogenetic analysis of Giribet *et al.* (2002) included representatives of Sclerosomatinae and Leiobuninae, and suggested paraphyly with the former nested within the latter. Gagrellinae has been separated from Leiobuninae by the presence of pseudoarticulations in the femora and a heavily sclerotised opisthosomal scute (Roewer 1910, 1923; Crawford 1992), but neither of these characters is universally reliable in distinguishing the subfamilies (Tourinho 2007). Crawford (1992) maintained their distinctiveness largely on biogeographical grounds.

The taxonomy of the Old World Gagrellinae has not been significantly revised since its treatment by Roewer (1954a,b, 1955a,b) and remains in a dire state of disarray (Crawford 1992; Klimeš 2006). As with other groups of Opiliones, Roewer used an artificial classification for Gagrellinae, with no consideration of genitalic characters. Foremost among the series of characters used by Roewer (1954a) to distinguish genera was the numbers of pseudoarticular nodules in the femora of the legs, particularly femur II. Subsequent authors have expressed doubts about the significance of this character (Martens 1987; Tourinho-Davis 2004; Klimeš 2006). Suzuki (1973) reported that the type specimen of the gagrelline *Psathyropus tenuipes* Koch 1878 possessed one nodule (characteristic of *Gagrella sensu* Roewer) in the left femur II and two nodules (*Psathyropus*) in the right femur II. Recent revisions of some of the Neotropical Gagrellinae have revealed the need for significant changes to the Roewerian system (Tourinho-Davis 2004). Martens (1987) identified a number of species groups on the basis of genitalic morphology among the Nepalese '*Gagrella*' that could warrant generic separation were the type species of the genus available for comparison. Unfortunately, the majority of south-east Asian taxa have not been re-examined, and Roewer's (1954a) classification remains the *status quo*. With about 700 species of Gagrellinae described from Asia (Tourinho-Davis 2004), most of them poorly described and all but unrecorded since their original descriptions, a sufficient revision of the subfamily would represent a monumental task, and it is not surprising that later authors have continued to use the Roewerian system without significant revision (e.g. Suzuki 1985). Using the key to

genera provided by Roewer (1954a), the Australian specimens would be assigned to the genus '*Gagrella*', which also includes the majority of the gagrelline species described from New Guinea. Unfortunately, the genus *Gagrella* as defined by Roewer did not include *G. signata* (Stoliczka 1869), the valid type species (see Crawford (1992) for a detailed discussion of the convoluted taxonomic history of this genus). Correct application of the rules of zoological nomenclature (International Commission on Zoological Nomenclature 1999) would mandate the use for this genus of the name *Hexomma* (Thorell 1876), which has been little used since its synonymisation with *Gagrella* by Thorell (1894). Furthermore, the type species of *Hexomma*, *H. vulcanicum* (Doleschall 1859), is poorly described and was regarded as unidentifiable by Roewer (1954a). As pointed out by Crawford (1992), it is also likely that many of the species currently included in *Gagrella sensu* Roewer will have to be recombined in future revisions, and the wholesale transfer of the almost 200 species-group names that have been included in *Gagrella* to *Hexomma* is probably not advisable. Martens (1987) sidestepped the nomenclatural issues associated with *Gagrella* by effectively treating *Gagrella* Stoliczka and *G. sensu* Roewer as synonyms. Though not a particularly satisfying solution, this compromise has been followed herein.

## **Methods**

Specimens used were obtained from the Queensland Museum (QM). Specimens were examined under alcohol using a Leica MZ6 microscope and drawings made using a camera lucida. Genitalia were examined under an Olympus BH-2 compound microscope. Measurements were taken of all specimens using a graticule and are given below as averages in millimetres with standard deviations in parentheses. Prosoma and total body lengths were both taken down the midline and width was measured at the widest part of the prosoma between the third and fourth legs. Leg measurements are given from leg I to IV. Genitalic terminology is based on Martens (1987). Comparisons between *G. cauricrepa* sp. n. and other species of Gagrellinae were based on descriptions in the literature, particularly Roewer (1954a,b, 1955a), except for *G. aura* (Rainbow 1913), specimens of which were available from QM.

## Taxonomic Description

### Family Sclerosomatidae

#### Subfamily Gagrellinae

**Comments.** Roewer (1954a) divided Asian Gagrellinae into two 'Gruppen' (equivalent to tribes), Gagrelleae and Zalepteae, distinguished by the presence (Gagrelleae) or absence (Zalepteae) of a large spine or spines on the dorsal scute of the opisthosoma. The significance of this distinction is doubtful, and was significantly challenged with the description by Martens (1987) of a genus *Nepalgrella* Martens 1987 supported by genitalic characters but including species with and without a dorsal spine. At present, no tribal division within Gagrellinae is recognised.

#### *Gagrella Stoliczka, 1869*

**Type species.** *Gagrella signata* Stoliczka 1869 through subsequent designation by Banks (1930; see Crawford 1992).

**Comments.** See above for discussion of the issues associated with this genus.

#### *Gagrella cauricrepa* new species

(Figs 227-231)

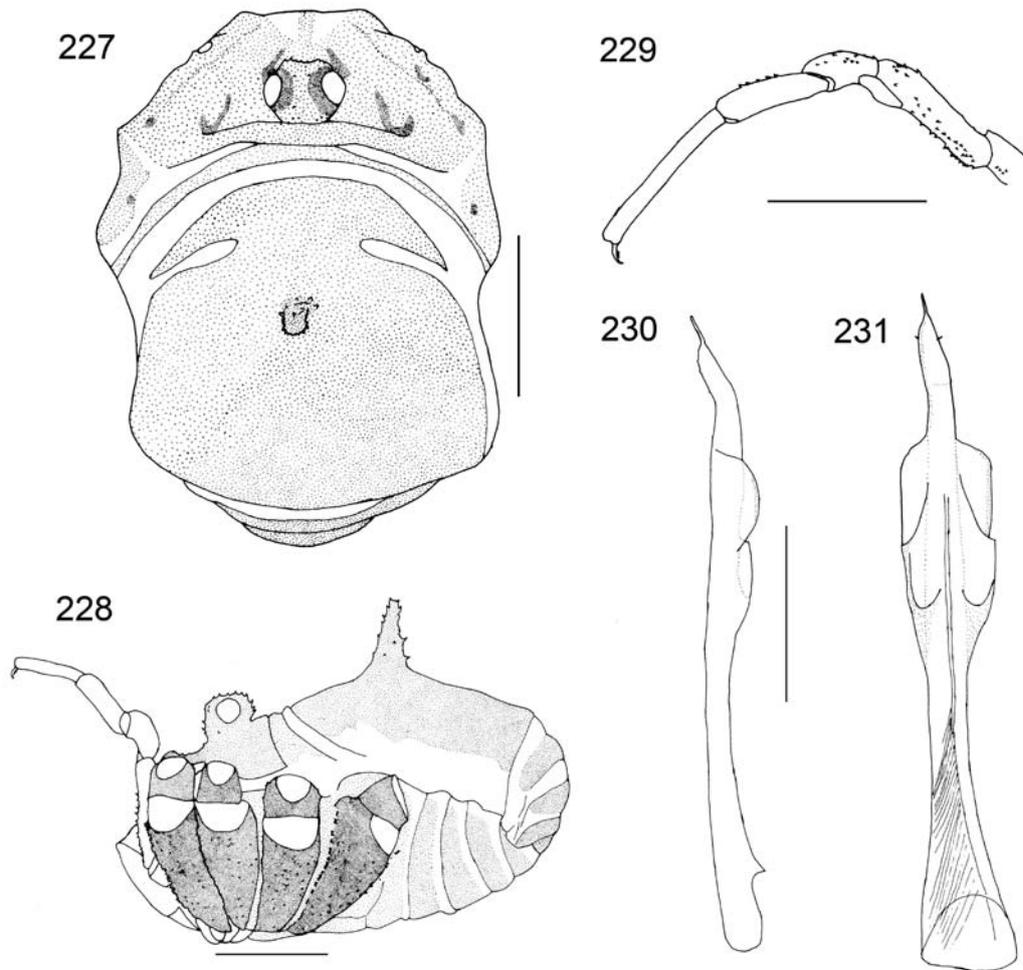
**Material examined.** *Male holotype.* Summit, Lamond Hill, Iron Range, NE Queensland, 12°43'59"S 143°13'01"E, 1 July 1976, R. Raven (QM S2950).

*Paratypes*, 4 males, 2 females, Gordon Ck, Iron Range, 12°43'00"S 143°19'00"E, 25 June 1976, V. Davies, R. Raven (QM S2951); 1 female, summit, Lamond Hill, Iron Range, 12°43'59"S 143°13'01"E, 1 July 1976, R. Raven (QM S2950); 2 females, West Claudie R., Iron Range, 12°44'24"S 143°14'40"E, 50 m, 3-10 December 1988, G. Monteith & D. Cook, rainforest (QM S2949).

**Diagnosis.** *G. cauricrepa* can be distinguished from all other Australian Eupnoi by the central dorsal spine on the opisthosoma. *Gagrella cauricrepa* can be distinguished from species of Gagrellinae found in or near New Guinea, or that key

out close to *G. cauricrepa* using the key of Roewer (1954a) due to the possession of anterior denticles on the ocularium, by the following features: *G. denticulatifrons* Roewer 1954a (from Finsch Coast, northern Papua New Guinea) lacks armament on the pedipalp patella and tibia. *Gagrella granobunus* Roewer 1954a (Perak, Malaysia) and *G. promeana* Roewer 1954a (Prome, Burma) have black chelicerae, and the former also has dark-brown pedipalp femur and patella. *Gagrella albertisii* Thorell 1876 (Maluku Islands, Indonesia to New Guinea), *G. dubia* Giltay 1930 (Sakoemi, Irian Jaya, Indonesia), *G. leopoldi* Giltay 1930 (between Lumira & Danau Kamakawalar, Irian Jaya, Indonesia), *G. fuscipes* Roewer 1910 (Jagei River, Papua New Guinea), *Eugagrella zilchi* Roewer 1954b (Madang, Papua New Guinea) and *Marthanella scripta* Roewer 1955a (Madang, Papua New Guinea) have the ocularium unarmed. *Gagrella amboinensis* (Doleschall 1857) (Maluku Islands, Indonesia to Bismarck Archipelago, Papua New Guinea) has an unarmed ocularium and lacks denticles on the pedipalp patella and tibia. *Gagrella aura* (Rainbow 1913) (Solomon Islands) has the ocularium unarmed and the opisthosomal scute a brighter, golden colour. *Gagrella neocera* Forster 1949b (Guadalcanal, Solomon Islands) has the ocularium unarmed and ventral denticles on the pedipalp tibia. *Gagrella amboinensis bicornuta* Strand 1910 (Toricelli Range, Papua New Guinea) and *G. duplex* Roewer 1915 (Madang, Papua New Guinea) have two median spines instead of one on the dorsum of the opisthosoma. *Metagagrella aurolucens* Roewer 1954b (Madang, Papua New Guinea) has the pedipalp unarmed, and the dorsal median spine is curved distinctly posteriad. *Dentobunus waigeuensis* Roewer 1955a (Waigeu, Indonesia) has a distinct pair of anterior-directed prodorsal spines on the ocularium. *Zaleptus marmoratus* Roewer 1910 (see introduction) lacks the median dorsal spine on the opisthosoma, has squarely blunted rather than trifid denticulations on the lateral margins of the coxae, and has legs with denticulation on the femora only.

**Male.** Prosoma length 1.15 (0.12), width 2.36 (0.10); total body length 3.50 (0.12). Entire dorsum heavily sclerotised, evenly covered with small granulations; non-sclerotised junctions between dorsal prosomal plate–metapeltidium, prosoma–



**FIGURES 227-231.** *Gagrella cauricrepa* (QM S2950). 227. Body, dorsal view. 228. Body, lateral view, showing chelicera and pedipalp. 229. Right pedipalp, ventromedial view (setation omitted). 230. Penis, lateral view. 231. Penis, ventral view. Scale bars for figs 227–229 = 1 mm; figs 230–231 = 0.5 mm.

opisthosoma, and partial divide between first and second segments of opisthosoma. Majority of dorsum golden-brown, prosoma with dark brown and sometimes golden-cream markings, triangular section of dorsal prosomal plate anterior to ocularium cream with two median golden-brown stripes. Supracheliceral lamellae with scattered small spines. Dorsal prosomal plate horizontal anterior to ocularium. Ocularium high, golden-brown or gold with black margins around eyes, with scattered small denticles. Ozopore slightly raised, visible from above, with small flanking lobes. Non-sclerotised segment boundaries cream. Opisthosoma with cream spots, concentrated along segment boundaries; first five segments of opisthosoma fused into scute. Large dark orange-brown central spine on posterior part of second opisthosomal segment, with blunt termination and densely covered in smaller black

denticles. Venter yellow-grey, with coxae darker than opisthosoma. Coxae orange or yellow-grey, mediodistal ends white; angular, densely denticulate. Lines of trifid denticulations along lateral margins of coxae, medial margin of coxapophysis IV and lateral margins of genital operculum. Venter of opisthosomal segments yellow-grey or orange mottled with purple; sclerotised anteriorly, non-sclerotised posteriorly.

*Chelicerae*. Segment I 0.44 (0.07), segment II 1.07 (0.03). Cream; unarmed.

*Pedipalps* (fig. 229). Femur 0.96 (0.03), patella 0.48 (0.03), tibia 0.71 (0.05), tarsus 1.03 (0.03). Cream; femur with numerous denticles concentrated on ventral surface and dorsodistally, patella with numerous dorsal denticles, tibia with few denticles dorsally only. Patella short and club-shaped, no apophysis.

*Legs*. Femora 8.47 (0.67), 15.15 (1.45), 8.08 (0.51), 11.23 (1.13); patellae 1.16 (0.04), 1.32 (0.03), 1.19 (0.03), 1.24 (0.01); tibiae 6.82 (0.54), 14.53 (1.54), 6.44 (0.38), 8.59 (0.72). Medial face of trochanters white; remainder of legs dark brown proximally, lightening to golden-brown distally. Articular membranes adjoining trochanters purple. Trochanters denticulate on anterior and posterior faces; leg I with small scattered denticles from femur to tibia; legs II-IV with denticles from femur to metatarsus. Femur II with two pseudosegments; tibia II with 9–11 pseudosegments; tibia IV undivided.

*Penis* (figs 2230-231). Glans moderately elongate, oblong in lateral view, with single small lateral bristle (*Sinnesborst* of Martens 1987) on each side about one third of the way from distal end. Alate portion with ventral lamella and dorsal mantle (*Ummantelung* of Martens 1987) taking up distal half of shaft except for short section at distalmost end before glans. Mantle along most of distal third forming two lateral wings, not fused to lamellae at any point, curved ventromediad. Lamellae mostly posterior to mantle, curved ventrally and attached to shaft both laterally and medially to form two lateral pockets. Ventral tendon elongate, attaching to distal end of muscle posterior to alate portion of shaft.

**Female.** Prosoma length 1.35 (0.15), width 2.63 (0.21), total body length 4.60 (0.56). External appearance as for male, except generally larger size and legs with metatarsi unarmed except dorsal longitudinal row of denticles on metatarsus IV.

*Chelicerae*. Segment I 0.48 (0.13), 1.12 (0.06).

*Pedipalps*. Femur 0.95 (0.06), patella 0.46 (0.01), 0.67 (0.03), 1.15 (0.03).

*Legs.* Femora 7.77 (0.47), 14.31 (0.60), 7.39 (0.41), 10.48 (0.37); patellae 1.17 (0.08), 1.30 (0.07), 1.14 (0.07), 1.25 (0.05); tibiae 6.00 (0.17), 13.85 (0.72), 5.82 (0.23), 7.81 (0.31).

**Variation.** A reasonable amount of variation in colour pattern can be seen, from lightly coloured specimens (including the holotype) with distinct patterns of cream markings on the dorsum to darker specimens with the dorsum nearly concolorous. As no significant variation can be seen in other characters and all specimens were collected in geographically proximate locations, this probably represents individual variation rather than having any taxonomic significance. Significant variation in colour pattern has been demonstrated even over the lifetime of a single individual for Sclerosomatidae as a result of cuticular hardening with age (Shultz 2008).

**Etymology.** From the Latin *cauricrepus*, blown by the northwest wind, to indicate the probable direction of derivation of this family in Australia.

### ***Zaleptus marmoratus* Roewer 1910**

*Zaleptus marmoratus* Roewer 1910: 140–141, 1923: 1043, 1955b: 136.

**Comments.** *Zaleptus marmoratus* Roewer 1910 was described from a single damaged specimen collected or donated by ‘Verreaux’ and attributed simply to ‘Australia’ in the Muséum national d’Histoire naturelle in Paris. Roewer (1910) placed a query against the locality in the original description, and later (Roewer 1955b) suggested that the specimen could have just as easily come from elsewhere in Australasia, such as New Guinea. Maison Verreaux was a family firm of commercial specimen collectors and taxidermists based in Paris. One member of the firm, Jules Verreaux, travelled to Australia between 1842 and 1847, and the *Z. marmoratus* specimen could have been among the over 10 000 biological specimens he collected on that trip (Norris 1996). Unfortunately, Jules Verreaux left no personal account of the exact localities he had visited in Australia, but there is no evidence for his having been further north than Moreton Bay in southern Queensland (Norris 1996), far south of the likely distribution of Gagrellinae in Australia (see comments on biogeography below). Numerous cases have been recorded of Maison Verreaux specimens bearing unreliable locality data (Banks 1998; Olson *et al.* 2005) and in at least one case the attribution of the wrong locality to specimens by Jules Verreaux may have been

deliberately fraudulent (Olson *et al.* 2005). In the case of *Z. marmoratus*, no other species of the genus *Zaleptus* has been recorded closer to Australia than Sumatra and no other member of the ‘Zaleptae’ group is known closer than Borneo or Java (Roewer 1955b). Jules Verreaux did travel in eastern Asia between 1832 and 1837, at least initially in the company of his brother Édouard. The greater part, if not all, of the material collected by Jules Verreaux at this time was lost with the wreck of the ship ‘Lucullus’ in 1838 (Anonymous 1874), but differing accounts exist of Édouard Verreaux’s movements at this time. Jules Verreaux’s obituary in *The Ibis* (Anonymous 1874) indicates that Édouard returned to Europe in 1837 with Jules, but Gunn and Codd (1981) stated that he returned to Paris in 1834. If the latter is correct, then some specimens could have been carried to Europe by Édouard. As well as material they collected themselves, Maison Verreaux were also receiving and reselling material from other collectors elsewhere in the world (Banks 1998; Olson *et al.* 2005). At least some south-east Asian material was handled by Maison Verreaux (Bowdler Sharpe 1875). The attribution of *Z. marmoratus* to Australia or even to the Australian region must therefore be regarded as suspicious.

### **Biogeography**

Though Gagrellinae have not previously been reliably recorded from Australia, their discovery in northern Queensland should not represent much of a surprise. Species of Gagrellinae have been described from New Guinea (Roewer 1954a,b, 1955a) and the Solomon Islands (Rainbow 1913; Forster 1949b). A land connection between New Guinea and Queensland bridging the Torres Strait would have been present when sea levels were only 10 m lower than the present time, and they have been at least that much lower for 91% of the past 250 000 years (Voris 2000). Closely related or shared taxa are known from both New Guinea and Australia in freshwater fish (McGuigan *et al.* 2000), flowering plants (Turner 1996; Swenson & Bremer 1997; Hill 2001), reptiles (Georges *et al.* 2002), spiders (Harvey & Waldock 2000) and insects (New 1990; Beebe & Cooper 2002), among others. Taylor (1972) concluded that Torres Strait had not been a significant barrier to dispersal for most insect groups. The apparent absence of Gagrellinae from Australia to date has therefore been unusual, though not unique (species of Uropygi (Arachnida) have been described from New Guinea and the Solomon Islands, but the order is currently

unknown in Australia – Rowland & Cooke 1973). The identification of Gagrellinae from the northern end of Cape York Peninsula was not unexpected. It is notable that the Iron Range, the origin of the current specimens, is one of the few areas of rainforest on Cape York Peninsula, and also the only known location in Australia for the Triatominae (Heteroptera), another pantropical group of arthropods that had previously been known from New Guinea (Monteith 1974). The presence of Gagrellinae in northern Queensland also corroborates another commonly seen pattern in Australian biogeography – that of a Gondwana-related element concentrated towards the southern part of the continent, with the appearance of a tropical or Asia-related element towards the northern end of the country. Such a pattern of distribution was noted in relation to Australian Opiliones, specifically Laniatores, by Forster (1955), with Triaenonychidae representing the Gondwanan element and ‘Phalangodidae’ (more accurately Grassatores *incertae sedis* as the family Phalangodidae has since been redefined to include a more restricted variety of taxa than previously: Ubick 2007) and Assamiidae the Asian elements. Similar biogeographical patterns are visible in Lycosidae (Araneae) (Framenau & Yoo 2006; Yoo & Framenau 2006) and *Anopheles* mosquitoes (Diptera: Culicidae) in northern Australia probably represent a relatively recent Asian derivative (Beebe & Cooper 2002).

In light of their wide distribution through southern Asia and Melanesia and the large number of species, Gagrellinae have the potential to be a very interesting group biogeographically. As it is currently constituted, the genus *Gagrella* includes species found from the Himalayas to tropical Australia. However, the poor state of gagrelline taxonomy and the almost certainly polyphyletic nature of *Gagrella* (Martens 1987) mean that any attempt to reconstruct gagrelline biogeography without a thorough revision of the subfamily would be premature.

## Acknowledgements

Thanks are due to the numerous people who arranged the loans and donations of specimens used in this study – Mark Harvey and Julianne Waldock (WAM), Graham Milledge (AMS), Owen Seeman (QM), Peter Lillywhite (MV), Phil Sirvid (MONZ), John Early (Auckland Institute and Museum), Nobuo Tsurusaki (Tohori University, Japan), Charles Griswold (CAS), Christian Komposch (Graz, Austria), Hieronymus Dastych (ZMH), Janet Beccaloni (BMNH). Thank you also to Mark Harvey, Jonathan Majer (Curtin University, Perth) and James Cokendolpher for their invaluable criticism and reviews of manuscripts; to Volker Framenau (WAM), Jeffrey Shultz (University of Maryland), Abel Pérez González (UFRJ, Rio de Janeiro), Peter Jäger (Senckenberg Museum, Frankfurt), Rose Docker and the other staff of the Australian Museum archive, and James Arnold (West Virginia Arachnid Survey) for help in research; and to Elaine Miller, Enid Holt and Charles Lacoste for their technical and administrative support. And thank you to all others who offered support and encouragement along the way – Shae Callan, Rebecca Graham, Karl Edwards, Brian Heterick, Jakkaphong Phosee, and countless more.

## References

- Anonymous (1874) Obituary. *Ibis*, 16, 464–472.
- Banks, N. (1891) A new genus of Phalangiidae. *Proceedings of the Entomological Society of Washington*, 2, 249–250.
- Banks, N. (1893) The Phalanginae of the United States. *Canadian Entomologist*, 25, 205–211.
- Banks, N. (1930) Phalangida from Borneo. *Sarawak Museum Journal*, new series, 4, 57–86, plates 11–12.
- Banks, R.C. (1998) Supposed northern records of the southern fulmar. *Western Birds*, 19, 121–124.
- Beebe, N.W. & Cooper, R.D. (2002) Distribution and evolution of the *Anopheles punctulatus* group (Diptera: Culicidae) in Australia and Papua New Guinea. *International Journal for Parasitology*, 32, 563–574.
- Bowdler Sharpe, R. (1875) *Catalogue of the Striges, or Nocturnal Birds of Prey, in the Catalogue of the British Museum*. Printed by order of the Trustees, London, United Kingdom.
- Canestrini, G. (1871) Nuove specie di Opilioni Italiani. *Bullettino della Società Entomologica Italiana*, 3(4), 381–385.
- Cokendolpher, J.C. (1984a) Clarification of the Colombian harvestman genus *Carmenia*, with a review of the New World Gagrellinae (Opiliones: Gagrellidae). *Florida Entomologist*, 67(3), 471–478.
- Cokendolpher, J.C. (1984b) Revision of the harvestman genus *Leptobunus* and dismantlement of the Leptobunidae (Arachnida: Opiliones: Palpatores). *Journal of the New York Entomological Society*, 92(4), 371–402.
- Cokendolpher, J.C. (2007a) Neopilionidae Lawrence, 1931. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 121–123.
- Cokendolpher, J.C. (2007b) Protolophidae Banks, 1893. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 127–128.

- Cokendolpher, J.C. & Lanfranco L., D. (1985) Opiliones from the Cape Horn Archipelago: new southern records for harvestmen. *Journal of Arachnology*, 13(3), 311–319.
- Cokendolpher, J.C. & Sissom, W.D. (2000) Further contributions to the study of *Dalquestia* (Opiliones, Sclerosomatidae). *Entomological News*, 111, 243–249.
- Cokendolpher, J.C. & Taylor, C.K. (2007) Monoscutidae. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 118–121.
- Cokendolpher, J.C., Tsurusaki, N., Tourinho, A.L., Taylor, C.K., Gruber, J. & Pinto-da-Rocha, R. (2007) Eupnoi: Historical systematic synopsis. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 108–114.
- Contreras-Medina, R. & Luna Vega, I. (2002) On the distribution of gymnosperm genera, their areas of endemism and systematic biogeography. *Australian Systematic Botany*, 15, 193–203.
- Cox, C.B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography*, 28(4), 511–523.
- Crawford, R.L. (1992) Catalogue of the genera and type species of the harvestman superfamily Phalangioidea (Arachnida). *Burke Museum Contributions in Anthropology and Natural History*, 8, 1–60.
- Curtis, D.J. & Machado, G. (2007) Ecology. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds.), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 280–308.
- De Geer, C. (1778) *Mémoires pour servir à l'histoire des insectes*, Tome 7. Pierre Hesselberg, Stockholm, xii + 950 pp., 49 pl.
- Delle Cave, L. (1979) On a remarkable *Galeodes barbarus* (Lucas) from Ethiopia (Arachnida, Solifugae). *Bulletin of the British Arachnological Society*, 4, 396–397.
- Doleschall, C.L. (1857) Bijdrage tot de kennis der Arachniden van den Indischen Archipel. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, Series 3, 3, 399–434, plates 1–2.
- Doleschall, C.L. (1859) Tweede Bijdrage tot de kennis der Arachniden van den Indischen Archipel. *Verhandelingen der Natuurkundige Vereeniging in*

- Nederlandsch Indie* [Acta Societatis Scientiarum Indo-Neêrlandicae], 5, 1–60, plates 1–18.
- Dunlop, J.A. (2006) Baltic amber harvestman types (Arachnida: Opiliones: Eupnoi and Dyspnoi). *Fossil Record*, 9(2), 167–182.
- Dunlop, J.A. (2007) Paleontology. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 247–265.
- Farris, J.S. (1979) The information content of the phylogenetic system. *Systematic Zoology*, 28(4), 483–519.
- Fink, W.L. (1979) Optimal classifications. *Systematic Zoology*, 28(3), 371–374.
- Forster, R.R. (1944) The genus *Megalopsalis* Roewer in New Zealand with keys to the New Zealand genera of Opiliones. *Records of the Dominion Museum*, 1(1), 183–192.
- Forster, R.R. (1947) A new harvestman of the subfamily Liobuninae from Australia. *Memoirs of the National Museum of Victoria*, 15, 174–177.
- Forster, R.R. (1948a) A new sub-family and species of New Zealand Opiliones. *Records of the Auckland Institute and Museum*, 3, 313–318.
- Forster, R.R. (1948b) A new genus and species of the family Acropsopilionidae (Opiliones) from New Zealand. *Transactions of the Royal Society of New Zealand*, 77(1), 139–141.
- Forster, R.R. (1949a) Australian Opiliones. *Memoirs of the National Museum of Victoria*, 16, 59–89.
- Forster, R.R. (1949b) Opiliones from the Solomon Islands. *Records of the Australian Museum*, 22, 141–147.
- Forster, R.R. (1950) Western Australian Opiliones. *Journal of the Royal Society of Western Australia*, 36, 23–29.
- Forster, R.R. (1954) The New Zealand harvestmen (sub-order Laniatores). *Canterbury Museum Bulletin*, 2, 1–329.
- Forster, R.R. (1955) Further Australian harvestmen (Arachnida: Opiliones). *Australian Journal of Zoology*, 3(3), 354–411.
- Forster, R.R. (1964) The Araneae and Opiliones of the subantarctic islands of New Zealand. In: Gressitt, J.L. (ed.), *Insects of Campbell Island*. B.P. Bishop Museum, Honolulu. *Pacific Insects Monograph*, 7, 58–115.

- Framenau, V.W. & Yoo, J.-S. (2006) Systematics of the new Australian wolf spider genus *Tuberculosa* (Araneae: Lycosidae). *Invertebrate Systematics*, 20, 185–202.
- Gardner, S.L. & Campbell, M.L. (1992) Parasites as probes for biodiversity. *Journal of Parasitology*, 78(4), 596–600.
- Georges, A., Adams, M. & McCord, W. (2002) Electrophoretic delineation of species boundaries within the genus *Chelodina* (Testudines: Chelidae) of Australia, New Guinea and Indonesia. *Zoological Journal of the Linnean Society*, 134, 401–421.
- Giltay, L. (1930) Notes préliminaires sur les Opilions recueillis aux Indes Néerlandaises par S. A. R. le Prince Léopold de Belgique. *Bulletin et Annales de la Société Entomologique de Belgique*, 69, 419–429.
- Giribet, G., Edgecombe, G.D., Wheeler, W.C. & Babbitt, C. (2002) Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics*, 18, 5–70.
- Giribet, G. & Kury, A.B. (2007) Phylogeny and biogeography. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 62–87.
- Giribet, G., Rambla, M., Carranza, S., Baguña, J., Riutort, M. & Ribera, C. (1999) Phylogeny of the arachnid order Opiliones (Arthropoda) inferred from a combined approach of complete 18S and partial 28S ribosomal DNA sequences and morphology. *Molecular Phylogenetics and Evolution*, 11, 296–307.
- Giribet, G., Vogt, L., Pérez González, A., Sharma, P. & Kury, A.B. 2009. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics*, 25, 1–30.
- Giribet, G. & Wheeler, W.C. (1999) On gaps. *Molecular Phylogenetics and Evolution*, 13, 132–143.
- Gnaspini, P., da Silva, M.B. & Pioker, F.C. (2004) The occurrence of two adult instars among Grassatores (Arachnida: Opiliones)—a new type of life-cycle in arachnids. *Invertebrate Reproduction and Development*, 45(1), 29–39.
- Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.

- González-Sponga, M.A. (1998) Arácnidos de Venezuela. Cuatro nuevos géneros y cuatro nuevas especies de la familia Pholcidae Koch, 1850 (Araneae). *Memoria Sociedad de Ciencias Naturales La Salle*, 57, 17–31.
- Govind, C.K. & Blundon, J.A. (1985) Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. *Biological Bulletin*, 168, 321–331.
- Gray, M.R. (2001) Glenn Stuart Hunt (1944–1999), an appreciation. *Records of the Western Australian Museum*, Supplement 64, 11–14.
- Gruber, J. (1974) Bemerkungen zur Morphologie und systematischen Stellung von *Caddo*, *Acropsopilio* und verwandter Formen (Opiliones, Arachnida). *Annalen des Naturhistorischen Museum in Wien*, 78, 237–259.
- Gruber, J. & Hunt, G.S. (1973) *Nelima doriae* (Canestrini), a south European harvestman in Australia and New Zealand (Arachnida, Opiliones, Phalangidae). *Records of the Australian Museum*, 28, 383–392.
- Gunn, M. & Codd, L.E.W. (1981) *Botanical Exploration of Southern Africa: An Illustrated History of Early Botanical Literature on the Cape Flora*. A. A. Balkema, Cape Town, South Africa.
- Harvey, M.S. & Waldock, J.M. (2000) Review of the spider genus *Yoroa* Baert (Araneae: Theridiidae: Hadrotarsinae). *Australian Journal of Entomology*, 39, 58–61.
- Hickman, V.V. (1957) Some Tasmanian harvestmen of the sub-order Palpatores. *Papers and Proceedings of the Royal Society of Tasmania*, 91, 65–79.
- Hill, R.S. (2001) Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): the contribution of the fossil record. *Australian Journal of Botany*, 49, 321–332.
- Hogg, H.R. (1910) Some New Zealand and Tasmanian Arachnida. *Transactions and Proceedings of the New Zealand Institute, new series*, 42, 273–283.
- Hogg, H.R. (1920) Some Australian Opiliones. *Proceedings of the Zoological Society of London*, 1920(1), 31–48, pl. 1–3.
- Huang, D., Selden, P.A. & Dunlop, J.A. (2009) Harvestmen (Arachnida: Opiliones) from the Middle Jurassic of China. *Naturwissenschaften*, 96(8), 955–962.
- Huber, B.A. (2004) Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (González-Sponga) (Pholcidae: Araneae). *Journal of Zoology*, 262, 317–326.

- Hunt, G.S. (1971) The genus *Nunciella* Roewer (Opiliones, Laniatores) with descriptions of a new species from Kangaroo Island, South Australia. *Proceedings of the Linnean Society of New South Wales*, 96, 53–65.
- Hunt, G.S. (1972) A new cavernicolous harvestman from Western Australia (Arachnida, Opiliones, Triaenonychidae). *Journal of the Australian Entomological Society*, 11, 232–236.
- Hunt, G.S. (1981) Male dimorphism and geographic variation in the genus *Equitius* Simon (Arachnida, Opiliones). *Dissertation Abstracts International B*, 41, 4375.
- Hunt, G.S. (1985) Taxonomy and distribution of *Equitius* in eastern Australia (Opiliones: Laniatores: Triaenonychidae). *Records of the Australian Museum*, 36, 107–125.
- Hunt, G.S. (1990a) *Hickmanoxyomma*, a new genus of cavernicolous harvestman from Tasmania (Opiliones: Triaenonychidae). *Records of the Australian Museum*, 42, 45–68.
- Hunt, G.S. (1990b) Taxonomic value of spiracle microstructure in the Megalopsalididae (Opiliones, Phalangioidea). In: Koponen, S., Lehtinen, P.T. & Rinne, V. (eds), *Proceedings of the XI International Congress of Arachnology, Turku, Finland, 7-12 August 1989. Acta Zoologica Fennica*, 190, 187–194.
- Hunt, G.S. (1991) Harvestmen (Opiliones) in arid and semi-arid Australia. *Australasian Arachnology*, 41, 3–5.
- Hunt, G.S. (1992) Revision of the genus *Holonuncia* Forster (Arachnida, Opiliones, Triaenonychidae) with description of cavernicolous and epigean species from eastern Australia. *Records of the Australian Museum*, 44, 135–163.
- Hunt, G.S. (1993) A new cavernicolous harvestman from lava tube caves in tropical Australia (Arachnida: Opiliones: Phalangodidae). *Memoirs of the Queensland Museum*, 33, 217–219.
- Hunt, G.S. (1995) Revision of the harvestman genus *Miobunus* from Tasmania (Arachnida: Opiliones: Triaenonychidae). *Records of the Western Australian Museum*, Supplement 52, 243–252.
- Hunt, G. S. & Cokendolpher, J.C. (1991) Ballarrinae, a new subfamily of harvestmen from the Southern Hemisphere. *Records of the Australian Museum*, 43, 131–169.
- Hunt, G.S. & Hickman, J.L. (1993) Revision of the genus *Lomanella* Pocock with implications for family level classification in the Travunioidea (Arachnida: Opiliones: Triaenonychidae). *Records of the Australian Museum*, 33, 551–556.

- International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature*, 4<sup>th</sup> ed. International Trust for Zoological Nomenclature, London.
- Kauri, H. (1954) Report from Professor T. Gislén's expedition to Australia in 1951-1952. 9. Harvest-spiders from S. W. Australia. *Lunds Universitets Årsskrift Ny Fjöld Avd. 2*, 50(11), 1–10.
- Kauri, H. (1961) Opiliones. In: Hanström, B., Brinck, P. & Rudebeck, G. (eds), *South African Animal Life: Results of the Lund University Expedition in 1950–1951*, vol. 8. Almqvist & Wiksell, Uppsala, pp. 9–197.
- Klimeš, L. (2006) A new *Umbopilio* species from Assam, NE India (Opiliones: Sclerosomatidae: Gagrellinae). *Zootaxa*, 1325, 147–156.
- Koch, C.L. (1835) [Arachniden], Heft 128. In: Herrich-Schäffer, G.A.W. (ed.), *Deutschlands Insecten*, Hefte 111–190, 1829–1844. F. Pustet, Regensburg.
- Koch, C.L. (1839) *Übersicht des Arachnidensystems*, Zweites Heft. C. H. Zeh'schen Buchhandlung, Nürnberg, 38 pp., 6 pl.
- Latreille, P.A. (1802) Histoire naturelle, générale et particulière des crustacés et des insectes, Tome 3. In: Buffon, L. (ed.), *Histoire naturelle, générale et particulière*, Tome 81. F. Dufart, Paris, 468 pp.
- Lawrence, R.F. (1931) The harvest-spiders (Opiliones) of South Africa. *Annals of the South African Museum*, 29(2), 341–508.
- Lee, S.Y. (1995) Cheliped size and structure: the evolution of a multi-functional decapod organ. *Journal of Experimental Marine Biology and Ecology*, 193, 161–176.
- Linder, H.P. & Crisp, M.D. (1995) *Nothofagus* and Pacific biogeography. *Cladistics*, 11, 5–32.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Tomus 1. Laurentius Salvius, Stockholm, iv + 824 pp.
- Mariappan, P., Balasundaram, C. & Schmitz, B. (2000) Decapod crustacean chelipeds: an overview. *Journal of Biosciences*, 25, 301–313.
- Marples, B.J. (1944) A new species of harvestman of the genus *Megalopsalis*. *Transactions of the Royal Society of New Zealand*, 73(4), 313–314.
- Martens, J. (1973) Opiliones aus dem Nepal-Himalaya. II. Phalangiidae und Sclerosomatidae (Arachnida). *Senckenbergiana Biologica*, 54, 181–217.

- Martens, J. (1976) Genitalmorphologie, System und Phylogenie der Weberknechte (Arachnida: Opiliones). *Entomologica Germanica*, 3(1–2), 51–68.
- Martens, J. (1978) Spinnentiere, Arachnida: Weberknechte, Opiliones. In: Senglaub, K., Hannemann, H.-J. & Schumann, H. (eds), *Die Tierwelt Deutschlands* vol. 64. Gustav Fischer Verlag, Jena, 464 pp.
- Martens, J. (1982) Opiliones aus dem Nepal-Himalaya. V. Gyantinae (Arachnida: Phalangiidae). *Senckenbergiana Biologica*, 62, 313–348.
- Martens, J. (1986) Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida). In: Barrientos, J.A. (ed.), *Actas X Congreso Internacional de Aracnologia (Jaca, Spain, September 1986)* vol. 1. Juvenil, Barcelona, pp. 289–310.
- Martens, J. (1987) Opiliones aus dem Nepal-Himalaya VI. Gagrellinae (Arachnida: Phalangiidae). *Courier Forschungsinstitut Senckenberg*, 93, 87–202.
- McGuigan, K., Zhu, D., Allen, G.R. & Moritz, C. (2000) Phylogenetic relationships and historical biogeography of melanotaeniid fishes in Australia and New Guinea. *Marine and Freshwater Research*, 51, 713–723.
- McInnes, S.J. & Pugh, P.J.A. (1998) Biogeography of limno-terrestrial Tardigrada, with particular reference to the Antarctic fauna. *Journal of Biogeography*, 25, 31–36.
- McLoughlin, S. (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany*, 49, 271–300.
- Mello-Leitão, C.F. de (1931) Notas sobre Arachnideos Argentinos. *Annaes da Academia Brasileira de Sciencias*, 3(2), 83–97, 2 pl.
- Meyer-Rochow, V.B. & Liddle, A.R. (1988) Structure and function of the eyes of two species of opilionid from New Zealand glow-worm caves (*Megalopsalis tumida*: Palpatores, and *Hendea myersi cavernicola*: Laniatores). *Proceedings of the Royal Society of London Series B—Biological Sciences*, 233, 293–319.
- Michener, C.D. (1979) Biogeography of the bees. *Annals of the Missouri Botanical Garden*, 66(3), 277–347.
- Monteith, G.B. (1974) Confirmation of the presence of Triatominae (Hemiptera: Reduviidae) in Australia, with notes on Indo-Pacific species. *Journal of the Australian Entomological Society*, 13, 89–94.
- Muona, J. (1991) The Eucnemidae of south-east Asia and the western Pacific—a biogeographical study. *Australian Systematic Botany*, 4, 165–182.

- Nation, J.L. (1983) A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. *Stain Technology*, 58(6), 347–351.
- New, T.R. (1990) Conservation of butterflies in Australia. *Journal of Research on the Lepidoptera*, 29, 237–253.
- Norris, K.R. (1996) Lectotype designation and characterisation of the Australian blowflies *Calliphora pubescens* Macquart and *Calliphora testaceifacies* Macquart (Diptera: Calliphoridae). *Australian Journal of Entomology*, 35, 49–59.
- Olson, S.L., Fleischer, R.C., Fisher, C.T. & Bermingham, E. (2005) Expunging the ‘Mascarene starling’ *Necropsar leguati*: archives, morphology and molecules topple a myth. *Bulletin of the British Ornithologists’ Club*, 125, 31–42.
- Phillipps, W.J. & Grimmett, R.E.R. (1932) Some new Opiliones from New Zealand. *Proceedings of the Zoological Society of London*, 1932, 731–740.
- Pinto-da-Rocha, R. & Giribet, G. (2007) Taxonomy. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 88–246.
- Pinto-da-Rocha, R. & Gruber, J. (2007) Caddidae Banks, 1893. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 115–118.
- Platnick, N.I. (1978) Gaps and prediction in classification. *Systematic Zoology*, 27(4), 472–474.
- Pocock, R.I. (1903a) On some new harvest-spiders of the order Opiliones from the southern continents. *Proceedings of the Zoological Society of London*, 1902(2), 392–413.
- Pocock, R.I. (1903b) Fifteen new species and two new genera of tropical and southern Opiliones. *Annals and Magazine of Natural History, series 7*, 11(65), 433–450, pl. 11–12.
- Rainbow, W.J. (1913) Arachnida from the Solomon Islands. *Records of the Australian Museum*, 10, 1–16.
- Ringuelet, R. A. (1959) Los arácnidos Argentinos del orden Opiliones. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”*. *Ciencias Zoológicas*, 5(2), 127–439, pl. 1–20.
- Roewer, C.F. (1910) Revision der Opiliones Plagiostethi (=Opiliones, Palpatores) I. Teil: Familie der Phalangiidae. (Subfamilien: Gagrellini, Leiobunini,

- Leptobunini). *Abhandlungen aus dem Gebiete der Naturwissenschaften, herausgegeben vom Naturwissenschaftlichen Verein in Hamburg*, 19(4), 1–294, pl. 1–6.
- Roewer, C.F. (1911) Übersicht der Genera der Subfamilie der Phalangiini der Opiliones Palpatores nebst Beschreibung einiger neuer Gattungen und Arten. *Archiv für Naturgeschichte, part I*, 77(suppl. 2), 1–106, pl. 1–3.
- Roewer, C.F. (1912) Revision der Opiliones Palpatores (=Opiliones Plagiostethi). II. Teil: Familie der Phalangiidae. (Subfamilien: Sclerosomini, Oligolophini, Phalangiini). *Abhandlungen aus dem Gebiete der Naturwissenschaften, herausgegeben vom Naturwissenschaftlichen Verein in Hamburg*, 20(1), 1–295, pl. 1–4.
- Roewer, C.F. (1915) 106 neue Opilioniiden. *Archiv für Naturgeschichte part A*, 81, 1–152.
- Roewer, C.F. (1923) *Die Weberknechte der Erde: Systematische Bearbeitung der Bisher Bekannten Opiliones*. Gustav Fischer, Jena, Germany, v + 1116 pp.
- Roewer, C.F. (1954a) Indoaustralische Gagrellinae (Opiliones, Arachnidae). (Weitere Weberknechte XVIII). 1. Teil. *Senckenbergiana Biologica*, 35, 181–236.
- Roewer, C.F. (1954b) Indoaustralische Gagrellinae (Opiliones, Arachnidae). (Weitere Weberknechte XVIII). 2. Teil. *Senckenbergiana Biologica*, 35, 237–292.
- Roewer, C.F. (1955a) Indoaustralische Gagrellinae (Opiliones, Arachnidae). (Weitere Weberknechte XVIII). 3. Teil. *Senckenbergiana Biologica*, 36, 71–121.
- Roewer, C.F. (1955b) Indoaustralische Gagrellinae (Opiliones, Arachnidae). (Weitere Weberknechte XVIII). 4. Teil (Schluß). *Senckenbergiana Biologica*, 36, 123–171.
- Roewer, C.F. (1956) Über Phalangiinae (Phalangiidae, Opiliones Palpatores). (Weitere Weberknechte XIX). *Senckenbergiana Biologica*, 37(3–4), 247–318.
- Rowland, J.M. & Cooke, J.A.L. (1973) Systematics of the arachnid order Uropygida (= Thelyphonida). *Journal of Arachnology*, 1, 55–71.
- Schenkel, E. (1963) Ostasiatische Opilioniiden aus dem Muséum d'Histoire Naturelle de Paris. *Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie*, 25(2), 483–494.

- Sclater, P.L. (1866) Notes upon the American Caprimulgidae. *Proceedings of the Zoological Society of London*, 1866, 123–145.
- Shear, W.A. (1975) The opilionid family Caddidae in North America, with notes on species from other regions (Opiliones, Palpatores, Caddoidea). *Journal of Arachnology*, 2, 65–88.
- Shear, W.A. (1982) Opiliones. In: Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms* vol. 2. McGraw-Hill Book Company, New York, pp. 104–110.
- Shultz, J.W. (1998) Phylogeny of the Opiliones (Arachnida): An assessment of the “Cyphopalpatores” concept. *Journal of Arachnology*, 26, 257–272.
- Shultz, J.W. (2008) *Leiobunum nigripes* is a junior synonym of *Leiobunum verrucosum* (Opiliones, Sclerosomatidae). *Journal of Arachnology*, 36(1), 184–186.
- Shultz, J.W. & Pinto-da-Rocha, R. (2007) Morphology and functional anatomy. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds.), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 14–61.
- Shultz, J.W. & Regier, J.C. (2001) Phylogenetic analysis of Phalangida (Arachnida, Opiliones) using two nuclear protein-coding genes supports monophyly of Palpatores. *Journal of Arachnology*, 29, 189–200.
- Šilhavý, V. (1970) Nouvelles recherches sur la famille des Neopilionidae Lawrence. *Bulletin du Muséum National d’Histoire Naturelle series 2*, 41(Suppl. 1), 171–175.
- Simon, E. (1879) Descriptions d’Opiliones nouveaux. *Annales de la Société Entomologique de Belgique*, 22(Comptes-Rendus), lxx–lxxv.
- Simon, E. (1884) Arachnides recueillis par la mission du Cap Horn en 1882–1883. *Bulletin de la Société Zoologique de France*, 9, 117–144, pl. 3.
- Simon, E. (1887) Arachnides. Mission scientifique du Cap Horn, 1882–1883. *Zoologie*, 6(2): 1–42, pl. I–II.
- Simon, E. (1902) Arachnoideen, excl. Acariden und Gonyleptiden. *Ergebnisse der Hamburger Magalhaensischen Sammelreise* vol. 2, *Arthropoden*, 17: 1–47. L. Friederichsen: Hamburg.
- Soares, B.A.M. & Soares, H.E.M. (1947) Alótipos e formas novas de Opiliões Paranaenses (Opiliones—Gonyleptidae, Phalangiidae). *Papéis Avulsos do Departamento de Zoologia*, 8(5), 63–84.

- Sørensen, W. (1886) Opiliones descripsit W. Sørensen. *In*: Koch, L. & Keyserling, E. von, *Die Arachniden Australiens nach der natur beschrieben und abgebildet* vol. 2. Bauer und Raspe: Nürnberg, pp. 53–86, pl. 5–6.
- Starega, W. (1964) Materialien zur Kenntnis der ostasiatischen Weberknechte (Opiliones). I–IV. *Annales Zoologici*, 22(17), 387–410.
- Starega, W. (1976a) Opiliones Kosarze (Arachnoidea). *Fauna Polski*, 5, 1–197.
- Starega, W. (1976b) Die Weberknechte (Opiliones, excl. Sironidae) Bulgariens. *Annales Zoologici*, 33, 287–433.
- Starega, W. (2002) Baltic amber harvestmen (Opiliones) from Polish collections. *Annales Zoologici*, 52(4), 601–604.
- Stoliczka, F. (1869) Contribution towards the knowledge of Indian Arachnoidea. *Journal of the Asiatic Society of Bengal*, 38(4 Pt 2), 201–251, plates 18–20.
- Strand, E. (1910) Spinnentiere aus Neuguinea (Opiliones, Psechridae und Clubionidae) gesammelt von Dr. Schlaginhaufen. *Abhandlungen und Berichte des Königl. Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden*, 13, 1–16.
- Suzuki, S. (1973) Opiliones from the South-west Islands, Japan. *Journal of Science of the Hiroshima University*, (Series B, Division 1)24, 205–279.
- Suzuki, S. (1985) A synopsis of the Opiliones of Thailand (Arachnida) II. Palpatores. *Steenstrupia*, 11, 209–257.
- Swenson, U., Backlund, A., McLoughlin, S. & Hill, R. S. (2001) *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics*, 17, 28–47.
- Swenson, U. & Bremer, K. (1997) Pacific biogeography of the Asteraceae genus *Abrotanella* (Senecioneae, Blennospermatinae). *Systematic Botany*, 22(3), 493–508.
- Taylor, C.K. (2004) New Zealand harvestmen of the subfamily Megalopsalidinae (Opiliones: Monoscutidae)—the genus *Pantopsalis*. *Tuhinga*, 15, 53–76.
- Taylor, C.K. (2008a) A new species of Monoscutinae (Arachnida, Opiliones, Monoscutidae) from New Zealand, with a redescription of *Monoscutum titirangiense*. *Journal of Arachnology*, 36, 176–179.
- Taylor, C.K. (2008b) A new species of Monoscutidae (Arachnida, Opiliones) from the wheatbelt of Western Australia. *Records of the Western Australian Museum*, 24(4), 375–380.

- Taylor, C.K. (2009a) Revision of the Australian Gagrellinae (Arachnida: Opiliones: Sclerosomatidae), with a description of a new species. *Australian Journal of Entomology*, 48, 217–222.
- Taylor, C.K. (2009b) *Australiscutum*, a new genus of Monoscutidae (Arachnida: Opiliones) from eastern Australia, with the first record of asymmetrical chelicerae in Opiliones. *Insect Systematics and Evolution*, 40, 319–332.
- Taylor, C.K. & Hunt, G.S. (2009) New genus of Megalopsalidinae (Arachnida: Opiliones: Monoscutidae) from north-eastern Australia. *Zootaxa*, 2130, 41–59.
- Taylor, R.W. (1972) Biogeography of insects of New Guinea and Cape York Peninsula. In: *Bridge and Barrier: The Natural and Cultural History of Torres Strait* (ed. D Walker), pp. 213–230. Australian National University, Research School of Pacific Studies, Publication BG/3, Canberra, Australia.
- Thorell, T. (1876) Descrizione di alcune specie di Opilioni dell' Arcipelago Malese appartenenti al Museo Civico di Genova. *Annali del Museo Civico di Storia Naturale di Genova, Serie I*, 9, 111–138.
- Thorell T. 1894. Förteckning öfver Arachnider från Java och närgränsande öar, insamlade af docenten D:r Carl Aurivillius; jemte beskrifningar å några sydasiatiska och sydamerikanska Spindlar. *Bihang till K. Svenska Vetenskaps-Akademiens Handlingar* **20**, 1–63.
- Tourinho, A.L. (2007) Sclerosomatidae Simon, 1879. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 128–131.
- Tourinho-Davis, A.L. (2004) A new genus of Gagrellinae from Brazil, with a comparative study of some subtropical and southernmost tropical South American genera (Opiliones, Eupnoi, Sclerosomatidae). *Revista Ibérica de Aracnología*, 9, 157–177.
- Turner, H. (1996) Sapindaceae and the biogeography of eastern Australia. *Australian Systematic Botany*, 8, 133–167.
- Ubick, D. (2007) Phalangodidae Simon, 1879. In: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (eds), *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge (Massachusetts) and London, pp. 217–221.
- Vinnersten, A. & Bremer, K. (2001) Age and biogeography of major clades in Liliales. *American Journal of Botany*, 88(9), 1695–1703.

- Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27, 1153–1167.
- Weidner, H. (1959) Die entomologischen Sammlungen des Zoologischen Staatsinstituts und Zoologischen Museums Hamburg. 1. Teil, Pararthropoda und Chelicerata, I. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 57, 89–142.
- Weston, P.H. & Crisp, M.D. (1994) Cladistic biogeography of waratahs (Proteaceae: Embothriaceae) and their allies across the Pacific. *Australian Systematic Botany*, 7, 225–249.
- White, A. (1849) Descriptions of apparently new species of Aptera from New Zealand. *Proceedings of the Zoological Society of London*, 17, 3–6 (reprinted 1850, *Annals and Magazine of Natural History series 2*, 5, 50–53).
- Yoo, J.-S. & Framenau, V.W. (2006) Systematics and biogeography of the sheet-web building wolf spider genus *Venonia* (Araneae: Lycosidae). *Invertebrate Systematics*, 20, 675–712.

Every reasonable effort has been made to acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.