



A new genus of scutigerial centipedes (Chilopoda) from Western Australia, with new characters for morphological phylogenetics of Scutigera

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Abstract

The scutigerial centipede *Allothereua incola* Verhoeff, 1925, originally described from the Kimberley region of north-western Australia, is abundantly represented in the Pilbara region of Western Australia. It forms the basis for a new genus, *Pilbarascutigera*, resembling *Thereuopoda* Verhoeff, 1904, and *Thereuopodina* Verhoeff, 1905, in the form of its female gonopods and in having short, triangular spicula on the tergal plates. *Pilbarascutigera* unites with *Thereuopoda* in cladistic analysis of morphological characters based on a pairing of slender, needle-like bristles (Tastborsten *sensu* Verhoeff) and spines on the posterior tergal plates and the arrangement of sensilla on the metarthron of the female gonopod. Scanning electron microscopic documentation of *P. incola* informs on numerous aspects of scutigerial morphology, including the female subanal plates, tergal prominences, and peristomatic structures.

Key words: Scutigera, Scutigerae, Thereuoneminae, *Pilbarascutigera*, Western Australia, Pilbara, phylogeny

Introduction

Taxonomic study of the scutigerial centipedes of Australia consists of a few papers by European and American zoologists working with small collections, all before 1940 (Lucas 1840; Newport 1844; Koch 1865; Haase 1887; Pocock 1901; Attems 1911; Brölemann 1912; Chamberlin 1920; Verhoeff 1925; Fahlander 1939). The extensive collections built up from surveys by Australian museums since the 1970s have not yet entered the taxonomic literature. Vast tracts of Australia, especially the arid parts of the country, are entirely undocumented with respect to scutigerial diversity.

Against this backdrop, herein we describe a scutigerial species collected in great abundance in surveys since 2000 by the Department of Environment and Conservation (Western Australia), Biota Environmental Sciences, and the Australian Museum in the Pilbara region, northwestern Western Australia (Fig. 1). Previous studies on Australian scutigerials found that the genera *Parascutigera* Verhoeff, 1904a, and *Allothereua* Verhoeff, 1905, accommodate most of the known species in northern and southern Australia, respectively, although several species were thought to represent monotypic genera endemic to Australia (e.g., *Prionopodella* Verhoeff, 1925; *Prothereua* Verhoeff, 1925; *Pesvarus* Würmli, 1974a). The Pilbara collections are assigned to the geographically closest published species, *Allothereua incola* Verhoeff, 1925, originally documented from the Kimberley region of Western Australia. *Allothereua incola* has always been anomalous in the context of Australian members of *Allothereua* with respect to both its distribution and its morphology. Other species of the genus are found in forests in southern Australia, whereas the types of *A. incola* occur in association with termite mounds in arid northern Australia. The morphological peculiarities of *A. incola*, enhanced by study of new collections from the Pilbara, serve as a basis for recognising a new genus, *Pilbarascutigera*, endemic to northwestern Australia.

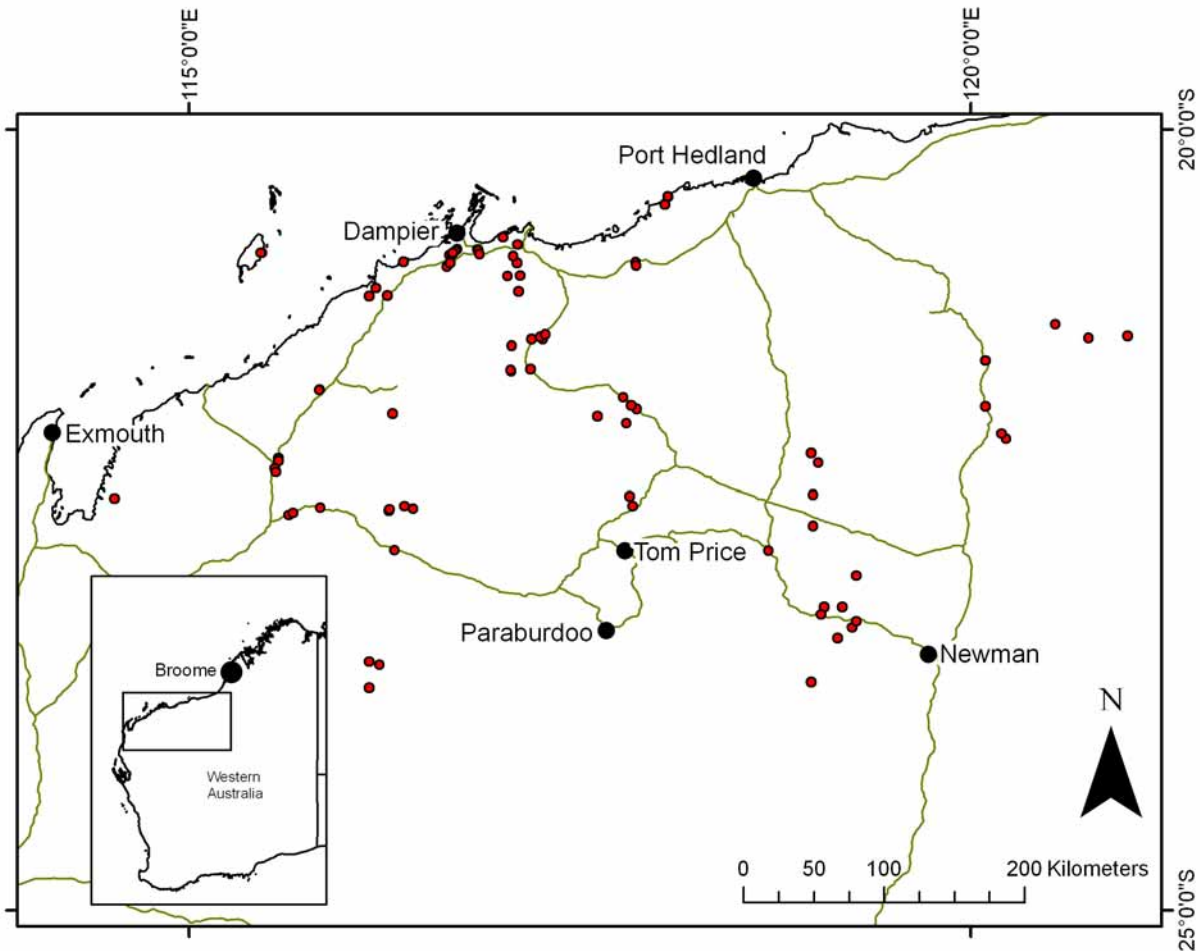


FIGURE 1. Distribution of *Pilbarascutigera*. Location of the Pilbara region indicated in inset (corresponding to large map) and type locality of *Pilbarascutigera incola* at Broome. Detailed map shows Pilbara region with localities for *P. incola* indicated by small closed circles.

Species identification in Scutigermorpha is fraught with problems. The most prolific student of the group, K. W. Verhoeff, characteristically over-split species without fully recognising the extent of ontogenetic and intra- and inter-population variation. The acknowledgement that scutigermorph species exhibit more variation than was perceived by Verhoeff [a problem already perceived by Muralevič (1910)] has led to a tendency to adopt polymorphic species, in many cases with broad geographic distributions and extensive synonymy (see e.g., Würmli 1978, 2005 for *Sphendononema*; Würmli 1979 for *Thereuopoda*). In evaluating the limits of *Pilbarascutigera incola* we have noted characters that vary in other genera, such as *Scutigera* in Europe and the Middle East (Würmli 1973, 1977) and *Thereuonema* in East Africa, the Middle East, and Asia (Würmli 1975). An understanding of variation is facilitated by the sheer abundance in the new collections – *Pilbarascutigera incola* is known from some 800 specimens, one population sample including more than 100 specimens, and pitfall sampling has been conducted at varied spatial scales throughout the Pilbara region.

Scanning electronic microscopy has not routinely been used as a tool in taxonomic work on Scutigermorpha. Because numerous morphological details of the group as a whole have not been documented by electron micrographs, the description of *Pilbarascutigera incola* is supplemented with extensive illustration.

Apart from the types at Naturhistoriska Riksmuseet, Stockholm, specimens described herein are housed in the collections of the Western Australian Museum, Perth (prefixed WAM), and the Australian Museum (AM KS), Sydney. Scanning electron microscopy used a LEO 435VP with a Robinson backscatter collector.

Descriptive terminology generally follows recommendations by Würmli (1974b). Proportions of the female gonopods follow measurements described by Würmli (1973, fig. 1). Terminology for peristomatic structures (epipharynx and hypopharynx) is as used by Koch & Edgecombe (2006). Tergal plates are abbreviated T1–T8 (Negrea 2003). Other abbreviations: Stn, Station; Hmst, Homestead.

Taxonomy

Order SCUTIGEROMORPHA Pocock, 1895

Family SCUTIGERIDAE Gervais, 1837

Subfamily THEREUONEMINAE Verhoeff, 1925

Pilbarascutigera n. gen.

Type species: Allothereua incola Verhoeff, 1925

Diagnosis: Thereuonemine with predominantly orange-brown pigmentation; anterior tergal plates having scattered setiform bristles (Stachelborsten *sensu* Verhoeff 1925) and slender, needle-like bristles (Tastborsten *sensu* Verhoeff) but lacking spines; TT5–7 (and TT3–4 in some specimens) with numerous spines, each paired with a Tastborste, along each side of midline, on stoma saddles, and on lateral parts of tergal plates; tergal spicula short, triangular, relatively sparse; anterior projection of cephalic sutures short, parallel; stoma saddles weakly vaulted; sinus between inner margins of mesarthron of female gonopod broad, parabolic to almost rectangular; margins of metarthron relatively straight in ventral view; female subanal plate drop-shaped, with blunt, rounded distal end; spines in lateral cluster on clypeal part of epipharynx uniformly elongate, slender.

Etymology: Compounding *Pilbara*, and the usual scutigeromorph suffix - *scutigera*.

Discussion: *Allothereua incola* Verhoeff, 1925, differs from other species of *Allothereua* in having relatively sparse, short spicula (Verhoeff 1925, pl. 1, fig. 8), slender, needle-like bristles paired with the spines on the tergal plates (especially TT5–7), and a relatively wide sinus between the inner margins of the mesarthron of the female gonopod (Verhoeff 1925, pl. 1, fig. 1). Verhoeff (1925) distinguished the fine bristles in paired association with a spine as “Tastborsten” (Figs. 42, 44, 68), in contrast to the thicker bristles described by Verhoeff as “Stachelborsten” that are paired with a spine in *Allothereua* (Edgecombe & Giribet 2006, fig. 4B). In *Allothereua* from southern parts of Australia, the spicula are variably setiform (Edgecombe & Giribet 2006, fig. 4B), as in *Parascutigera* from New Caledonia (Edgecombe & Giribet 2006, fig. 4D), rather than short and triangular as in *Pilbarascutigera* (Figs. 42, 43).

The female gonopod of the types of *Pilbarascutigera incola* (Verhoeff 1925, pl. 1, fig. 1) is matched by many specimens from the Pilbara region (Fig. 62). However, the parabolic sinus between the mesarthron inner margins in these specimens is at one end of a range of variation found in the Pilbara samples, and other specimens, irrespective of size, have a relatively wider sinus with an angular (Fig. 61) or almost transverse (Fig. 63) proximal part that significantly differs from the narrow, parallel-sided sinus in species of *Allothereua* and *Parascutigera*. As was recognized in Verhoeff’s (1925, p. 8) key to genera of Thereuoneminae, the wider sinus is shared with *Thereuopoda* and *Thereuopodina*, two genera that also occur in northern Australia.

Distinction of *Pilbarascutigera* and *Thereuopoda* is straightforward, the former having weakly (versus strongly) vaulted stoma saddles, much shorter spiracles, an absence of spines on the anterior tergal plates (consistent absence on T1; usually absent on T2 and sometimes absent on T3 and T4 in *P. incola*), and the first appearance of spines on the stoma saddle of TT3, 4 or 5 (versus first appearance on TT1 or 2 in *Thereuopoda*, with consistent abundance on T2). *Pilbarascutigera* has shorter cephalic sutures (Figs. 3, 4, 21) than the two valid species of *Thereuopoda* *fide* Würmli (1979), and the sutures lack an outward kink (*cf.* Verhoeff 1937, pl. 20, fig. 48; Verhoeff 1939, figs. 1, 5; Würmli 1979, fig. 25). *Pilbarascutigera* has relatively elongate setae on

the ventral side of the leg 15 tarsus, in contrast to the short, spine-like setae in this position in *Thereuopoda* (Murakami 1971, fig. 3G). *Pilbarascutigera* also lacks spines that are found on the proximal half of the first antennal flagellum in *Thereuopoda* (Murakami 1971, fig. 3C; Figs. 64, 65 herein). The metarthron of the female gonopod in *Pilbarascutigera* is less curved than in *Thereuopoda* (see, e.g., Verhoeff 1943, fig. 4; Unsöld & Melzer 2003, fig. 2G–I for *T. longicornis*) or *Thereuopodina*. The subanal plate of the female has a blunt, rounded distal end in *Pilbarascutigera* (Fig. 53), less elaborate than the variably pointed (Fig. 66) or projecting end in *Thereuopoda* (see Würmli 1979, figs. 13–22 for variability in shape of the subanal plate in *Thereuopoda*).

Thereuopoda resembles *Pilbarascutigera* in having Tastborsten paired with the spines on the posterior tergal plates (Fig. 68 for *Thereuopoda longicornis*; Murakami 1971, fig. 3A for *T. clunifera*). *Thereuopodina* (e.g., *T. queenslandica*: Fig. 69) resembles *Thereuonema* (Würmli 1975, figs. 5, 15; Edgecombe & Giribet 2006, fig. 2F) and *Allothereua* in having relatively thicker bristles paired with the spines, as is also shared by non-thereuonemines such as *Scutigera* (Edgecombe & Giribet 2006, fig. 2E). The triangular shape of the spicula in *Pilbarascutigera* is shared by *Thereuopoda* (Verhoeff 1937, pl. 23, fig. 64) and *Thereuopodina* (Fig. 69). *Thereuopodina* also has more vaulted stoma saddles than does *Pilbarascutigera*, approaching the condition seen in *Thereuopoda*.

Pilbarascutigera and *Thereuopoda* unite to the exclusion of other scutigeromorph taxa in the distribution of sensilla coeloconica on the metarthron of the female gonopod. In *Pilbarascutigera incola* these sensilla are scattered two-deep along the ventral surface of the metarthron (Fig. 58). Likewise, in *Thereuopoda* sensilla are arranged two-deep (Verhoeff 1937, pl. 22, figs. 56, 58, 60; Verhoeff 1939, fig. 2; Fig. 70 herein) along most or all the length of the metarthron or are even more densely scattered (Verhoeff 1943, fig. 4). In contrast, in *Thereuonema*, the sensilla are arranged in a single row along the length of the metarthron (Verhoeff 1936, fig. 5; Fig. 71 herein), and this single-row arrangement can be confirmed in *Allothereua* (Fig. 73) and *Thereuopodina* (Fig. 72), as well as non-thereuonemines such as *Scutigera* (Fig. 74) and members of the Scutigerinidae (Fig. 75). All scutigeromorphs examined also have a row of sensilla along the outer margin of the metarthron (Fig. 72). These data suggest that a single row of sensilla on the ventral surface is plesiomorphic relative to the proliferation of sensilla in *Pilbarascutigera* and *Thereuopoda*.

A distinctive morphology of spines on the clypeal part of the epipharynx is seen in *P. incola*. The spines in the lateral cluster are uniformly elongate and slender (Fig. 15), in contrast to the condition in *Thereuopoda*, *Thereuopodina* and *Allothereua*, in which a group of elongate, slender spines grades into a larger cluster of shorter, conical spines (Edgecombe & Giribet 2006, fig. 3D for *Thereuopoda longicornis*). Other scutigeromorphs have more uniformly conical spines (e.g., *Prothereua annulata*: Koch & Edgecombe 2006, fig. 7d).

***Pilbarascutigera incola* (Verhoeff, 1925) new comb.**

Figs. 2–63

Allothereua incola Verhoeff, 1925: 18–19, pl. 1, figs. 1, 8.

Types: WESTERN AUSTRALIA: Broome: ♀, ♂, juvenile ♂, in alcohol apart from slide mounts of parts of ♀; Naturhistoriska Riksmuseet, Stockholm.

Other material: WESTERN AUSTRALIA: Pilbara. Collected by pitfall where range of dates is indicated. Department of Environment and Conservation Pilbara Survey except where other collectors indicated; numbers prefixed by 'T' = WAM. T57730, ♂, Barrow Island, NW of Town Point, 20°47'18"S 115°27'43"E, leg. R. Teale, G. Harold, 18.xi.2003; T57731, ♂, Barrow Island, terminal tanks, 20°47'24"S 115°27'22"E, leg. R. Teale, G. Harold, 18.ii.2003; T69857, 4 ♀♀, ♂, Bungaroo, 26.9 km S of Pannawonica, 21°49'08"S 116°17'59"E, leg. Z. Hamilton, 14–20.iii.2005; T69858, 6♀♀, 2♂♂, T75216, ♀, Waramboo, 50.5 km W of Pannawonica, 21°40'00"S 115°50'06"E, leg. D. Kamien, 14–20.iii.2005; T69859, 3 ♀♀, 2♂♂, Waramboo,

50.9 km W of Pannawonica, 21°40'09"S 115°49'54"E, leg. D. Kamien, 14–20.iii.2005; T69861–69867, Dampier Salt Biological, leg. D. Kamien, Z. Hamilton: T69861, 3 ♀♀, 3.7 km WSW of Karratha, 20°46'02.6"S 116°42'53"E, 27.x.–2.xi.2005; T69862, 2 ♀♀, 2 ♂♂, 19.8 km WSW of Karratha, 20°48'09.6"S 116°39'55"E, 28.x.–3.xi.2005; T69863, ♂, 13.7 km WSW of Karratha, 20°46'02.6"S 116°42'53"E, 27.x.–2.xi.2005; T69864, 2 ♀♀, ♂, 18.0 km WSW of Karratha, 20°47'43.1"S 116°40'51"E, 27.x.–2.xi.2005; T69865, ♂, 13.7 km WSW of Karratha, 20°46'02.6"S 116°42'53"E, 27.x.–2.xi.2005; T69866, ♀, 15.3 km WSW of Karratha, 20°46'36.7"S 116°42'05"E, 27.x.–2.xi.2005; T69867, ♀, ♂, 17.4 km WSW of Karratha, 20°47'21.9"S 116°41'03"E, 27.x.–2.xi.2005; T69869, ♀, Exmouth Gulf (Straits Saltfield), 30 km NW of Yanrey Hmst, 22°21'36"S 114°31'12"E, leg. R. Teale, 17–26.viii.2004; T76419, 5 ♀♀, ♂, Nullagine River, N of Nullagine, 21°46'13"S 120°05'31"E, 5.viii.–17.xi.2003; T76420–T76422, Millstream NP: T76420, 5 ♀♀, 4 ♂♂, 21°32'48"S 117°03'33"E, 15.vii.–23.xi.2003; T76421, 3 ♀♀, 4 ♂♂, 21°32'25"S 117°03'25"E, 23.xi.2003–8.v.2004; T76422, 9 ♂♂, 21°18'37"S 117°16'35"E, 16.vii.–23.xi.2003; T76423, 4 ♀♀, 2 ♂♂, Coolawanyah Stn, SW of hmst, 21°50'00"S 117°36'39"E, 6.v.–11.x.2004; T76424, ♀, ♂, Cane River Reserve, 22°11'19"S 115°33'13"E, 27.ix.–27.xi.2003; T76425, 30 ♀♀, 7 ♂♂, Mt Stuart Stn, E of hmst, 22°25'48"S 116°16'47"E, 26.xi.2003–2.v.2004; T76426, T76427, Mt Stuart Stn, NE of hmst: T76426, 26 ♀♀, 6 ♂♂, 22°24'29"S 116°22'29"E, 26.xi.2003–2.v.2004; T76427, 2 ♀♀, 22°25'30"S 116°25'57"E, 26.xi.2003–1.v.2004; T76428, T76429, Hamersley Range, SE of Mt Lockyer, 22°32'09"S 118°59'31"E: T76428, 9 ♀♀, 3 ♂♂, 30.xi.2003–22.v.2004; T76429, 5 ♀♀, 8 ♂♂, 22.v.–19.x.2004; T76430, 5 ♀♀, Ophthalmia Range, Giles Point, 23°15'03"S 119°08'41"E, 20.xi.2003–25.v.2004; T76431, 2 ♀♀, 2 ♂♂, Hamersley Range, NE of Mt Robinson, 23°03'14"S 119°03'37"E, 1.ix.–19.xi.2003; T76432, 14 ♀♀, 8 ♂♂, Marillana Stn, Weeli Wollie Creek, 22°51'08"S 119°15'54"E, 31.viii.–19.xi.2003; T76433, 8 ♀♀, 5 ♂♂, Mundabullanga Stn, NE of hmst, 20°25'49"S 118°03'50"E, 14.xi.2003–12.v.2004; T76435, 3 ♀♀, 4 ♂♂, 1 indet., Macroy Stn, E of Mt Negri, 20°50'55"S 117°51'16"E, 11.vii.–13.xi.2003; T76436, 13 ♀♀, 5 ♂♂, Mardie Stn, NW of hmst, 21°03'56"S 116°09'02"E, 28.xi.2003–11.v.2004; T76595, T76596, crown land reserve, SE of Dampier, 20°46'05"S 116°50'31"E: T76595, 16 ♀♀, 6 ♂♂, undet. juvs., 12.xi.2003–10.v.2004; T76596, ♀, 10.v.–2.x.2004; T76597–T76599, crown land reserve, NW of Mt Prinsep, 20°46'18"S 116°50'59"E: T76597, 56 ♀♀, 53 ♂♂, 3 indet., 12.xi.2003–10.v.2004; T76598, 12 ♀♀, 9 ♂♂, 1.vii.–12.xi.2003; T76599, 4 ♀♀, 10 ♂♂, 1 indet., 10.v.–2.x.2004; T76600, ♀, crown land reserve, NE of Mt Prinsep, 20°47'40"S 116°51'24"E, 10.v.–3.x.2004: T76601, T76602, Mt Welcome Stn, W of Mt Roe, 20°56'24"S 117°02'05"E, 10.v.–3.x.2004: T76601, 5 ♀♀, 2 ♂♂; T76602, 3 ♀♀, 3 ♂♂; T76606, T76607, Mt Welcome Stn, E of Mt Roe, 20°56'04"S 117°06'54"E, 12.xi.2003–9.v.2004: T76606, ♀, ♂; T76607, 3 ♀♀, ♂; T76610, 2 ♀♀, 2 ♂♂, Mt Welcome Stn, W of Mt Roe, 20°48'29"S 117°04'21"E, 5.vii.–12.xi.2003; T76003, T76005, water reserve, W of Cooya Pooya, 21°02'11"S 117°06'22"E: T76603, 7 ♀♀, 3 ♂♂, undet. juv., 12.xi.2003–10.v.2004; T76605, ♂, 2.vii.–12.xi.2003; T76008, T76009, Mt Welcome Stn, W of Mt Gregory, 20°51'09"S 117°05'45"E: T76608, ♀, ♂, 12.xi.2003–9.v.2004; T76609, ♀, 2 ♂♂, 9.v.–3.x.2004; T76611–T76613, Mt Welcome Stn, W of Roebourne: T76611, 4 ♀♀, 4 ♂♂, 20°48'29"S 117°04'21"E, 6.x.2004–23.v.2005; T76612, ♂, 20°44'11"S 117°05'56"E, 6.vii.–13.xi.2003; T76613, ♀, 5 ♂♂, 20°41'18"S 117°00'25"E, 6.vii.–13.xi.2003; T76614, T76615, Mundabullangana Stn, NE of hmst, 8.vii.–14.xi.2003; T76614, ♀, 20°25'49"S 118°03'50"E; T76615, ♀, 20°25'43"S 118°03'42"E; T76616, ♂, Mundabullangana Stn, N of hmst, 20°28'49"S 118°02'26"E, 12.v.–2.x.2004; T76617, 3 ♀♀, 11 ♂♂, 2 undet. juv., Macroy Stn, E of Mt Negri, 20°50'56"S 117°51'16"E, 13.v.–3.x.2004; T76618, ♀, Mundabullangana Stn, SW of hmst, 20°52'12"S 117°51'32"E, 13.v.–3.x.2004; T76620, ♀, crown land res., NW of Mt Wilkie, 20°50'41"S 116°22'03"E, 23.ix.–28.xi.2003; T76621, ♀, Karratha Stn, N of hmst, 20°52'34"S 116°38'50"E, 5.x.2004–20.v.2005; T76622, 5 ♀♀, 2 ♂♂, SW of Mt Regal, 20°51'14"S 116°40'08"E, 22.ix.–28.xi.2003; T76624, T76625, Mardie Stn, Eramurra Creek, 21°03'43"S 116°15'54"E; T76624, 5 ♀♀, 6 ♂♂, 24.ix.–27.xi.2003; T76625, 25 ♀♀, 21 ♂♂, 4 indet., 11.v.–4.x.2004; T76627, ♂, Mardie Stn, NW of hmst, 21°03'56"S 116°09'02"E, 24.ix.–28.xi.2003; T76630, T76631, Meentheena Stn, NW of hmst, 21°14'46"S 120°32'21"E: T76630, 5 ♀♀, 3 ♂♂, 16.xi.2003–18.v.2004; T76631, 4 ♀♀, 8 ♂♂, 2 undet. juv., 18.v.–

13.x.2004; T76632–T76634, uncleared CALM land, W of Yigalong Ck, 21°20'01"S 120°45'08"E: T76632, 2 ♂♂, 31.vii.–16.xi.2003; T76633, 2 ♀♀, 16.xi.2003–18.v.2004; T76634, ♀, 18.v.–13.x.2004; T76635, T76636, Warrawagine Stn, near Pulgorah Cone, 21°19'19"S 121°00'08"E: T76635, 4 ♀♀, 3 ♂♂, 30.vii.–16.xi.2003; T76636, 4 ♀♀, ♂, 16.xi.2003–17.v.2004; T76638, 5 ♀♀, Bonney Downs Stn, NW of hmst, 21°58'46"S 120°13'27"E, 18.xi.2003–28.viii.2004; T76640, 2 ♀♀, 2 ♂♂, Bonney Downs Stn, NE of hmst, 21°56'52"S 120°11'39"E, 20.v.–19.x.2004; T76642, 3 ♂♂, Corruna Downs Stn, E of hmst, 21°28'48"S 120°05'27"E, 19.v.–20.x.2004; T76644, T76649, Coolawanyah Stn, SW of hmst: T76644, ♂, 21°52'56"S 117°47'40"E, 6.v.–13.x.2004; T76649, ♀, 21°50'00"S 117°36'39"E, 5.ix.–25.xi.2003; T76645, T76646, Mt Florance Stn, NW of hmst, 21°47'12"S 117°51'44"E: T76645, ♀, 2 ♂♂, 3.ix.–24.xi.2003; T76646, 2 ♀♀, 5.v.–10.x.2004; T76647, T76648, Coolawanyah Stn, Chichester Range: T76647, ♀, 21°45'59"S 117°49'31"E, 4.ix.–24.xi.2003; T76648, ♀, ♂, 21°42'51"S 117°46'32"E, 5.v.–11.x.2004; T76653–T76659, T76664, T76666–T76671, Millstream Chichester NP: T76653, ♂, 21°20'23"S 117°15'36"E, 23.xi.2003–8.v.2004; T76654, T76655, 21°19'41"S 117°14'35"E: T76654, 2 ♀♀, 2 ♂♂, 16.vii.–23.xi.2003; T76655, ♀, 4 ♂♂, 23.xi.2003–8.v.2004; T76656–T76658, 21°20'29"S 117°11'19"E: T76656, 2 ♀♀, 17.vii.–23.xi.2003; T76657, 2 ♀♀, 23.xi.2003–8.v.2004; T76658, 2 ♀♀, 5 ♂♂, 8.v.–13.x.2004; T76659, ♀, 3 ♂♂, 21°20'29"S 117°11'19"E, 13.x.2004–12.v.2005; T76664, 9 ♀♀, 3 ♂♂, 21°32'48"S 117°03'33"E, 23.xi.2003–8.v.2004; T76666, 3 ♂♂, 21°32'25"S 117°03'25"E, 8.v.–11.x.2004; T76667–T76669, 21°23'03"S 117°03'38"E: T76667, 4 ♀♀, 18.vii.–23.xi.2003; T76668, 9 ♀♀, 3 ♂♂, 23.xi.2003–7.v.2004; T76669, 2 ♀♀, ♂, 7.v.–11.x.2004; T76670, T76671, 21°18'37"S 117°16'35"E: T76670, 2 ♀♀, 2 ♂♂, 23.xi.2003–8.v.2004; T76671, 3 ♀♀, 10 ♂♂, 8.v.–11.x.2004; T76673, T76674, T76676–T76678, Hamersley Range, SE of Mt Robinson: T76673, ♀, 23°11'07"S 119°14'17"E, 30.viii.–20.xi.2003; T76674, 3 ♀♀, 5 ♂♂, 23°08'46"S 119°15'57"E, 2.ix.–20.xi.2003; T76676, 2 ♂♂, 23°06'12"S 119°02'20"E, 2.ix.–20.xi.2003; T76678, ♂, 23°03'14"S 119°10'37"E, 25.v.–16.x.2004; T76680, ♀, 5 ♂♂, Marillana Stn, Weeli Wollie Creek, 22°51'08"S 119°15'54"E, 24.v.–16.x.2004; T76684, 4 ♀♀, 3 ♂♂, Hamersley Range, SE of Mt Lockyer, 23°32'06"S 118°58'38"E, 11.viii.–20.xi.2003; T76685, 4 ♀♀, 5 ♂♂, Mulga-Downs Stn, near Outcamp, 22°20'05"S 118°59'19"E, 21.xi. 2003–24.v.2004; T76687, 3 ♀♀, ♂, Mulga-Downs Stn, NW of hmst, 22°04'08"S 118°58'43"E, 23.v.–29.x.2004; T76688, 8 ♀♀, 3 ♂♂, 2 undet. juv., Mulga-Downs Stn, SW of hmst, 22°08'05"S 119°01'27"E, 21.xi. 2003–23.v.2004; T76691–T76696, T76702, Mt Stuart Stn: T76691, 6 ♀♀, 5 ♂♂, SE of hmst, 23°24'17"S 116°08'54"E, 2.v.–7.x.2004; T76692, ♀, ♂, SE of hmst, 23°34'17"S 116°08'54"E, 2.v.–7.x.2004; T76693, ♀, 2 ♂♂, NW of hmst, 22°25'09"S 115°50'16"E, 3.v.–7.x.2004; T76694, 7 ♀♀, 7 ♂♂, NE of hmst, 23°25'31"S 116°12'55"E, 1.v.–10.x.2004; T76695, 4 ♀♀, ♂, NE of hmst, 22°26'15"S 116°16'27"E, 1.v.–10.x.2004; T76696, 2 ♀♀, 2 ♂♂, E of hmst, 22°25'48"S 116°16'47"E, 9.ix.–26.xi.2003; T76702, ♀, 5 ♂♂, E of hmst, 22°25'48"S 116°16'47"E, 2.v.–10.x.2004; T76704, ♂, Cane River Reserve, 22°06'15"S 115°34'04"E, 3.ix.–27.xi.2003; T76706, 4 ♀♀, ♂, Cane River Reserve, 22°07'12"S 115°34'12"E, 27.xi.2003–30.iv.2004; T76798, ♀, Cane River Reserve, 22°10'11"S 115°32'39"E, 30.iv.–30.ix.2004; T76709, T76710, Cane River Reserve, 22°11'36"S 115°33'13"E: T76709, 3 ♀♀, 28.ix.–27.xi.2003; T76710, 2 ♀♀, 2 ♂♂, 29.iv.–30.ix.2004; T76712–T76714, Nanutarra Stn, NE of hmst: T76712, ♀, 5 ♂♂, 22°27'50"S 115°38'04"E, 1.v.–1.x.2004; T76713, ♀, 29.ix.–26.xi.2003; T76714, ♂, 22°27'08"S 115°39'41"E, 1.v.–1.x.2004; T76719, ♂, Cape Preston, site 2, 21°00'55"S 116°11'32"E, 10–25.iv.2000; T76734, ♂, Ophthalmia Range, Giles Point, 23°15'03"S 119°08'41"E, 25.v.–16.x.2004; AM KS 92757, ♀, Juna Downs Stn, Great Northern Hwy, approx. 8 km S of Kanijini Dr turnoff, 22°41'36"S 118°42'19"E, CVA volunteers, 23–28.ix.2005; AM KS 92758, ♀, Hamersley Stn, Pindering paddock, 22°24'28"S 117°50'07"E, leg. S. Lassau, M. Elliott, L. Kampen, M. Bulbert, 14–22.iv.2005; AM KS 92759, ♀, Hamersley Stn, Pindering paddock, 22°20'50"S 117°48'59"E, leg. S. Lassau, M. Elliott, L. Kampen, M. Bulbert, 14–22.iv.2005; AM KS 97166, 97167, 2 ♀♀, Roebourne-Wittenoom Rd, 14.9 km S of Tom Price Rwy Rd junction, 21°31'58.6"S 117°10'48.5"E, leg. M. Bulbert, J. Gollan, S. Ginn, G. Brown, 21–31.v.2006; AM KS 97168, ♂, Nanutarra-Wittenoom Rd, 119.6 km W of Paraburdoo-Tom Price Rd junction, 22°41'28.5"S 116°18'49.2"E, leg. M. Bulbert, J. Gollan, S. Ginn, G. Brown, 22.v.–1.vi.2006.

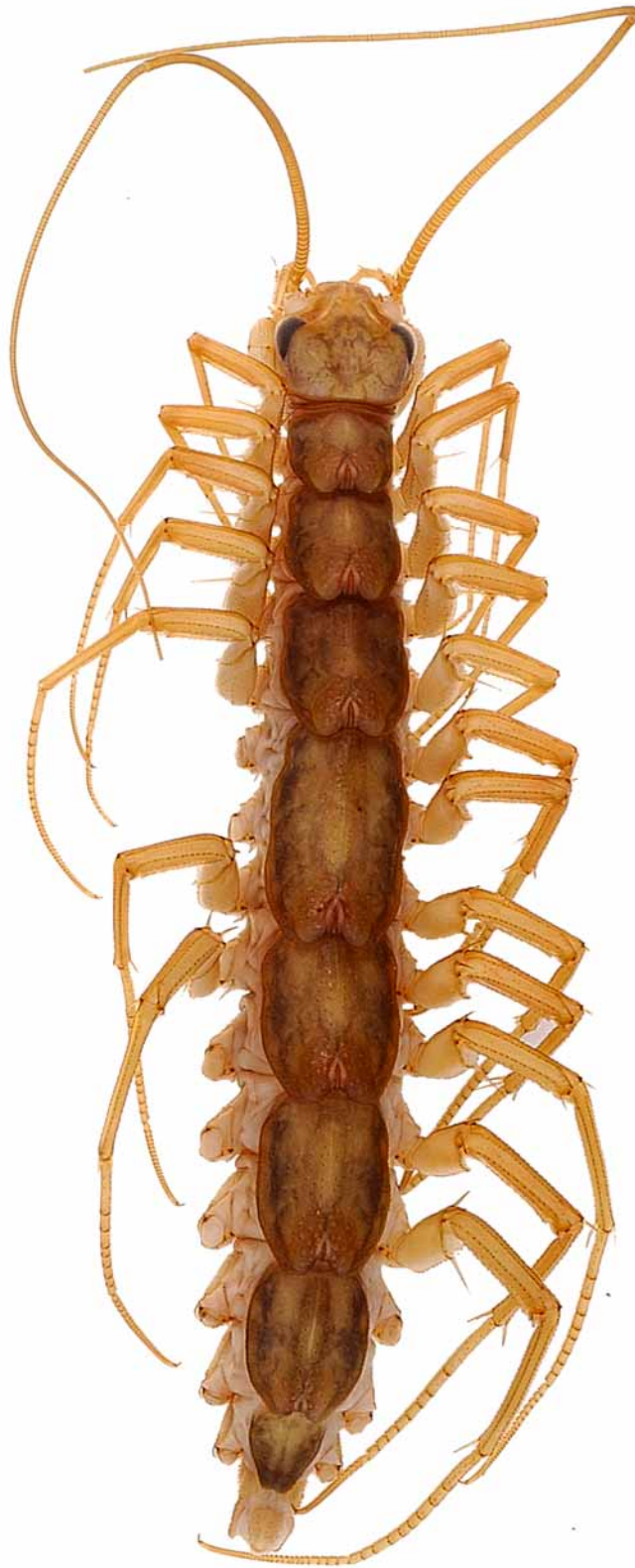


FIGURE 2. *Pilbarascutigera incola* (Verhoeff, 1925). WAM T75216, female. Body length 28 mm.

Description: Length up to 31 mm in males, 28 mm in females.

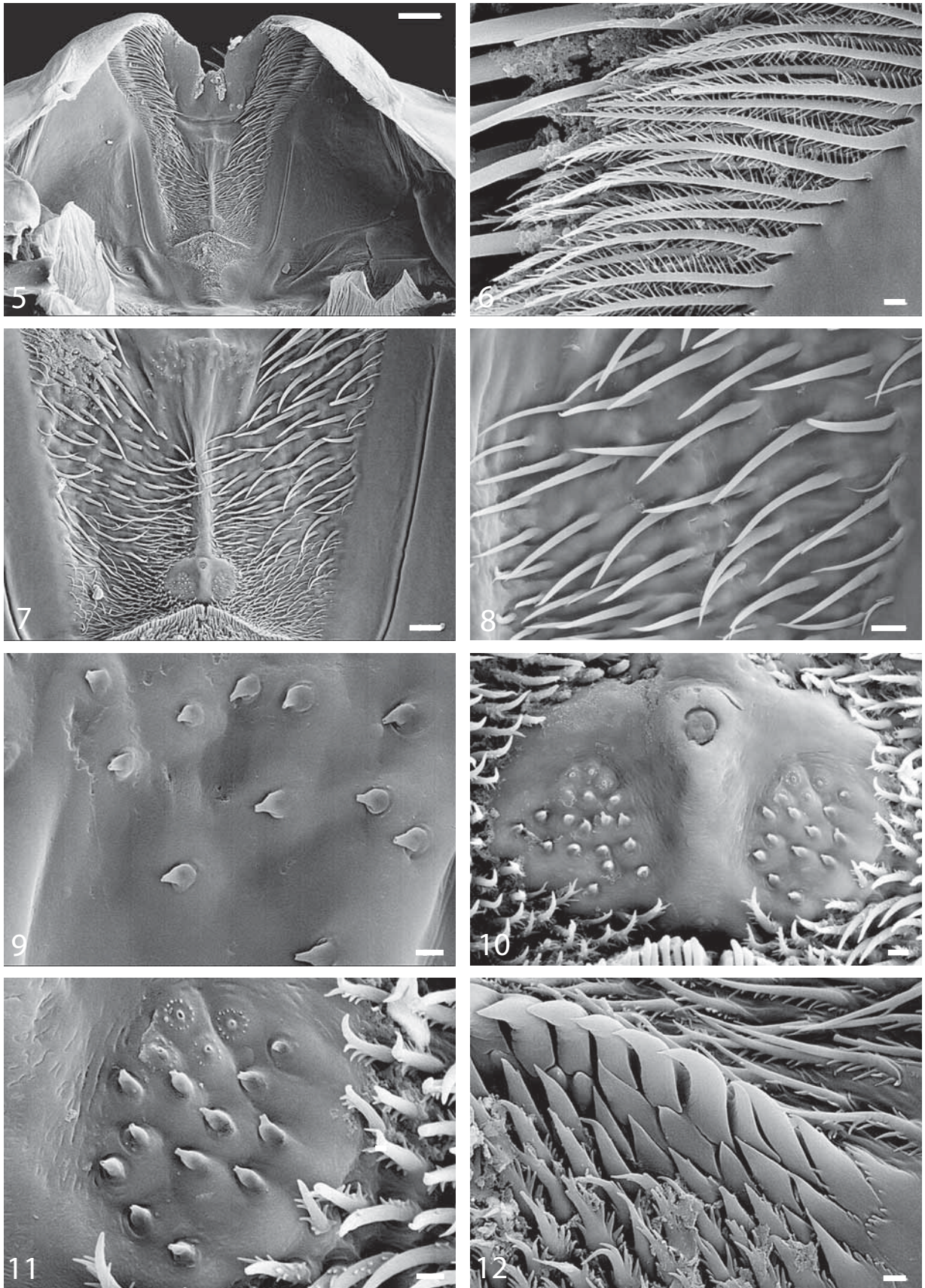
Colour: Head capsule typically orange-brown with radiating dark brown network covering most or all of dorsal side of head behind sutures; some populations with rather uniformly orange head capsule, radiating network of darker pigment confined to posterolateral part of head; tergal plates with yellowish-orange, bright

orange or pale tan medial band with diffuse dark brown, blackish or orange-brown pigment that becomes more concentrated as a pair of longitudinal bands on more posterior segments; stoma saddles generally orange-yellow or pale tan/whitish, often with diffuse blackish, red-brown or reddish pigment; lateral flanks of tergal plates pale orange, each side with a variably strong mottled longitudinal band of blackish, dark brown or reddish-brown pigment. Legs pale to moderate orange, sometimes yellow, usually without significant concentric banding, rarely with well defined bluish bands on femur, tibia, and basal article of tarsus I. Sternites yellow-orange in anterior segments, more intensely orange in posterior segments.

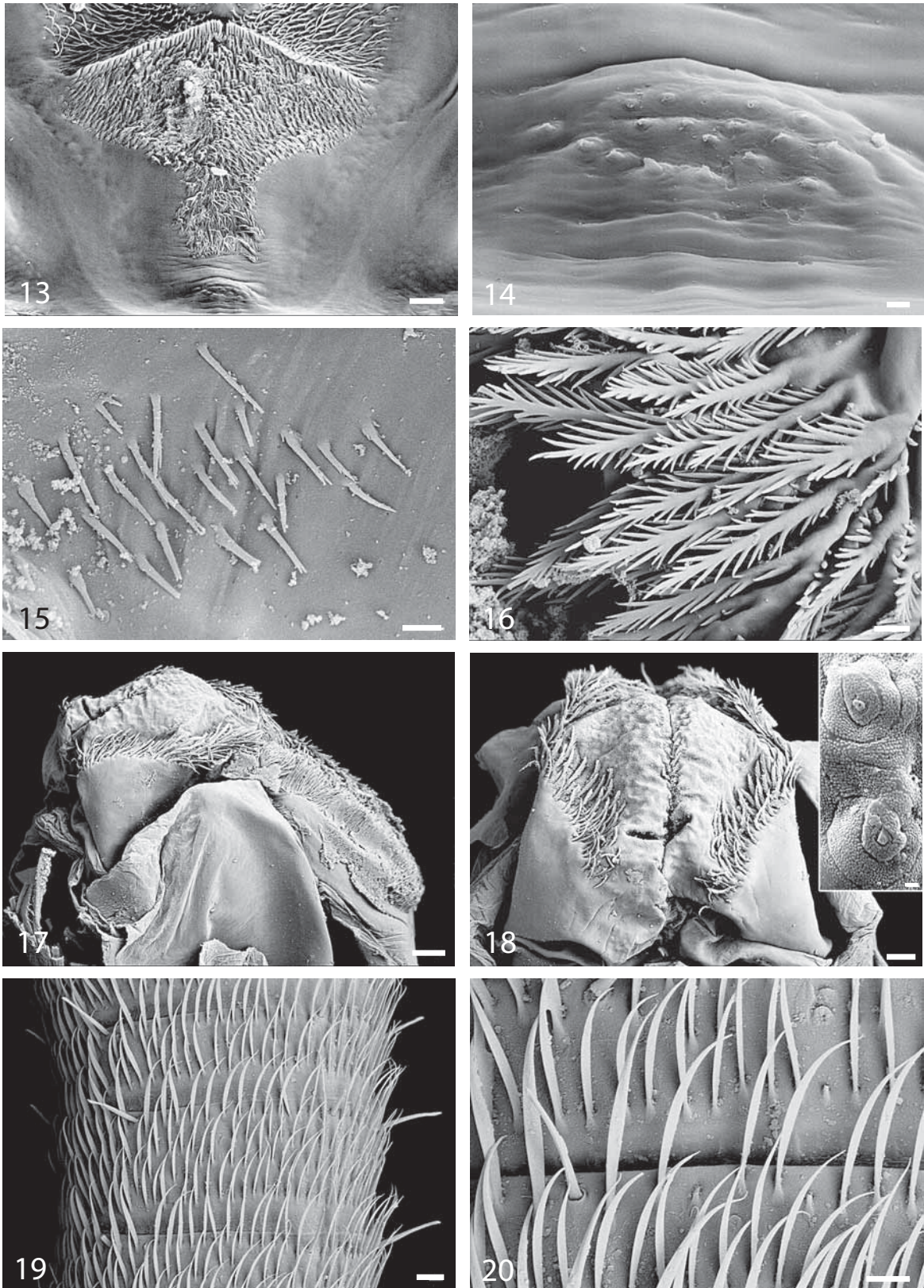


FIGURES 3–4. *Pilbarascutigera incola* (Verhoeff, 1925). Pigmentation of head and T1. 3, WAM T75216, female; 4, WAM T69865, male. Scales 100 μ m.

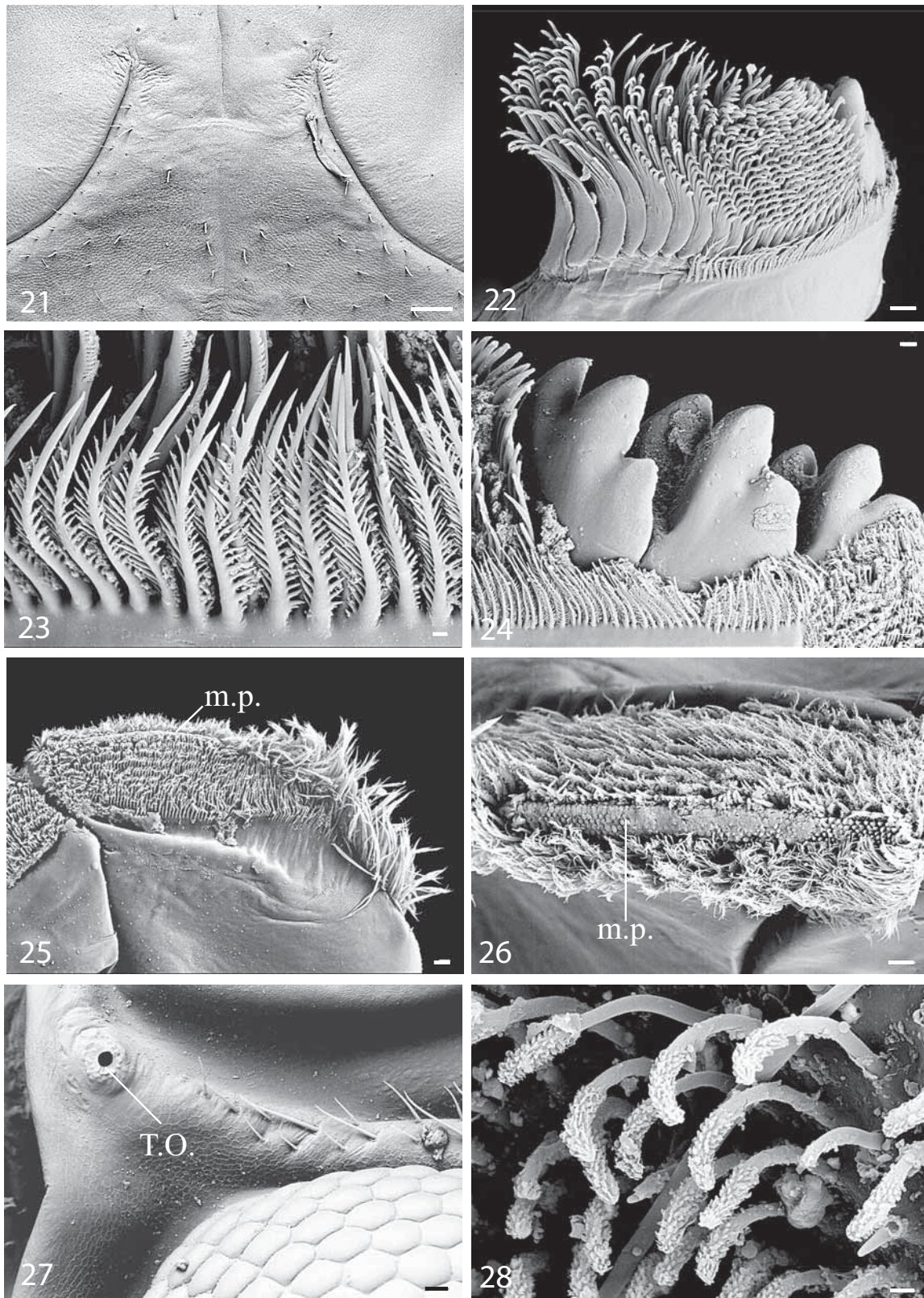
Head capsule: Anterior projection of sutures short, triangular, pointing straight anteriorly (Fig. 21). Posteromedian impression moderately deep. Antenna 1.2–1.5 times body length. First flagellum with 56–124 articles apart from specimens in which node is undifferentiated with extreme asymmetry (e.g., 65/173 or 174/78 articles) between left and right antennae, mean 75 articles (N=84, specimens >14 mm body length); asymmetry between numbers of articles in first flagellum on each side of a specimen usually less than 10 articles, ranging to 26; ring-like articles with two or three whorls of densely arranged hairs with a flattened section and gentle curvature (Fig. 19) and a few trichoid setae in a single whorl encircling distal end of article (Fig. 20); hairs on distal part of second flagellum in either one or two whorls per article, these differing whorl numbers typically on alternating articles. Tömösváry organ small, in typical position between eye and base of antenna (Fig. 27); median pore encircled by a few rings of small swellings.



FIGURES 5–12. *Pilbarascutigera incola* (Verhoeff, 1925). WAM T69858, female. 5, ventral view of epipharynx, scale 100 μm ; 6, labral bristles, scale 3 μm ; 7, labral trapezoid, scale 30 μm ; 8, simple spines on labral trapezoid, scale 10 μm ; 9, bottle-shaped sensilla in distal cluster on labral trapezoid, scale 3 μm ; 10, 11, proximal sensilla clusters on labral trapezoid, scales 3 μm ; 12, chevron-shaped row of spines at border between labral and clypeal parts of epipharynx, scale 4 μm .



FIGURES 13–20. *Pilbarascutigera incola* (Verhoeff, 1925). 13, 14, 16–18, WAM T69858, female. 13, field of branching spines on clypeal part of epipharynx, scale 10 μm ; 14, cluster of sensilla on medial clypeal part of epipharynx, scale 2 μm ; 16, branching bristles beside median excavation on hypopharynx, scale 6 μm ; 17, 18, lateral and distal views of hypopharynx, scales 30 μm , 60 μm ; inset shows sensilla on distal tip, scale 1 μm . 15, 19, 20, WAM T69862, female. 15, lateral cluster of spines on clypeal part of epipharynx, scale 20 μm ; 19, distal part of first flagellum of antenna, scale 20 μm ; 20, hairs and a single trichoid seta on two articles from proximal part of second antennal flagellum, scale 10 μm .



FIGURES 21–28. *Pilbarascutigera incola* (Verhoeff, 1925). WAM T69858, female, except 21, 27, WAM T69859, male. 21, cephalic sutures, scale 100 μm ; 22–26, mandible. 22, gnathal edge, scale 30 μm ; 23, fringe of pectinate bristles, scale 3 μm ; 24, mandibular teeth, scale 10 μm ; 25, 26, Haarpolster, with molar plate (m.p.), scales 10 μm ; 27, eye and Tömös-váry organ (T.O.), scale 20 μm ; 28, brush-like setae on inner margin of distal article of telopodite of first maxilla, scale 4 μm .

Epipharynx: Lateral bar of labral trapezoid with narrow longitudinal groove along whole length of bar (Fig. 7). Labral bristles differentiated into narrow outer band of short, pectinate bristles and wider inner band of longer simple bristles (Fig. 6). Two clusters of sensilla along midline of labral trapezoid: more distal unpaired, transverse group of a few dozen bottle-shaped sensilla (Fig. 9) at termination of median ridge (Fig. 7), and proximal cluster composed of three aggregations of sensilla at proximal sclerotized bulge (Fig. 10); proximal aggregations comprise a lateral pair of groups of mostly bottle-shaped sensilla and a few button-shaped sensilla (Fig. 11), and slightly distal to the lateral aggregations a median side-by-side pair of button-shaped sensilla. Chevron-shaped spine row of triangular and distally-curved denticles at border between labral and clypeal part of epipharynx (Fig. 12); immediately proximal to spine row is dense median field of pectinate spines composed of broadly rhomboid distal portion with pectinate spines and narrow, subparallel-sided proximal portion (Fig. 13) with multifurcating spines. Broadly ovate cluster of nipple- and bottle-shaped sensilla on medial part of clypeal triangle (Fig. 14), a short distance behind dense field of branching spines (Fig. 13); ovate groupings of about 10 nipple-shaped sensilla form pair of lateral clusters set in weak depression at a level of about midlength of dense median spine field. Pair of lateral spine fields (Fig. 15) proximal to lateral clusters of sensilla within clypeal part of epipharynx; spines uniformly slender, elongate; a few pores of apparently epidermal glands in spine field. Median transverse band of six or seven spines, some bifid, immediately in front of mouth.

Hypopharynx: Elongate, deeply projecting into preoral chamber (Fig. 17). Bars of lateral sclerotised fork with lateral bulges. Median excavation on proximal part of frontal surface bordered laterally by flattened bipectinate bristles (Fig. 16); pectinate bristles form in addition a few rows on distal part of hypopharynx (Fig. 18). Paramedial rows of button-like sensilla on tip of tongue, each sensillum with an ovate rim that is in turn enclosed by an incomplete, horseshoe-shaped rim (Fig. 18, inset). Cluster of sensilla-like structures in front of mouth between median excavation and converging flattened bars of proximal fork with more or less rhomboid arrangement.

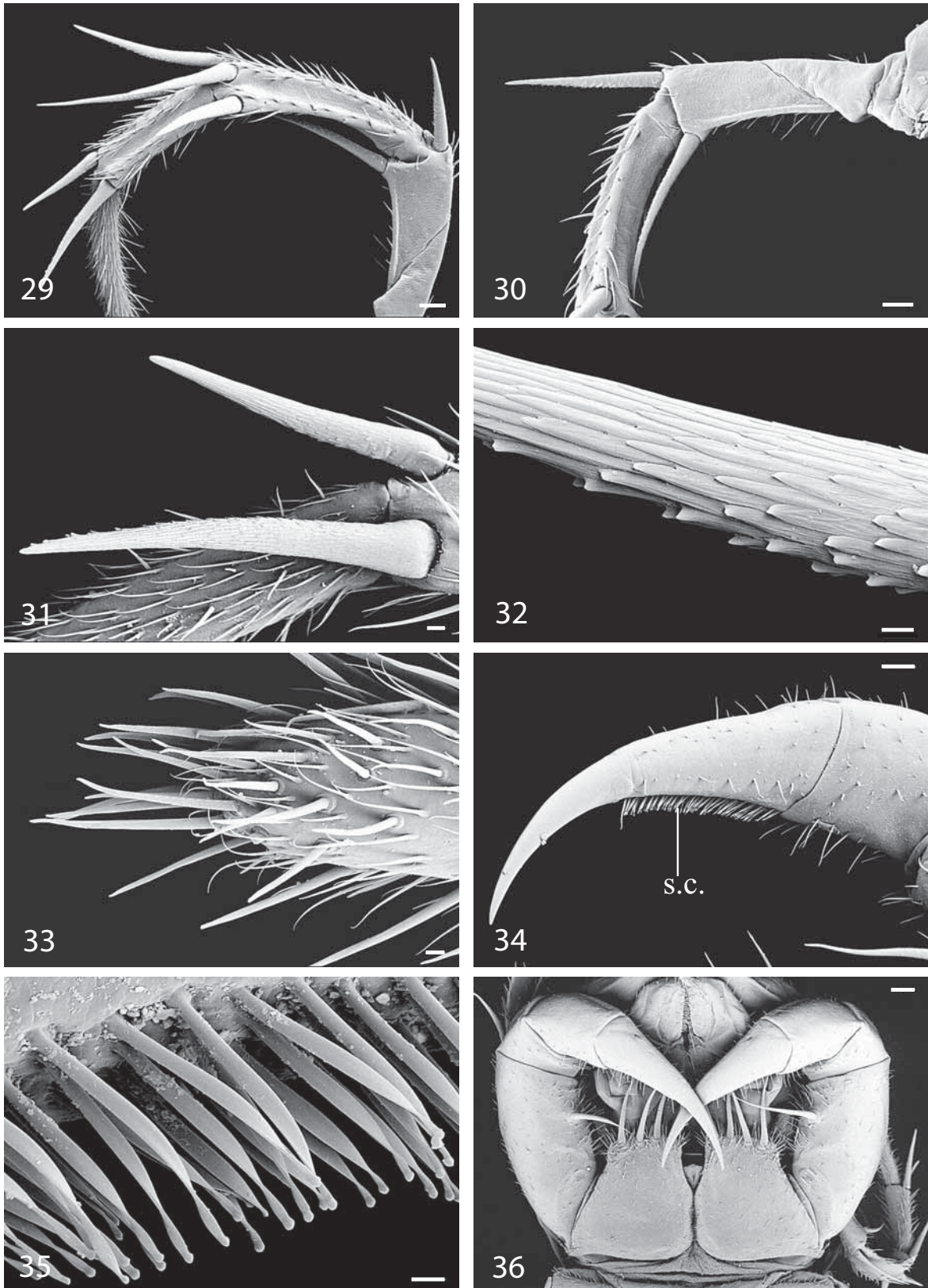
Mandible: About 20 pectinate lamellae in large specimens (Fig. 22); individual spines at tips of pectinate lamellae with ridge on inner side and many small, blunt marginal serrations. Three teeth, each with three cusps, surface smooth (Fig. 24). Narrow fringe of pectinate bristles along dorsal half of pectinate lamellae and against teeth; each bristle with many short lateral branches along all but terminal part (Fig. 23). Haarpolster has narrow molar plate along most of its length (Figs. 25, 26); surface of molar plate composed of about six dense spine rows. Haarpolster bristles arranged in numerous imbricated bands of pectinate bristles.

First maxilla: Dense field of brush-like setae on inner margin of distal article of telopodite with typical scutigeromorph structure (basal half smooth, distal half with many short back-curved spines: Fig. 28). Coxal process with short, simple setae evenly scattered over its ventral surface.

Second maxilla: Typical scutigerid arrangement of elongate spine bristles at distal ends of podomeres (dorsal and ventral spine bristles on prefemur; four spine bristles on femur; two dorsal spine bristles on tibia: Figs. 29–31). All spine bristles with similar surface details, spiniform scales, short proximally, becoming more elongate distally (Fig. 32) to confer a ridged or fluted surface to distal third of spine bristle. Tarsus densely setose, with slender, distally curved, setiform spines between longer trichoid setae at tip (Fig. 33).

Maxillipede: Four spine bristles on anterior margin of coxa about equal in length to coxa (Fig. 36); surface ornament of spine bristles similar to those on second maxilla. Spine comb (Dornenkamm of Borucki 1996) along inner side of tarsus (Fig. 34); spines twisted distally, terminating in a rounded bulb (Fig. 35). Poison calyx cylindrical; poison duct extending to base of tarsus.

Tergal plates: Outlines as shown in Fig. 2. Stoma saddles weakly inflated. Spiracles relatively short (Fig. 41). Spines first appear on T3 in most specimens, exceptionally T2, in which case they are few and confined to the lateral part of the tergal plate or include one to three spines on stoma saddle; spines consistently paired with a Stachelborste or, more commonly, a Tastborste; pairing of spine and Stachelborste most common on anteromedian part of TT3–4, with more posterior parts of those plates having spines paired with Tastborsten;



FIGURES 29–36. *Pilbarascutigera incola* (Verhoeff, 1925). WAM T69858, female, except 36, WAM T69859, male. 29–33, second maxilla. 29, scale 100 µm; 30, trochanter, prefemur and femur, scale 100 µm; 31, tibial spine bristles, scale 20 µm; 32, detail of a femoral spine bristle, scale 10 µm; 33, distal end of tarsus, scale 10 µm. 34, maxillipede tarsus and pretarsus, showing spine comb (s.c.), scale 100 µm; 35, detail of spine comb, scale 10 µm; 36, maxillipedes, scale 200 µm.

TABLE 1. Number of spines on stoma saddle for TT1–7. 64 specimens (128 stoma saddles) of body length >14 mm examined from across geographic range of species. N refers to number of stoma saddles bearing spines.

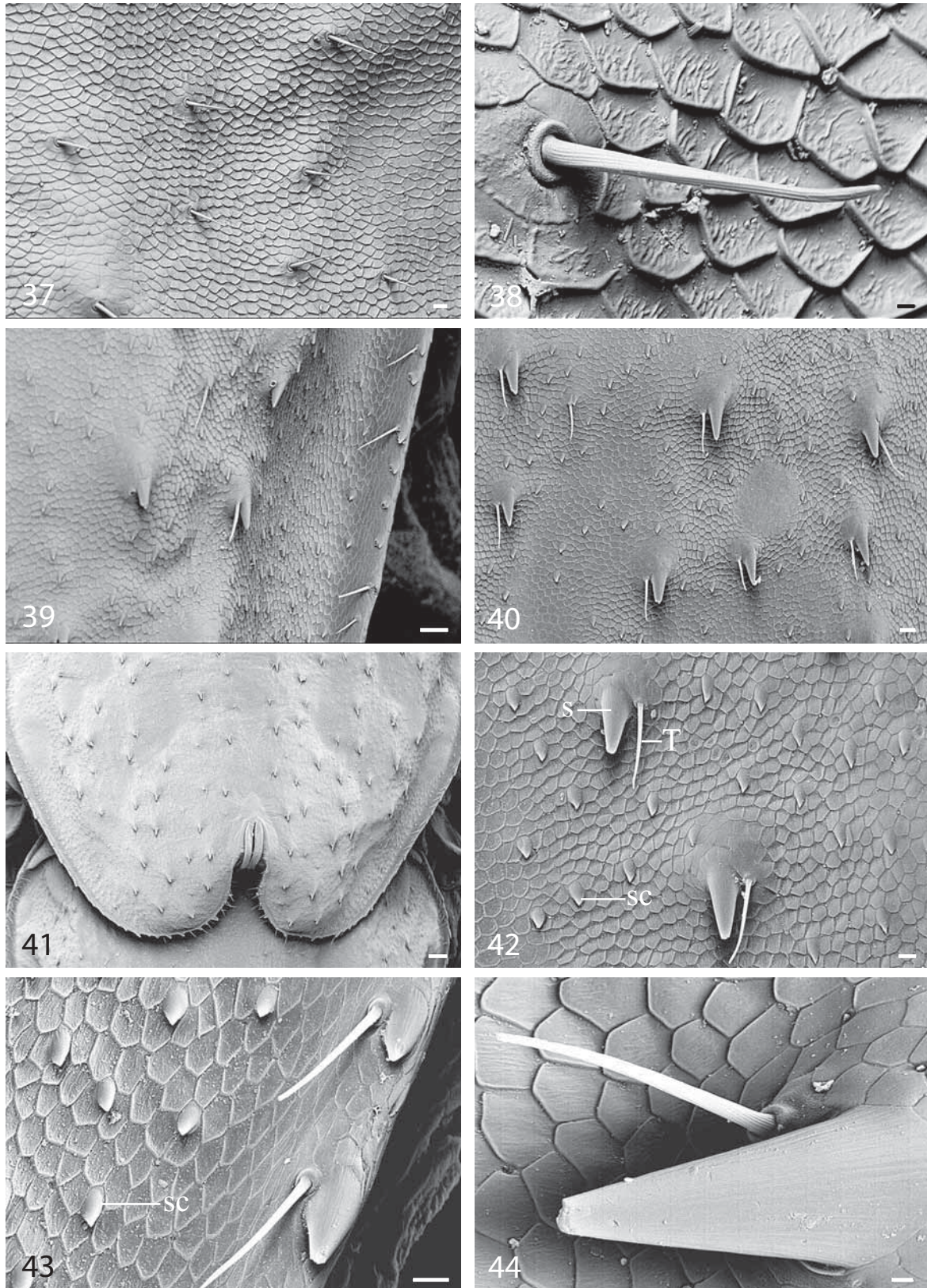
Tergal plate	N	Range	Mean
1	0	-	-
2	6	0–3	0.15
3	56	0–12	2.47
4	114	0–22	8.50
5	128	4–27	13.00
6	127	6–29	15.37
7	116	2–24	12.01

consistent pairing of Tastborste and spine on TT5–8 (Fig. 44); Tastborsten generally slightly longer than their associated spine. Numerous isolated Tastborsten (not associated with spines) on tergal plates (Fig. 40). TT4–7 with more or less even distribution of spines/Tastborsten on medial and lateral parts of tergal plate as well as on stoma saddles (Fig. 41). Spines usually first appear on stoma saddle of T3 or T4, sometimes on T5, rarely on T2 stoma saddle; number of spines on stoma saddles as shown in Table 1. Spicula small, triangular, each separated by several polygonal scales that lack spicula (Fig. 43), in some specimens spicula weaker on medial than lateral parts of tergal plates. Margins of TT1 and 2 with alternating Tastborsten and Stachelborsten; spines fringe margin from posterior $\frac{1}{2}$ – $\frac{2}{3}$ of T3– or T4–T8; marginal spines quite varied in size, from small to moderately large, each spine paired with a Tastborste (Fig. 43).

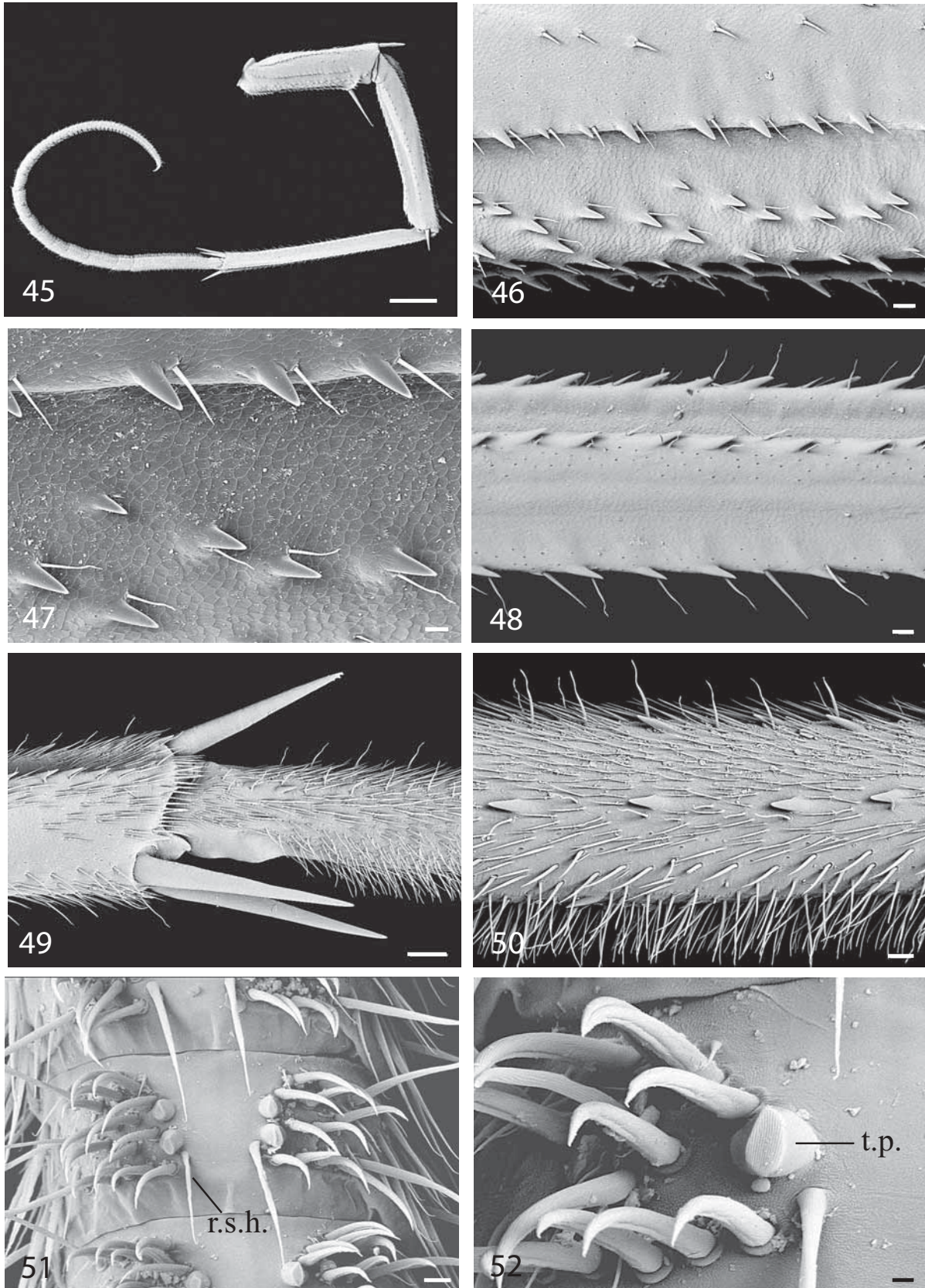
Legs: Tarsus I and II segmentation as shown in Tables 2 and 3. Leg 15 with up to 359 tarsomeres. Prefemoral spine bristles (“end spines”) 2/1 on legs 1–14, 1/1 on leg 15. Femoral spine bristles 1/2 on all legs. Tibial spine bristles 0/1 on leg 1, 1/1 or $\frac{1}{2}$ on leg 2 (posterior ventral spine bristle short when present), consistently $\frac{1}{2}$ from leg 3, posterior ventral spine bristle becoming about as long as anterior ventral spine bristle (Fig. 49) from leg 5. Spine rows on prefemur (Fig. 47), femur (Fig. 48) and tibia consistently with spine/Tastborste pairing. Basal article of tarsus 1 with spines (single distal posterior spine) first appearing on legs 3–6, irregularly increasing on more posterior legs to maximum of 8–16 spines in longitudinal posterior row in leg 14 (Fig. 50); numbers on each leg variable (e.g., leg 8 with 3–7 spines in longitudinal posterior row).

TABLE 2. Number of segments in tarsus I. N refers to number of legs.

Leg	N	Range	Mean
1	63	10–22	17.1
2	55	9–20	13.9
3	60	7–18	11.4
4	56	7–14	10.6
5	57	6–22	10.0
6	49	7–14	9.6
7	37	7–15	9.2
8	36	7–11	8.8
9	28	7–12	8.8
10	27	8–13	9.3
11	22	8–11	9.3
12	23	8–11	9.6
13	21	8–12	10.0
14	22	8–13	10.5



FIGURES 37–44. *Pilbarascutigera incola* (Verhoeff, 1925). Tergal prominences. 37, 38, 44, WAM T69858, female. 37, Tastborsten on lateral part of T1, scale 10 μm ; 38, isolated Tastborste on T1, scale 2 μm ; 44, spine and Tastborste on T7, scale 3 μm . 39–43, WAM T69859, male. 39, lateral part of T3, scale 30 μm ; 40, medial part of T5, scale 20 μm ; 41, T6, scale 100 μm ; 42, medial part of T6, showing spines (s), Tastborsten (T) and spicula (sc), scale 10 μm ; 43, margin of T6, scale 10 μm ; 44, spine and Tastborste on T7, scale 3 μm .



FIGURES 45–52. *Pilbarascutigera incola* (Verhoeff, 1925). WAM T69858, male. 45–50, leg 14, anterior side except 48, 50, posterior side. 45, scale 1 μm ; 46, 47, prefemur, scales 30 μm , 20 μm ; 48, tibia, scale 30 μm ; 49, tibial spine bristles, scale 100 μm ; 50, tarsus I, first article, scale 30 μm . 51, 52, leg 10, tarsus II, ventral view, showing resilient sole hairs (r.s.h.) and tarsal papillae (t.p.). 51, scale 10 μm ; 52, scale 10 μm .

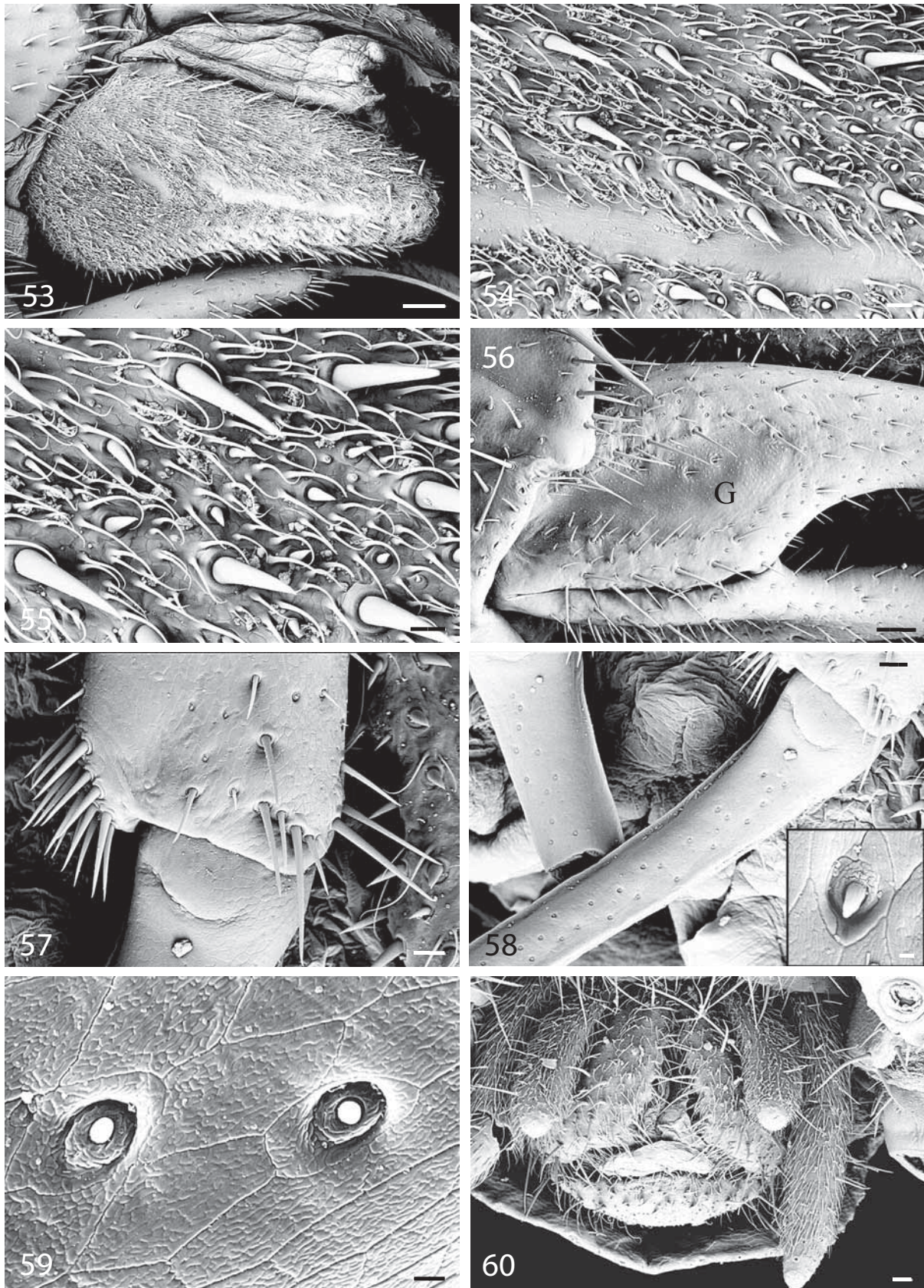
TABLE 3. Number of segments in tarsus II.

Leg	N	Range	Mean
1	56	20–39	31.1
2	53	20–36	30.0
3	58	23–34	28.8
4	51	16–33	27.6
5	55	11–33	27.1
6	49	19–34	26.9
7	40	19–31	26.2
8	34	17–32	27.1
9	26	25–37	28.8
10	23	25–33	29.1
11	23	22–34	29.9
12	22	24–38	32.4
13	22	18–38	33.3
14	23	20–42	36.2

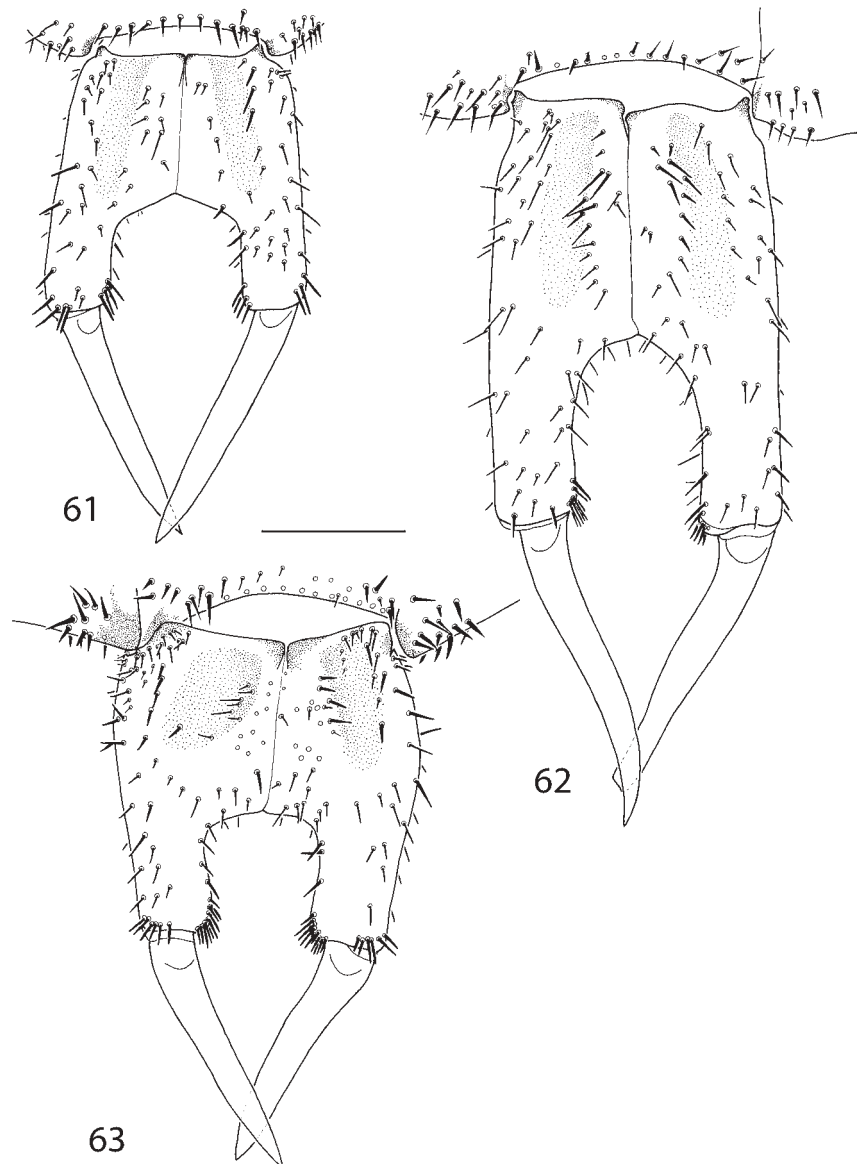
Tarsus II of legs 1–14 with tarsal papillae (Tarsalzapfen) on successive segments excepting first and last few segments on each leg; papillae usually paired, exceptionally arranged as two pairs per segment (Fig. 51). Cluster of setae on ventrolateral side of tarsi II arranged in two or three transverse bands of three or four setae per band (Fig. 52). Resilient sole hairs (federnden Sohlenhaare of Verhoeff 1904b) originating near postero-medial edge of tarsal papilla, extending to about half length of the succeeding segment.

Sternites: Posterior margin with gentle to moderate concavity medially, on each side of a posteriorly-convex extent. Longitudinal median furrow in anterior half or more of sternites; sternites scattered with setae except for on posterior part of anterior segments; margin fringed by many short setae; sternal setae finer on more posterior segments, which bear minute multifurcating spinulae (Haardörchen of Verhoeff) and scattered Tastborsten.

Female: Gonopod with maximum length 1.7–2.5 times maximum width (ratio A/B of Würmli 1973, fig. 1); longitudinal median suture in proarthron complete. Lateral margins of proarthron gently divergent posteriorly (Fig. 61), nearly parallel sided (Fig. 62), or gently convergent posteriorly (Fig. 63). Subtriangular depression (Grube of Verhoeff) on proarthron shallow, bearing at most just a few short setae (Fig. 56). Proarthron 1.0–1.45 times length of mesarthron (ratio C/D of Würmli 1973). Coarsest setae on proarthron slightly thicker than those on mesarthron apart from cluster at distomedial corner of mesarthron, this cluster usually composed of 10–15 setae (Fig. 57). Sinus between mesarthron usually broadly parabolic, its apex typically weakly pointed but sometimes distinctly pointed (Fig. 61) or, less commonly, approximately transverse (Fig. 63); width of mesarthron 0.5–0.8 maximum width of sinus (ratio F/G of Würmli 1973). Mesarthron with numerous sensilla (apparently sensilla coeloconica; cf. Ernst & Rosenberg 2003) between its setae, including conical sensilla (Fig. 58, inset); sensilla surrounded by narrow, circular rim. Proarthron + mesarthron 1.0–1.7 times length of metarthron (ratio C+D/E of Würmli 1973). Outer margin of metarthron nearly straight for much of its length. Ventral surface of metarthron scattered with small, blunt sensilla coeloconica (Fig. 59); single row of sensilla coeloconica along outer margin of metarthron; a few setae on dorsal side of metarthron. Subanal plate drop-shaped, maximum height slightly more than half its length, with blunt, rounded distal end and nearly symmetrical dorsal and ventral margins (Fig. 53); smooth, non-setose band along middle of subanal plate in its posterior half to two-thirds (Fig. 54); setae of varied size on outer surface of subanal plate, predominantly slender subspiniform setae and short, conical, spiniform setae, between which are slender, curved hairs (Fig. 55); setation becoming coarser posteroventrally, with spiniform setae concentrated on posterior third of subanal plate. Telson elongate triangular with rounded posterior apex in both sexes, bearing abundant setae and slender, curved hairs as on subanal plate.



FIGURES 53–60. *Pilbarascutigera incola* (Verhoeff, 1925). WAM T69858, female, except 60, WAM T69859, male. 53, subanal plate, scale 100 μm ; 54, 55, setae and hairs on subanal plate, scales 20 μm ; 56, syntelopodite of gonopod, showing depression, Grube (G), scale 40 μm ; 57, distal end of mesarthron, scale 20 μm ; 58, metarthron, scale 30 μm , inset shows sensillum coeloconicum on mesarthron, scale 1 μm ; 59, sensilla coeloconica on metarthron, scale 2 μm . 60, male gonopods, scale 30 μm .

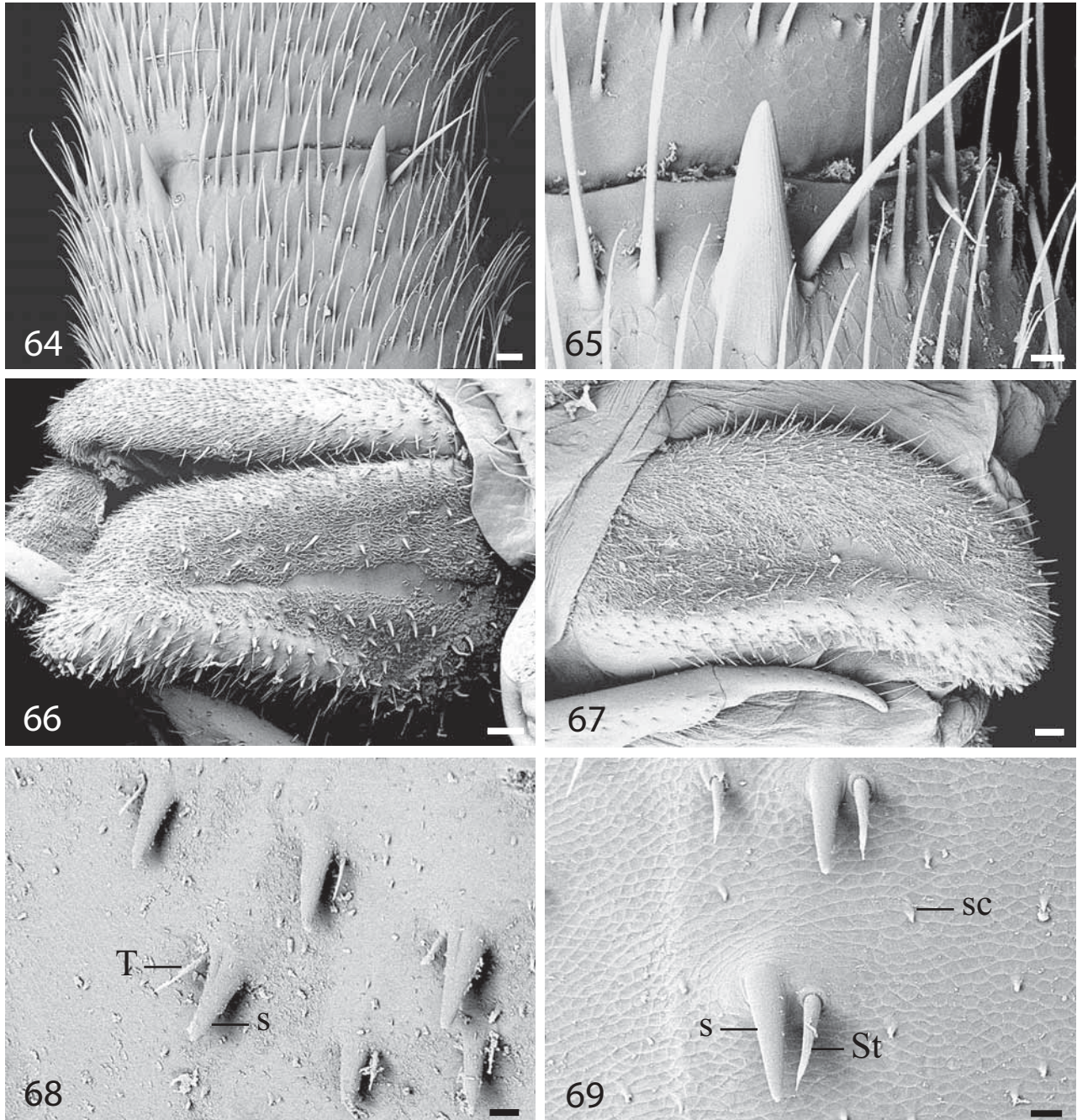


FIGURES 61–63. *Pilbarascutigera incola* (Verhoeff, 1925). Female gonopods, scale for all 200 μm . 61, WAM T69862; 62, WAM T69864; 63, WAM T75216.

Male: Typically scutigerid gonopod styles on first and second genital segment (Fig. 60); both pairs of gonopods densely covered with setae; terminal part with short, spiniform setae between longer setae. Subanal plate with parabolic outline, relatively shorter than in female, non-setose band along its length at midwidth.

Discussion: The large sample size allowed recognition that several characters that differ between many Pilbara specimens and the types of *Pilbarascutigera incola* also vary within populations. This is most notable with respect to how far anteriorly unpaired spines first appear on the tergal plates, with spines generally but inconsistently appearing on more anterior plates in Pilbara specimens. The types of *P. incola* have Stachelborsten but not spines on TT1–3; T4 has Stachelborsten on the midline and stoma saddles but lacks spines on those regions, although a few spines are paired with longer Stachelborsten laterally; T5 has the spines paired with Tastborsten or some of the spines paired with Stachelborsten; TT6 and 7 have the spines paired with Tastborsten. Most Pilbara specimens have the first appearance of a Tastborste/spine pairing on T3 rather than on T5, and usually have spines developed in rows along the midline and on the stoma saddles of TT3 and 4. However, Pilbara specimens include those with no spines on the midline or stoma saddle of T4, as in the types

of *P. incola*, and the first appearance of the spine/bristle pairing on the midline and stoma saddles ranges from TT3 to 5 even within single populations. Concerning variability in spine numbers on the stoma saddles, 15 matus stage specimens from northwest of Mt Prinsep near Karratha (WAM T76597) have 0–3 spines on the saddles of T2, 4–12 spines on the saddles of T3, 7–18 spines on T4, 12–24 spines on T5, 15–25 spines on T6, and 10–24 spines on T7.



FIGURES 64–69. Thereuoneminae. 64, 65, *Thereuopoda clunifera* (Wood, 1862). Two articles from first flagellum of antenna, showing pair of spines, scales 20 μ m, 10 μ m. 66, 68, *Thereuopoda longicornis* (Fabricius, 1793). 66, female subanal plate, scale 100 μ m; 68, T7 stoma saddle, showing spines (s) paired with Tastborsten (T), scale 20 μ m. 67, 69, *Thereuopodina queenslandica* Verhoeff, 1925, female subanal plate, scale 100 μ m; 69, medial part of T7, showing spines (s) paired with Stachelborsten (St), and spicula (sc), scale 20 μ m.

Variability is shown across the Pilbara with respect to whether slender Stachelborsten are present on TT1 and 2 (more pigmented and distinctly thicker than the Tastborsten on those plates) or more robust Stachelborsten, but this variation intergrades within and between samples. Pigmentation is variable, notably with respect to the degree to which dark longitudinal bands are developed on the tergal plates, the head has a dark mottled network, and red pigmentation is observed on the stoma saddles (see Figs. 3 and 4 for typical orange-brown versus more uniformly orange specimens). Exceptionally specimens with bands on the legs are observed in samples that otherwise lack distinct bands, and the banded specimens are otherwise typical of the species. Female gonopod proportions are variable at all localities, notably with respect to the shape of the inner margin of the mesarthron and the orientation of the lateral margin of the pro- and mesarthron, and the intergradation between specimens does not provide a basis for identifying more than a single species. The considerable degree of variability in the number of tarsal segments (see Tables 2 and 3), even within populations, is consistent with previous criticism of the taxonomic value of this character (Muralevič 1910; Chamberlin 1920), in contrast to the works of Verhoeff, who employed rather narrow tarsal segment counts even at the generic level. The data in tables 1–3, as well as counts of antennal segmentation, were restricted to specimens that represent the pseudomaturus and matus stages of Verhoeff (1904b). Antennal and tarsal segmentation show a general pattern of increased segmentation with size, though much less consistently than was the case for the few specimens of *Scutigera coleoptrata* and *Podotheruea insularum* recorded by Verhoeff (Verhoeff 1902–1925); most of the range of variation is observed within the matus stage, as was likewise observed by Murakami (1959) in *Thereuopoda clunifera*.

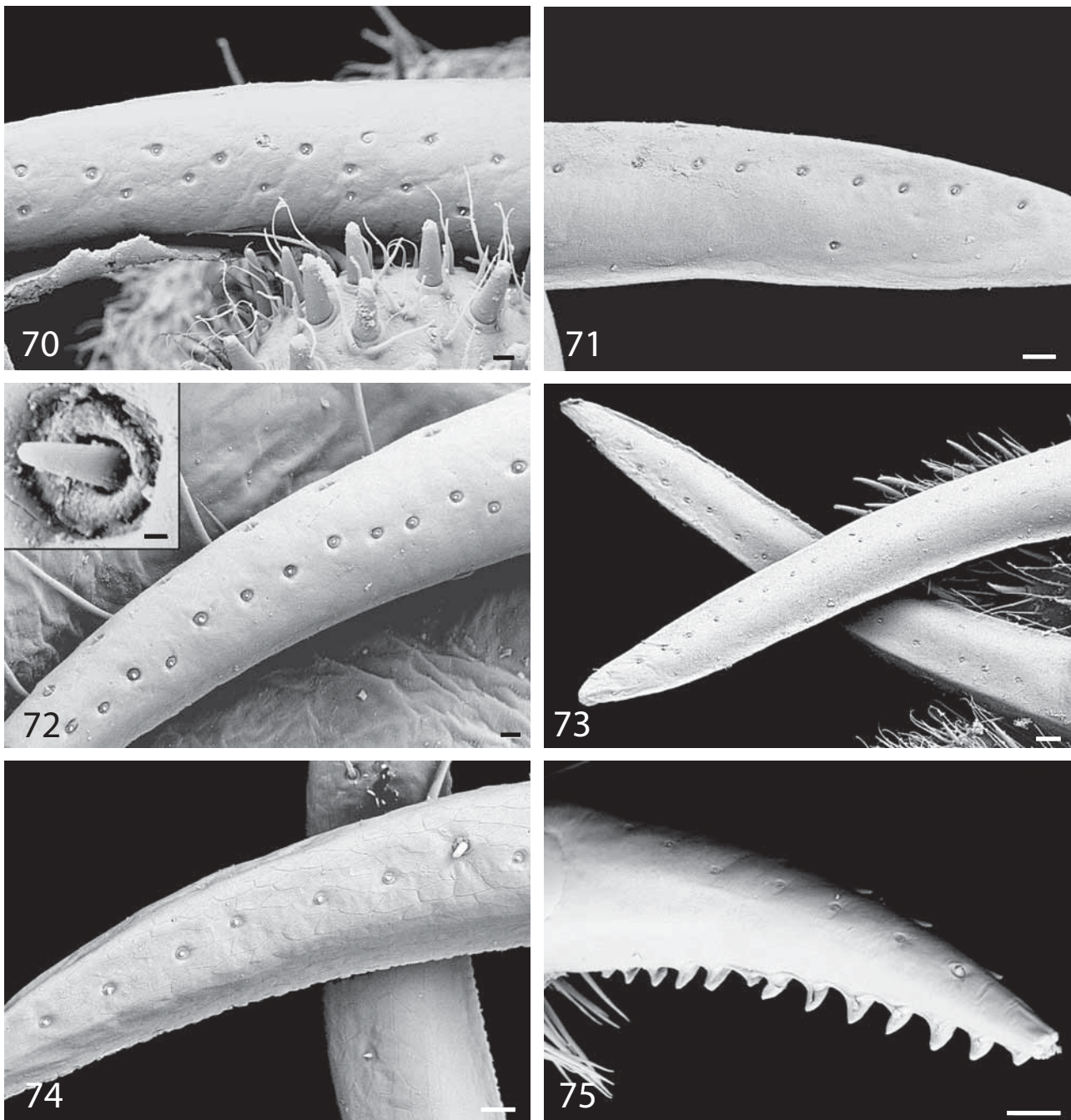
Phylogenetic relationships

Discussion above suggested a relationship between the new genus and *Thereuopoda* rather than with *Allothereua*, to which *Pilbarascutigera incola* had previously been assigned. To explore these alternatives more formally, character data for *P. incola* were analysed in a modified version of a dataset for scutigero-morph relationships developed for combined morphological and molecular analysis (Edgecombe & Giribet 2006).

Several changes are made to the taxonomic sample in the new analysis. The outgroup sample is confined to five pleurostigmophoran chilopods; a diplopod outgroup is excluded. Along with the newly added terminal *Pilbarascutigera incola*, *Tachythereua* Verhoeff, 1905, is also added, based on its sole species, *T. hispanica* (Meinert, 1886). The exemplar taxon for *Thereuopodina* Verhoeff, 1905, is *T. queenslandica* Verhoeff, 1925, rather than the unnamed congener used previously. Two autapomorphic characters are excluded (formerly informative because multiple exemplars of certain species were included to examine molecular variation within species). One character is redefined to code for additional character states of the tergal spicula (character 20 in the Appendix). Four new characters are added to code for variation in taxa allied to *Thereuopoda*. These characters are: the presence of spines on the proximal half of the first antennal flagellum (character 2); a pairing of spines with either Stachelborsten or Tastborsten on the posterior tergal plates (character 17); the shape of the female subanal plates (character 31), and; the arrangement of sensilla on the metarthron of the female gonopod (character 34). Character 18, describing the morphology of paired spines at the base of tergal bristles, is newly added for resolving relationships of *Allothereua* and *Parascutigera*; the alternative character states are depicted by Edgecombe & Giribet (2006: Fig. 2C,D for state 0; Fig. 4D for state 1). The modified dataset codes for 57 characters (Appendix, Table 4). Discussion of the characters that vary between scutigero-morphs is presented by Edgecombe & Giribet (2006).

Parsimony analysis used PAUP*4.0b10 (Swofford 2002) with the branch and bound search strategy. Support for nodes was evaluated by parsimony jackknifing, with 1000 jackknife replicates using a branch and bound search, each with 37% character deletion and 'jac' resampling. Multistate characters were coded as

unordered except for characters 25 and 47, which were ordered (0-1-2). The cladograms were rooted between Scutigermorpha (16 terminal taxa) and Pleurostigmophora (5 terminal taxa).



FIGURES 70–75. Ventral surface of metarthron of female gonopod, showing arrangement of sensilla coeloconica. 70, *Theureuopoda longicornis* (Fabricius, 1793), scale 10 μm ; 71, *Thereuonema turkeстана* Verhoeff, 1905, scale 10 μm ; 72, *Theureuopodina queenslandica* Verhoeff, 1925, scale 10 μm ; inset shows detail of a sensillum, scale 1 μm ; 73, *Allothereua maculata* (Newport, 1844), scale 20 μm ; 74, *Scutigera coleoptrata* (Linnaeus, 1758), scale 10 μm ; 75, *Madagassophora hova* (Saussure & Zehntner, 1902), scale 30 μm .

Four shortest cladograms of 79 steps (Consistency Index 0.861; Retention Index 0.945; Rescaled Consistency Index 0.815) were retrieved with the analytical procedures described above. The strict consensus of these is shown in Fig. 76.

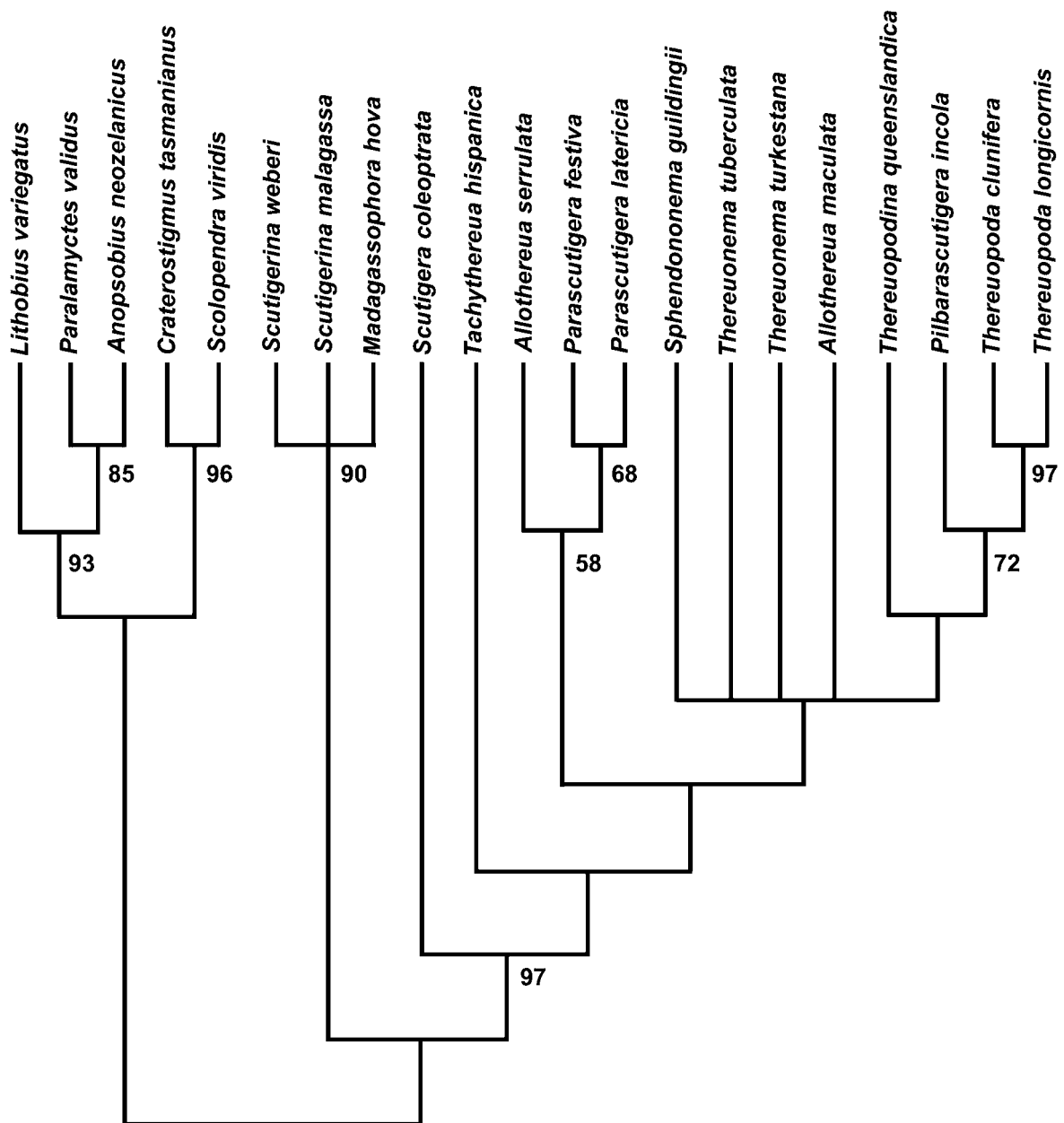


FIGURE 76. Strict consensus of four shortest cladograms based on character data in Table 4. Numbers in italics at nodes are jackknife frequencies greater than 50%.

A sister group relationship between *Pilbarascutigera* and *Thereuopoda* is found in all shortest cladograms, with *Thereuopodina* being sister to that clade. The relationship between *Pilbarascutigera* and *Thereuopoda* has a moderate jackknife frequency (72%) and is supported in all shortest cladograms by two synapomorphies: the pairing of tergal spines and Tastborsten (Figs. 44, 68), rather than spines paired with thicker bristles (Stachelborsten: Fig. 69), and the proliferation of sensilla on the metarthron of the female gonopod (Figs. 58, 70). These apomorphies (characters 17 and 34, respectively) are unique and unreversed. Four unambiguous, unreversed apomorphic characters unite *Thereuopoda* to the exclusion of *Pilbarascutigera* (characters 2, 4, 22, and 31) and the jackknife value for *Thereuopoda* is particularly strong (97%). The alliance between these two genera and *Thereuopodina* is supported by the wide sinus between the mesarthron margins on the female gonopod (character 32), though this character exhibits homoplasy on all shortest cla-

dograms. Regarding other taxa closely allied to *Thereuopodina*, *Pilbarascutigera* and *Thereuopoda*, the monophyly of *Thereuonema* is shown in the strict consensus (Fig. 76) as ambiguous. In three of the four shortest cladograms, the two sampled species of *Thereuonema* form a clade supported by elongate, needle-like tergal spicula (character 20, state 2), but in one cladogram they are unresolved. As had been anticipated from analyses of molecular sequence data (Edgecombe & Giribet 2006, figs. 13, 14), *Allothereua* is resolved as para- or polyphyletic. *Allothereua serrulata* groups with *Parascutigera* based on the elongate spines at its bristle bases (character 18) and its dense tergal spicula (character 21), whereas *A. maculata* (sensu Verhoeff, 1925) exhibits plesiomorphic states for both of these characters and instead groups with the large clade including *Thereuonema*, *Thereuopodina*, *Thereuopoda* and *Pilbarascutigera*. Were *Pilbarascutigera incola* retained in *Allothereua*, as has been the case since its original description (Verhoeff, 1925), *Allothereua* would be even more blatantly non-monophyletic.

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APPENDIX. Characters used in phylogenetic analysis (dataset in Table 4).

1. Proportions of antennal articles: 0) as long as wide; 1) much wider than long.
2. Spines on proximal half of first antennal flagellum: 0) absent; 1) present.
3. Anterior (antennal) branch of antennocellar suture: 0) present; 1) absent.
4. Course of projections on cephalic sutures: 0) posterior part subparallel; 1) posterior part divergent.
5. Ventral spine bristle on prefemur of second maxilla: 0) absent; 1) present.
6. Pair of distal spine bristles on tibia of second maxilla: 0) absent; 1) present.
7. Cluster of sensilla at apex of proximal fork in hypopharynx: 0) absent; 1) present.
8. Sclerotised lateral bulge in proximal fork in hypopharynx: 0) absent; 1) present.
9. Lateral bar of labral trapezoid: 0) with a groove; 1) with tubercles.
10. Structure of bristles on labral trapezoid: 0) wide field of pectinate bristles; 1) all simple; 2) narrow outer band of pectinate bristles strongly differentiated from wide inner band of simple bristles.
11. Labral trapezoid with two median sensillar clusters: 0) absent; 1) present.
12. Arrangement of tripartite sensilla clusters on proximal labral part of epipharynx: 0) median sensilla in-between lateral clusters; 1) median sensilla completely distal to lateral clusters.
13. Median sensilla of tripartite cluster on proximal labral part of epipharynx: 0) antero-posteriorly aligned pair; 1) side-by-side pair; 2) diamond-shaped group of four sensilla.
14. Lateral field of spines on clypeal part of epipharynx: 0) absent; 1) present.
15. Position of median sensillar cluster on clypeal part of epipharynx: 0) transverse bands of sensilla immediately proximal to dense median spine field; 1) transversely ovate cluster of sensilla distinctly separated from dense median spine field; 2) transverse bands of sensilla within dense median spine field.
16. Large unpaired tergal spines associated with bristles: 0) large spines absent; 1) large spines present.
17. Kind of bristle paired with spines on TT5–7: 0) Stachelborsten; 1) Tastborsten.
18. Length of paired spines at bases of bristles (scored from TT6–7): 0) short, flat, triangular spines; 1) elongate, conical spines, some half or more length of bristle.
19. Tergal spicula (hairs): 0) absent; 1) present.
20. Form of tergal spicula: 0) short triangular spines; 1) setiform, tapering hairs, shorter than bristles; 2) needle-like hairs, as long as bristles.
21. Density of spicula: 0) one spiculum for each of several cuticular scales; 1) spicula at margins of most scales.
22. Vaulting of stoma saddles: 0) weak or moderate; 1) strong.
23. Median embayment in posterior margin of sternites: 0) shallow or lacking; 1) strong.
24. Coxa and sternites of posterior segments with dense covering of hairs between bristles: 0) hairs absent; 1) hairs present.
25. Carinae on legs: 0) absent; 1) weak; 2) strong. ORDERED
26. Paired spine bristles at end of first tarsal segment: 0) absent; 1) present.
27. Tarsal papillae: 0) absent on all legs; 1) present on legs 1–14; 2) on legs 1–9 only.
28. Density of setal cluster associated with tarsal papillae (scored from midlength of tarsus II of leg 10): 0) sparse, arranged in transverse bands of two setae; 1) dense, arranged in transverse bands of three or more setae.
29. Resilient sole-hairs: 0) absent; 1) one pair per segment, with base distomedial to tarsal papilla; 2) two pairs per segment, one with base distomedial to tarsal papilla, one with base proximolateral to tarsal papilla.
30. Spine bristles at distal end of tibia: 0) all legs with two spine bristles in 1/1 arrangement; 1) several posterior legs with 3 spine bristles in 1/2 arrangement.
31. Shape of female subanal plate: 0) dorsal and ventral margins curved, posterior termination rounded; 1) ventral margin straighter than curved dorsal margin, posterior termination pointed or with process.

32. Sinus between inner sides of mesarthron of female gonopod: 0) sinus broad, semicircular or parabolic; 1) sinus deep, narrow, parallel-sided.
33. Single row of spines along inner margin of metarthron of female gonopod: 0) spine row absent; 1) spine row present.
34. Arrangement of sensilla on ventral surface of metarthron of female gonopod: 0) in single row for most of or entire length of metarthron; 2) two- or more deep for most of or entire length of metarthron.
35. Form of male gonopods on first genital segment: 0) segmented; 1) lamelliform; 2) slender styles.
36. Form of male gonopods on second genital segment: 0) absent; 1) blunt cones; 2) slender styles.
37. Maxillary organ: 0) absent; 1) present.
38. Single large tergal plate over trunk segments 7–9: 0) separate plates; 1) single plate.
39. Tarsus form: 0) one or two articles; 1) flagelliform, multiarticulate.
40. Position of spiracles: 0) pleural; 1) dorsal opening on tergum.
41. Shaft organ on antennal scape: 0) absent; 1) present.
42. Spine comb (Dornenkamm) on maxillipede tarsus: 0) absent; 1) present.
43. Projection of hypopharynx as an elongate tongue: 0) short hypopharynx; 1) elongate hypopharynx.
44. Chevron-shaped row of transversely compressed, triangular denticles at border between labral and clypeal parts of epipharynx: 0) absent; 1) present.
45. Flattening of head capsule: 0) domed; 1) flattened.
46. Trochanter on second maxilla: 0) separated from prefemur; 1) fused to prefemur with incomplete articulation.
47. Coxosternite of maxillipede sclerotised in midline: 0) coxae separated in midline; 1) coxosternal plates meeting medially, hinge flexible; 2) midline sclerotised, inflexible. ORDERED
48. Tarsungulum on maxillipede: 0) separate tarsus and pretarsus; 1) tarsus and pretarsus fused.
49. Coxal organs: 0) absent; 1) present.
50. Distribution of coxal organs: 0) on last four pairs of legs; 1) on last two pairs of legs; 2) on last pair of legs only.
51. Single transverse seta projecting medially from labral side piece: 0) absent; 1) present.
52. Plumose setae on inner surface of tarsus of second maxilla: 0) absent; 1) present.
53. Female gonopod and egg manipulation: 0) forcipulate gonopod, used to manipulate single eggs; 1) gonopod lacking, mother humps egg cluster.
54. Form of female gonopod: 0) three articles, the basal article bearing spurs (macrosetae), terminal article with a broad claw; 1) two articles, the proximal article of each gonopod pair partly joined, the distal article a spine.
55. Pleurite of maxillipede segment: 0) discontinuous ventromedially; 1) continuous ventromedially.
56. Distal spinose projections on anterior side of tibia of legs 1–11: 0) absent; 1) present.
57. Maxillipede tooth plates: 0) absent; 1) present.

TABLE 4. Character data, numbered as in Appendix.

<i>Lithobius variegatus rubriceps</i>	0-0-00----	0--0-0--0-	--00000-0-	----000000	0000111110	1100000
<i>Paralamyctes validus</i>	0-0-00----	0--0-0--0-	--00000-0-	----000000	0000111110	1100110
<i>Anopsobius neozelanicus</i>	0-0-00----	0--0-0--0-	--000-0-0-	----000000	0000111111	1100110
<i>Craterostigma tasmanianus</i>	0-0-00----	0--0-0--0-	--000-0-0-	-----00000	0000112112	001-001
<i>Scolopendra viridis</i>	0---00----	0--0-0--0-	--00000-0-	-----00000	0000112112	001-001
<i>Sphendononema guildingii</i>	0010111001	1121210010	0100211111	010?121111	111100000-	0001000
<i>Scutigera weberi</i>	100-000010	100000-00-	-011111020	0010111111	111100000-	0001000
<i>Scutigera malagassa</i>	100-000010	100000-00-	-011111020	0010111111	111100000-	0001000
<i>Madagassophora hova</i>	100-000010	100000-011	1011111020	0010111111	111100000-	0001000
<i>Scutigera coleoptrata</i>	1010111102	111111000-	-000212011	0000221111	111100000-	0001000
<i>Tachythereua hispanica</i>	1010111102	1??111000-	-010201111	0000221111	111100000-	0001000
<i>Thereuonema tuberculata</i>	1010111102	1111110012	0000201111	0100221111	111100000-	0001000
<i>Thereuonema turkeстана</i>	1010111102	1111110012	0000201111	0100221111	111100000-	0001000
<i>Thereuopoda clunifera</i>	1111111102	1111111010	0100201111	1001221111	111100000-	0001000
<i>Thereuopoda longicornis</i>	1111111102	1111111010	0100201111	1001221111	111100000-	0001000
<i>Allothereua maculata</i>	1010111102	1111110011	0000201111	0100221111	111100000-	0001000
<i>Allothereua serrulata</i>	1010111102	1111110111	1000201111	0100221111	111100000-	0001000
<i>Parascutigera festiva</i>	1010111102	111110-111	1000201011	0100221111	111100000-	0001000
<i>Parascutigera latericia</i>	1010111102	111110-111	1000201011	0100221111	111100000-	0001000
<i>Thereuopodina queenslandica</i>	1010111102	1111110010	0000201111	0000221111	111100000-	0001000
<i>Pilbarascutigera incola</i>	1010111102	1111111010	0000201111	0001221111	111100000-	0001000