

Morphological and systematic study of the tribe Australiosomatini (Diplopoda: Polydesmida: Paradoxosomatidea: Paradoxosomatidae) and a revision of the genus *Australiosoma* Brölemann

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Abstract. The collection of several paradoxosomatid species in the context of ecological studies prompted an investigation into the morphology and species-level characteristics of Australian millipedes in the tribe Australiosomatini Brölemann, 1916 (Polydesmida: Paradoxosomatidae). Three new species are described: *Akamptogonus caragoon*, sp. nov., *Australiosoma fulbrighti*, sp. nov. and *Australiosoma combei*, sp. nov. Notes or re-descriptions are provided for nine additional species belonging to the tribe. Scanning electron microscopy was utilised to examine details of the antennal sensory fields, the fifth sternite lamella and associated pores. The presence of the fifth sternite lamella in adult males is considered a synapomorphy for the family Paradoxosomatidae, whereas the prominent tubercle on the first femur in males (adenostyle) represents a synapomorphy of the subfamily Australiosomatinae. With the description of two new species in the genus *Australiosoma* Brölemann, 1913 a revision of the genus was undertaken with the purpose of constructing a species-level phylogeny. The most commonly described and utilised species-specific characteristics were scored in a data matrix and analysed using PAUP. The analysis resulted in a single, fully resolved tree of the following structure: *Hoplatrìa clavigera* ((*A. clavigerum*, *A. inusitatum*) (((*A. rainbowi*, *A. nodulosum*) *A. michelseni*) (*A. laminatum* (*A. combei*, *A. fulbrighti*))).

Additional keywords: Australia, millipede.

Introduction

The millipede family Paradoxosomatidae Daday, 1889, with ~142 genera and more than 560 described species, the largest family of the Diplopoda (Hoffman 1980, 1982), has a recorded natural range covering all continents excluding North America and Antarctica. Currently the family is organised into three subfamilies (Jeekel 1968: fig. 1; Hoffman 1980, 1999), two of which are known from Australia, the Paradoxosomatinae Daday, 1889 and Australiosomatinae Brölemann, 1916. All known endemic Australian Paradoxosomatidae are contained within the subfamily Australiosomatinae. Although some species from the subfamily Paradoxosomatinae have successfully invaded glasshouses worldwide, e.g. *Oxidus gracilis* C. L. Koch, 1847, no species from this subfamily are known to be endemic to Australia. Members of two tribes in the subfamily Australiosomatinae, the Australiosomatini and Antichiropodini Brölemann, 1916, are distributed throughout Australia, including Tasmania, with some 94 nominal species assigned to 36 genera (Australiosomatini 20 genera; Antichiropodini 16 genera).

Systematic history of the subfamily Australiosomatinae

Brölemann (1913) first described the genus *Australiosoma* (placed in the Polydesmoidea Pocock, 1894) based on the type species *A. rainbowi* Brölemann, 1913, and included a total of five species in this taxon. The group was split into two subgenera based upon the number of gonopod branches (two branches in the subgenus *Di clad osoma* Brölemann, 1913 and three branches in *Australiosoma sensu stricto*). Brölemann (1916) argued that the endemic Australian Paradoxosomatidae are distinct from those of other countries, implying that they form a monophyletic group, and arranged these species into two tribes, the Australiosomatini (as Australiosomini) and Antichiropodini (as Antichiropini). At that time, the Australiosomatini (Brölemann, 1916: 540) contained the genera *Australiosoma* and *Helicorhabdosoma* Brölemann, 1916 (now *Helicorthomorpha* Attems, 1914) and the Antichiropodini contained the genera *Antichiropus* Attems, 1911 and *Haplogonosoma* Brölemann, 1916 (Brölemann 1916: 539). Attems (1914: 186, couplet 9 in the key; 1929: 262) recognised that the Australian paradoxosomatid genera can be separated from other paradoxosomatids by the adeno-

style (a tubercle, see Fig. 13) on the femur of the first leg in males. Verhoeff (1924: 13, 1928a: 1601, 1941: 5) noted that the femoral adenostyle on the first leg pair of males occurs in all then known genera of the Australiosomini and Antichiropodini. He characterised the Australiosomatini (as Australiosominae) by the free strong solenomere and the strongly developed tibiotarsus. Jeekel (1964: 108) noted that the adenostyle is also present in *Dendrogonopus* Jeekel, 1964 and thus also occurs in the third tribe of the subfamily Australiosomatinae, tribe Aschistodesmini (Fig. 1).

Jeekel (1968), following Brölemann and Verhoeff, separated the tribes employing the following characters: Australiosomatini: tibiotarsus present, femorite short,

solenomere of medium length. The Antichiropodini were distinguished by a reduced or absent tibiotarsus, a long femorite and a very long solenomere. Jeekel (1968) subdivided the Australiosomatini into five groups based on gonopod characters, such as the number of branches and their relative lengths and positions (see Jeekel 1968: fig. 1). Jeekel hypothesised about the primitive condition of the gonopods in Australiosomatini, including the reductive tendencies of the femorite, the enlargement of the femoral process and bifurcation of the tibiotarsus.

Currently, the Australiosomatini are characterised by the following combination of characters: a short or somewhat elongate gonopod prefemur, thick and rather short to almost

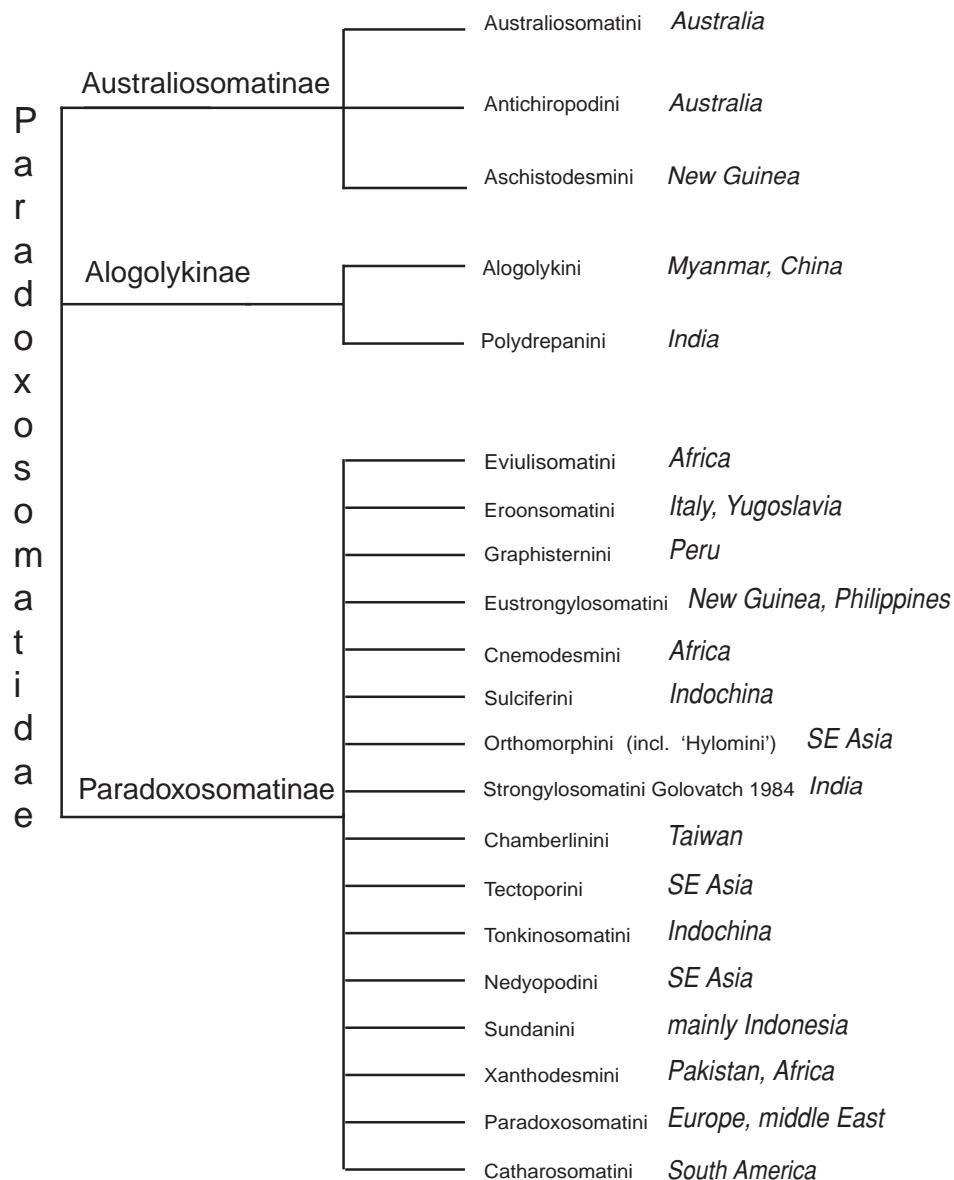


Fig. 1. Proposed relationships within the family Paradoxosomatidae, from Jeekel (1968) and Hoffman (1980), modified to incorporate classification changes by Golovatch (1984) and Golovatch and Enghoff (1994).

entirely absent femorite and a strongly developed solenomere (Jeekel 1968, 1987). In many genera, the gonopod femorite is provided with a strong femoral process arising from the anterior side of the femorite. In addition to these gonopod features, the paranota are moderately developed. The various distinguishing characters employed by previous authors demonstrate that the Australiosomatini are not defined by unequivocal apomorphies.

Representatives of the tribe have been collected from all regions within Australia, with most attention to the Queensland (Jeekel 1987) and South Australian (Jeekel 1985) fauna. The tribe currently includes 20 genera and 56 species (the number of species for each genus are listed below in italics): *Akamptogonus* Attems, 1914, 1; *Archicladosoma* Jeekel, 1984, 1; *Australiosoma* Brölemann, 1913, 6; *Boreohesperus* Shear, 1992, 1; *Cladethosoma* Chamberlin, 1920, 7; *Di clad osoma* Brölemann, 1913, 1; *Di clad osomella* Jeekel, 1982, 1; *Gigantowales* Verhoeff, 1937, 2; *Heterocladosoma* Jeekel, 1968, 7; *Hoplatessara* Verhoeff, 1928, 8; *Hoplatria* Verhoeff, 1941, 1; *Isoclad osoma* Jeekel, 1984, 3; *Myallosoma* Verhoeff, 1928, 2; *Oncoclad osoma* Jeekel, 1985, 3; *Orocladosoma* Jeekel, 2000, 1; *Para australiosoma* Verhoeff, 1924, 1; *Perittogonopus* Jeekel, 2003, 1; *Phyllocladosoma* Jeekel, 1968, 3; *Somethus* Chamberlin, 1920, 3; *Streptoclad osoma* Jeekel, 1980, 3. Jeekel listed three additional species as ‘more or less probably’ belonging to the tribe Australiosomatini (Jeekel 1987: 39): *Strongylosoma dubium* (C. L. Koch, 1867); *Strongylosoma rubripes* (C. L. Koch, 1867); and *Eustrongylosoma transversefasciatum* (Silvestri, 1898). The uncertain placement of these species appears to be due to missing type material or type material comprising only female specimens.

Jeekel (1987: 13) addressed the interrelationship and provided a key to the Queensland Australiosomatini, represented by the genera *Phyllocladosoma*, *Cladethosoma*, *Heteroclad osoma*, *Streptoclad osoma* and *Para australiosoma*. These genera were suggested to be well characterised and ‘apparently phylogenetically rather isolated from one another’ (Jeekel 1987: 12). The interrelationship was determined by examination of characters not shared by all Queensland Australiosomatini, including various conditions of the acropodite, tibiotarsus, femoral process and solenomere. For example, the whole acropodite may or may not be ‘torted 180° or more in relation to the prefemur, involving a different course of the sperm channel and different positions towards one another of the various gonopod branches’ (Jeekel 1987: 12).

With respect to the current work, ecological studies by the senior author (MR) yielded numerous Australian paradoxosomatid specimens. Identifying the specimens resulted in the discovery of three new species. Investigation of morphological details, especially the fifth sternite lamella in males, prompted an analysis of the current phylogenetic scheme of the tribe Australiosomatini, with a special focus on the genus *Australiosoma*.

Materials and methods

Specimens examined included millipedes collected during ecological studies and type material borrowed from museums. Material was not obtained by sorting through the extensive backlog at various Australian institutions (see Sierwald and Reft 2004); such a task was outside the scope of this study. Millipedes were hand-collected in the Sydney Basin region during May 2000. Collection times were synchronised with observed peak activity periods of 06:00 hours to 12:00 hours, with most success on overcast days or during light rain. Specimens were located in leaf litter, fallen logs and on trees during random walk searches. Specimens were euthanised by cooling and then preserved in 70% ethanol in glass vials of appropriate size, cotton plugged and placed in parfait jars filled with 70% ethanol.

Specimens were examined using light and scanning electron microscopy (SEM). Scanning electron micrographs of the gonopods did not reveal features, such as setae or pores, that were not already observed using light microscopy. However, the SEM image imparts a three-dimensional view of the structures, whereas the line drawings indicate overlaying structures. Additional characteristics explored in the current study include the cuticle structure, spiracles, gnathochilarium, antennae, epiproct and in males, the lamella on the fifth sternite, the gonopore and legs. Gonopods were dissected and drawn with the aid of a Leica MZ12 microscope and a camera lucida. Pencil drawings were digitised using Adobe Illustrator. Specimen samples for electron microscopy were cleaned with an ultrasonic cleaner and dehydrated through a series of 80%, 90%, 95% and 100% alcohol. Specimens were mounted on SEM stubs using carbon conductive tabs and air-dried for 24–72 hours in a desiccator cabinet. Specimens were sputter-coated with gold for 240 seconds and observed in an AMRAY 1810 with digital image capture. Morphological measurements were made with an ocular micrometer. All measurements are in millimetres.

Genera are treated alphabetically, except for *Australiosoma*, for which new species descriptions and the phylogenetic analysis are presented at the end of the results section. Specimens cited herein are housed in institutions listed under ‘abbreviations’.

Abbreviations

AM	Australian Museum, Sydney, Australia.
AMNH	American Museum of Natural History, New York, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
NMW	Naturhistorisches Museum Wien, Vienna, Austria
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
ZMA	Zoological Museum, University of Amsterdam, Netherlands
ZMB	Museum für Naturkunde an der Humboldt-Universität zu Berlin, Berlin, Germany
ZMH	Zoologisches Museum Hamburg, Hamburg, Germany
ZSM	Zoologische Staatssammlung des Bayerischen Staates, München, Germany
NSW	New South Wales, Australia
SA	South Australia, Australia
Qld	Queensland, Australia

Phylogenetic analysis

For the phylogenetic analysis of *Australiosoma* the character matrix (Table 1) was prepared in McClade 4.02 (Maddison and Maddison 2001). The matrix contains 19 characters: eight binary and 11 multistate characters. Outgroup comparison was made using the species *Hoplatria clavigera* Verhoeff, 1941, the only representative of this genus, based on

the suggestion by Jeekel (1982) that this genus is apparently related to *Australiosoma*. The matrix was analysed using PAUP v4.0b10 (Swofford 2002). All multistate characters were treated as unordered and optimisation followed ACCTRAN. Branch and bound and heuristic searches were employed and resulted in a single most parsimonious tree.

Results

Morphology

To date, millipede morphology remains poorly described. With the exception of the male gonopods, most morphological character suites (e.g. distribution of sense cones, female copulatory organs, setal patterns and mandibular structures) have not been examined in detail, except in the case of a few species within the 145 currently recognised families (Shelley 2003). For many organ systems, the last comprehensive treatment dates back almost a century (e.g. Hennings 1904, 1906 studies on the Tömösváry organs), when scanning electron microscopy, providing a wealth of morphological data for many other groups, was unavailable. The last comprehensive morphological treatment dates back to Verhoeff (1928a, 1932), who summarised the knowledge at that time. Recent taxonomic treatments often focus on a few species and distinguishing characters and rarely provide morphological data from other parts of the millipede body; however, notable exceptions exist (e.g. Enghoff 1979; Köhler and Alberti 1990). A case in point is an important synapomorphy of the family Paradoxosomatidae, the lamella at the fifth sternite of males.

Lamella

Attems (1937) noted that males in most genera of the family Paradoxosomatidae (*sensu* Attems, then called Strongylosomidae) carry a lip-like transverse protuberance on the fifth sternite (calling it either 'Lamelle' or 'Fortsatz'). In some genera, males carry two setose tubercles (Attems 1937) instead of a single flat protuberance. Hoffman (1982: 720) noted for the family Paradoxosomatidae that the 'anterior sterna of males normally have paired or single processes and paired gland openings'. Despite its phylogenetic importance,

this character has rarely been examined or illustrated in paradoxosomatid studies and is cited in the literature intermittently at varying taxonomic levels (Brölemann 1913; Verhoeff 1924, 1928b; Attems 1931; Schubart 1944; Jeekel 1982, 1984, 1985, 1987, 2000, 2002; Shear 1992). Illustrations of this structure have been published almost exclusively by Golovatch (1984, 1994, for example) and Golovatch and Enghoff (1994). These illustrations demonstrate that the morphological details of the fifth sternite lamella in males vary at the species and at the genus levels and may provide numerous character states for phylogenetic analyses.

All adult males in species and genera examined in the current study possess this structure, referred to here as the fifth sternite lamella (Figs 6–10, 47–55). In the Australiosomatini, variation in the lamella exists in the caudal view and lateral profile. Large individuals appear to have a more prominent lamella and the direction of projection is more obvious (Figs 47–55). The anterior surface bears numerous setae relative to the less setose posterior surface. However, the examined species exhibit variation in the density of setae on both surfaces. The observed variation in shape is likely to represent species-specific characters; our current observations are restricted to a single species within each of the five genera examined. The lack of numerous conspecific specimens from multiple species hampers the assessment of intra- and interspecific variation in the structure.

Previous studies described two shallow impressions on the posterior surface (Brölemann 1913). Scanning electron micrographs revealed the presence of two large pores on the posterior surface (Fig. 10) as already noticed by Verhoeff (1936) in *Helicorthomorpha* Attems 1914 (listed as *Kochliopus*) and *Nedyopus* Attems, 1914. These pores appear to be deep and often possess setae.

Antennal cones and sense organs

Millipede antennae typically carry four sense cones on the last antennomere. In addition, a variety of specialised setae located often apically at the distal antennomeres are illustrated for individual species in various millipede orders (Verhoeff 1928a: 785–798, figs 368–383), however, they are hardly ever described in detail. The millipede antennae represent another largely unexplored suite of character states. Scanning electron microscopic examination of the taxa treated here revealed fields of sense cones in addition to the typical four sense cones at the antennal tip, the latter occurring in almost all millipede groups (see Verhoeff 1928a; Eisenbeis and Wichard 1985: plate 69, *Polyxenus*). In addition to the typical tip sense cones, we observed a separate field of small cones at the outer side on the penultimate (fourth) antennomere and the third antennomere (Figs 19–21). Similar fields of sense cones are reported from other genera of the Polydesmida (Verhoeff 1928a) and occasionally from other millipede groups, e.g. Siphoniulida (Sierwald *et al.* 2003).

Table 1. Coding for the 19 morphological characters used in phylogenetic analysis

Taxa	Characters	
	0000000001	1111111111
	1234567890	123456789
<i>Australiosoma rainbowi</i>	2010211221	110211101
<i>Australiosoma clavigerum</i>	2010111210	010101001
<i>Australiosoma laminatum</i>	0000311210	211111001
<i>Australiosoma michaelsoni</i>	1201211120	210211001
<i>Australiosoma inusitatum</i>	0210211110	011102002
<i>Australiosoma nodulosum</i>	0000311221	020202111
<i>Australiosoma combei</i>	2100311111	010112201
<i>Australiosoma fulbrighti</i>	2010411211	011111201
<i>Hoplatria clavigera</i>	0000000000	000000000

Spiracles

All millipedes breathe through segmentally arranged tracheae that open at the base of each leg pair with a pair of spiracles. The spiracles are located on the sternites, laterally to the leg coxae. The actual tracheal opening is located at the base of the spiracle pit and often features a closing mechanism (Attems 1930; Verhoeff 1932). All helminthomorph millipedes lack spiracles on body rings 1–3; body ring 4 carries a single spiracle pair whereas there are two pairs on body rings 5–18 in the Polydesmida. There is no spiracle above the gonopod. The spiracles of most millipedes possess additional features. We found dense hair-like or coral-like structures inside the spiracles, often protruding from the openings (Figs 11–12), a trait more commonly present in the anteriormost spiracle. *Polydesmus angustus* Latzel, 1884 possess distinctly different chitinous elements inside their spiracles (Eisenbeis and Wichard 1985: plate 67).

Male legs

In many millipede groups adult males possess several distinct sexually dimorphic features. The coxae of the second leg pair bear a gonopore from which spermatozoa are discharged (Fig. 3). In the Australiosomatinae there is a distinct tubercle, the adenostyle, on the ventral surface of the femur of the first leg (Figs 13, 24–25), a feature that represents a synapomorphy for all members of the subfamily Australiosomatinae (see discussion above). Additional secondary sexual characteristics include the presence of setal ‘pads’ or ‘brushes’ on the tarsus and apical portion of the tibia of legs (Figs 16–18). The arrangement of setae on the tarsus and tibia (compare Figs 16 and 17) and the number of legs bearing setal pads, either limited to the pregonopodial legs or occurring on all but the final leg pairs, at equal or varying density, appears to be species- or genus-specific. Recent studies by Mesibov (2004) also indicate a potential wealth of generic level characters in details of leg spination features in dalodesmid Polydesmida. Such studies require multiple specimens for each taxon, which were not available in the current study.

Gonopod structure

As in all adult males of the order Polydesmida, the anterior leg pair of the seventh ring is modified to form gonopods consisting of the basal coxite with cannula and the distal telopodite. The basal unbranched section of the telopodite, the prefemur, is termed ‘femorite’ by Jeekel (1968) and its length is variable in different genera. The distal section of the telopodite, the acropodite, carries several branches in Australiosomatini identified as the solenomere (also called solenomerite) with a sperm groove (also called sperm channel, sperm canal or prostatic groove by other authors), a femoral process and a tibiotarsus that may be bifurcated, thus forming two branches (Figs 2, 26–46; Jeekel 1968: fig. 1). The solenomere may carry additional processes.

The terminology used to designate the acropodite branches varies greatly (Brölemann 1913; Verhoeff 1928*a*, 1937, 1941; Attems 1931; Jeekel 1982, 1984) with different authors employing alternative names for identical structures (Table 2). In the current study, branch identification follows the most recent treatment of the group by Jeekel (1968: see fig. 1; Table 2). The diverse usage of terms, especially the reversed identification of the tibiotarsus and the femoral process illustrates a major handicap plaguing millipede systematics at the family level and below. Primary homology-hypotheses regarding various sections, branches and processes of gonopods are almost non-existent, hampering the use of these complex structures for phylogenetic analyses. Hoffman (1990: 40) discussed various homology-hypotheses regarding the telopodite of the family Oxydesmidae Cook, 1895 (Polydesmida), concluding that, ‘...there are few, if any reliable landmarks’. Traditionally, the distal end of the sperm groove was taken as an indication for the tarsus (Hoffman 1965). But, ‘...what has been called the solenomerite has been variously identified as the tarsus, tibiotarsus, or an adventitious process not homologous to any podomere’ (Hoffman 1990: 40).

Other morphological features

The gnathochilarium (Fig. 14) consists, as in all members of the order Polydesmida, of the paired stipites and lamellae linguales, the mentum and the central cone. The palps of the stipites carry a varying number of sensory cones in assorted arrangements (e.g. in two rows of four and five (Fig. 15)). Whether these different patterns represent genus- or species-specific character states remains to be explored, and awaits additional suitable material for examination of intraspecific variability. It is important to note that these characters are potentially useful to delineate taxa at various hierarchical levels. Paranota show the typical family trait of being moderately developed with the second paranota margin being

Table 2. Comparison of paradoxosomatid gonopod terminology (and implied homology hypotheses?) employed by different authors

Terminology given in the original language used (German, English and French respectively). (See also Jeekel 1982, 1984.) Note that Brölemann (1916) used a different podomere notation, labelling the prefemur ‘Fémur’ and the femorite *sensu* Jeekel ‘Tibia’. He distinguished between the solenomere and the other processes as ‘rameau seminal’ and ‘rameau secondaire’ respectively

Rowe and Sierwald (this study)	Femoral process	Tibiotarsus
Jeekel (1982, 1984)	Femoral process	Tibiotarsus
Verhoeff (1928)	Tibiotarsus	Lateral rami of femur
(1937)	Tibiotarsus	Postfemorale Fortsätze
(1941)	Tibiotarsus	Parsolänomerite
Attems (1931)	Tarsus	Seitenäste der Tibia
	Tarsalast	Nebenäste der Tibia
Brölemann (1913)	Tarsal branch	Tibial branch
Brölemann (1916)	Rameau secondaire	Rameau secondaire
Chamberlin (1920)	Tibial branch	Tarsal branch

lower than others, as well as the typical pore formula (rings 5, 7, 9, 10, 12, 13, 15–19). Pore-bearing paranota are more strongly developed than the paranota of rings without defensive gland pores (see Fig. 3). The epiproct or telson also exhibits the setal pattern typical of the family (Figs 22–23; see also Eisenbeis and Wichard 1985: plate 67). The cuticular structure observed in the current study shows a porous surface, possibly the openings of epidermal glands (Fig. 5). This structure appears similar to that observed in other millipedes (Eisenbeis and Wichard 1985: plate 63).

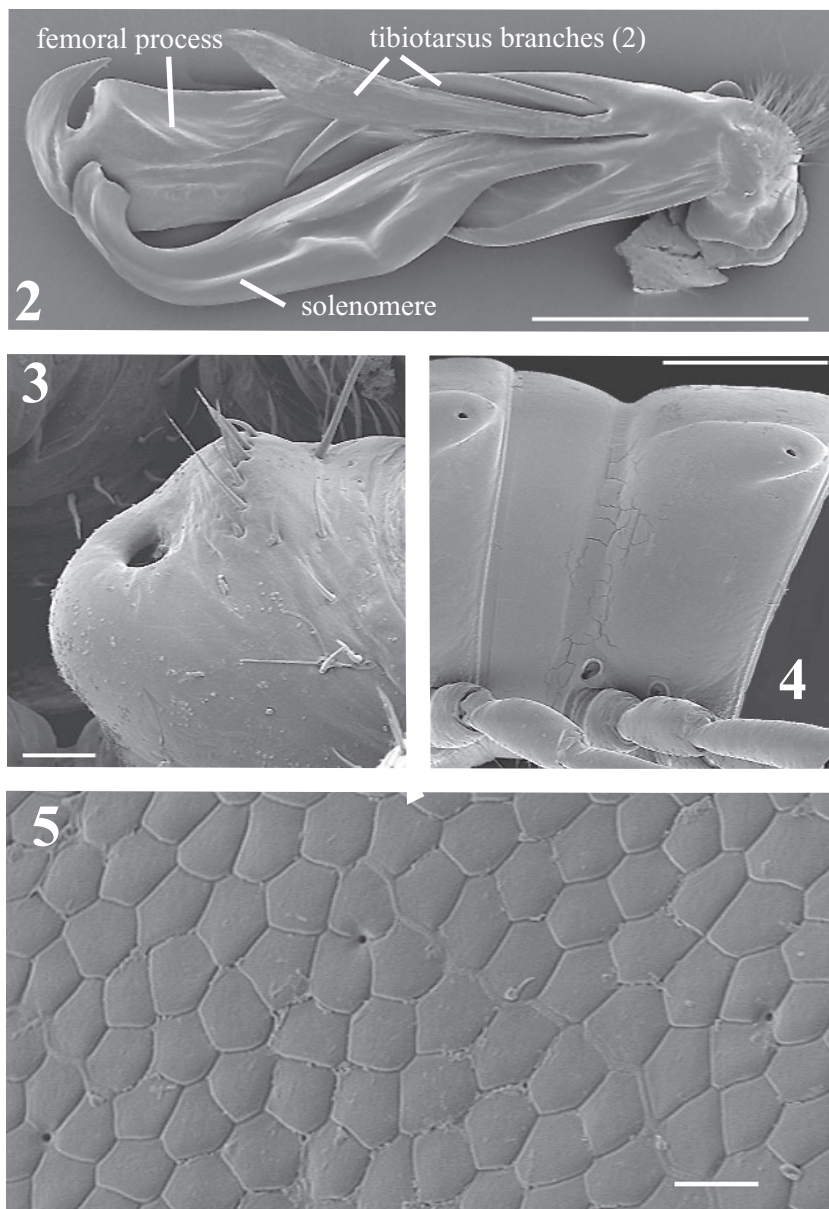
Taxonomy

Genus *Akamptogonus* Attems

Akamptogonus Attems, 1914: 221.

Tricladosoma Brölemann, 1916: 591; synonymised by Attems, 1937: 252, junior objective synonym. Type species: *Polydesmus novarae* Humbert & deSaussure, 1869.

Zelanodesmus Chamberlin, 1920: 10; synonymised by Jeekel, 1964: 106; Jeekel, 1968: 23. Type species: *Zelanodesmus rotornanus* Chamberlin, 1920.



Figs 2–5. Morphology of Australiosomatini. 2, ‘Typical’ Australiosomatini gonopod structure, *Cladethosoma clarum*, scale bar = 1 mm; 3, gonopore, coxa of second leg pair, *Hoplatessara musgravei*, scale bar = 100 μ m; 4, body ring in lateral view, pore-bearing paranota, *Heterocladosoma bifalcatum*, scale bar = 1 mm; 5, cuticle structure, *Cladethosoma clarum*, scale bar = 10 μ m.

Type species: *Polydesmus (Strongylosoma) novarae* Humbert & deSaussure, 1869, by original designation.

Diagnosis

The solenomere is slim and narrow in side view, with the sperm canal extending more-or-less straight to the apex. Metazonites are smooth, either lacking or with shallow transverse sulcus. Pleural keels present on anterior segments, absent on posterior segments.

Remarks

The current diagnosis of *Akamptogonus* is unclear. Attems (1937) listed several somatic characters that are higher-level taxon characters, such as the segment number, pore formula, lamella between the anterior leg pair on the fifth sternite and adenostyle on the femur of first leg pair. Additionally, he noted there is no clear border between the femur and acropodite. Jeekel (1964) defined *Akamptogonus* on the basis of a relatively elongate femorite, relative shortness of the solenomere and a well developed femoral division of the gonopods. The genus was compared to *Australiosoma* based on similarity of the gonopod branches and many species have been transferred between these two genera. However, *Akamptogonus* remains a distinct genus (Jeekel 1964).

The genus is relatively poorly known, up until now containing only a single Australian species (after Jeekel 2000; see also Mesibov 2002) and has had a long history of rearrangement. Attems (1914: 221) described the genus *Akamptogonus*, including four species and one subspecies, in addition to the type species. Attems (1937: 252) reviewed the genus and listed a total of nine species, two located in Australia and seven from India, Papua New Guinea and the Solomon Islands. Subsequently, Jeekel (1965) transferred *A. nigrovirgatus* (Carl, 1902) to the new genus *Pogonosternum* as the type species. Jeekel (1968) transferred the species *Australiosoma kosciuskovagus* to *Akamptogonus*, restoring the number of Australian species in the genus to two. However, *A. kosciuskovagus* was again transferred and is currently classified as *Orocladosoma kosciuskovagus* (Jeekel, 2000). During an attempt to resolve the heterogeneity of the old genus *Strongylosoma* Brandt, 1833, Jeekel (1964) re-classified several species originally described as *Akamptogonus* into new genera. The literature provides relatively detailed descriptions and diagnoses of the new genera but does not provide much information regarding the current status of *Akamptogonus*.

Akamptogonus caragoon, sp. nov.

(Fig. 33)

Material examined

Holotype. ♂, Australia: NSW: North Ryde, Macquarie University, 33°46'28.63"S 151°44'43.75"E, v.2000, coll. M. Rowe (AM KS87598).

Paratype. **Australia: NSW:** ♀, same data as holotype (AM KS91586).

Diagnosis

Elongate femorite, acropodite with two branches (solenomere and tibiotarsus), solenomere curved with broad non-tapering tip bearing no additional processes, sperm channel following straight path to apex, tibiotarsus slightly longer in length than solenomere and tapering at tip, somatic characters as for *A. novarae*. *Akamptogonus caragoon* is identified as belonging to the genus *Akamptogonus* based on the long femorite and short branches of the gonopod and somatic characters.

Description

Male (holotype)

Measurements. Collum 0.75 long, 2.2 wide; tergite 1.25 long, 1.9 wide.

Colour. Head pale light-brown, darkening at vertex, with paler labral region, area below antennae and gnathal lobes. Antennomeres 1–4 light-brown, fifth and terminal article slightly darker, whitish intersegmental tissue and terminal article tip. Collum brown with margins and lateral ridge paler. Body rings with brown dorsal surface on metazonite, light-brown dorsal surface on prozonite, slightly darker band caudad on prozonite. Thin, dark, mid-dorsal line, almost suture-like. Lateral surface of rings light-brown, with slightly darker metazonite. Ventral surface and sternites pale, almost whitish. Paranota anteriorly pale brown grading to whitish posteriorly. Entire leg pale, almost white. Epiproct midline with light-brown band grading to yellowish towards apex, flanked by brown lateral surface. Interior paraproct with pale brown speckling, pale margins and hypoproct pale, almost white. (Specimen may have undergone some minor bleaching due to alcohol preservation.)

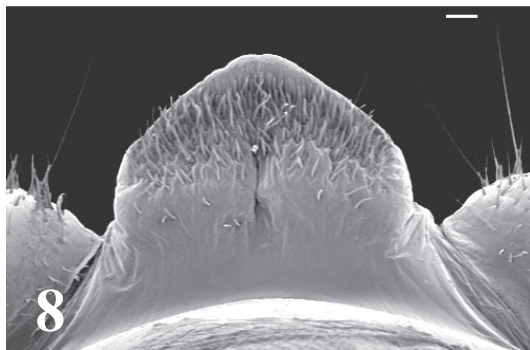
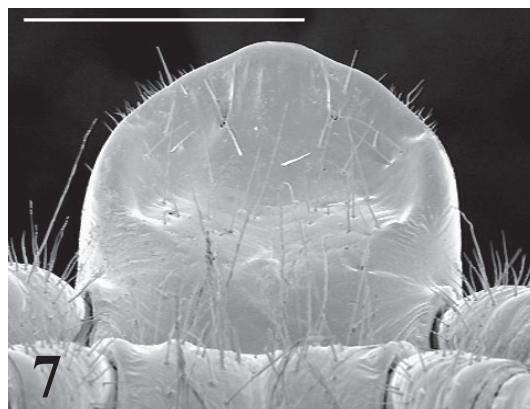
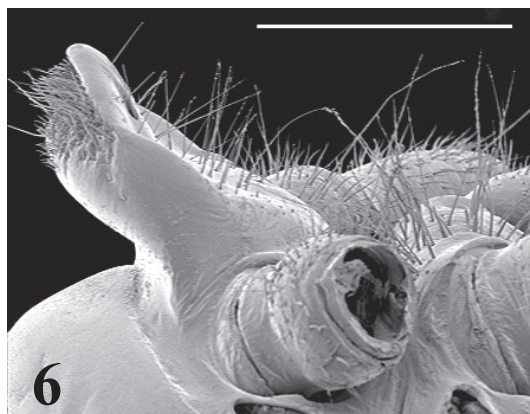
Head and antennae. Labrum midpoint with three small rounded projections. Headplate with numerous setae in clypeal region, setae denser just above labrum, fewer setae extending up between antennal sockets, vertex bald. Gnathal lobes with few setae. Epicranial groove present. Suture extending from vertex of headplate down midline to point level with antennal sockets. Antennomeres of equal length, each widening a little apically, setae moderate with few longer setae on apical region, penultimate segment with sensory field on outer apical region.

Collum. Surface smooth, shiny, without setae, cuticle with pores. Marginal rim with pre-marginal furrow on lateral side and extending anteriorly, fading towards middle of anterior border.

Body rings. Surface smooth, without setae. Mid-ring constriction forming prominent transverse sulcus, with coarse ribbing dorsally and reaching laterally until approximately level with paranota. Dorsum with median suture. Pleural keels, little more than a swelling, present on second

and third rings. Anterior spiracles with complex structure or projection. Single spiracle on fourth ring lacking projection and larger and flatter than others.

Paranota. Paranota of second ring strongly developed, with anterior margin relatively straight and rounded, anterolateral edge with small rounded projection. Posterolateral edge rounded and extending slightly beyond ring margin. Paranota of third and fourth rings well developed and relatively straight in lateral view. Paranota of rings 5–17 small and narrowly extended laterally, less prominent on rings 18



Figs 6–8. Fifth sternite lamella in males. 6, Lateral view, *Hoplatesara musgravei*, scale bar = 1 mm; 7, posterior view, *H. musgravei*, scale bar = 1 mm; 8, anterior view, *Cladethosoma clarum*, scale bar = 100 μ m.

and 19. Lateral poriferous paranota dorsoventrally wider anteriorly, tapers in caudal half, with lateral projection increasing. Pore-less paranota less prominent laterally and dorsoventrally narrower, relatively straight to slightly crescent-shaped in lateral view.

Sternites and legs. Lamella present on sternite of fifth ring between coxae of anterior leg pair, numerous short setae on anterior surface and fewer longer setae on posterior surface. Setae present on fourth and subsequent sternites between coxae. Coxae of sixth sternite set slightly wider than others, particularly on posterior leg pair. Legs with setae on all segments, predominately on ventral surface, with slight increase in length at apex of each segment. Some setae on dorsal surface, becoming denser on tarsus. Single long seta at ventral apical surface of coxae and prefemur and dense pads of setae on apical portion of tibia and tarsus on pregonopodial legs, pads thinning on posterior legs.

Anal ring. Dorsolateral epiproct relatively straight; in dorsal view relatively long, broad at base, sides initially straight, tapering, concave towards blunt apex. Setae not on tubercles, total of 14 setae arranged in three rows, first proximal row of six, mid row of four and posterior row of four setae at apex. Hypoproct rounded with two setae at posterior margin and paraproct with two setae at ridged margin.

Gonopods (Fig. 33). Cannula on mesal side of coxae forming a loop. Prefemur with numerous bunched setae on mesal region, distinct demarcation between prefemur and acropodite region. Relatively elongate femorite extending for half length of entire acropodite, bifurcating into two branches. Mesal branch, tibiotarsus, widely curved and tapering towards a point. Outer branch, solenomere, strongly developed and extending past tibiotarsus, curving mesad with slightly expanded and laminate apex. Sperm channel course straight, extending to solenomere apex.

Female (paratype)

Specimen colouration matches male colouration. Otherwise similar to male but lacking dense setal pads on tibiae and tarsi of legs. Females exhibit greater body width than males (10th tergite).

Measurements. Collum 1.1 long, 2.15 wide; tergite 1.9 long, 2.4 wide.

Remarks

Although homology of the gonopod branches is uncertain, *A. caragoon* is distinguished from *A. novarae* by the lack of the third branch: the femoral process. Colouration and somatic characters are as for *A. novarae*. Despite this somatic similarity to *A. novarae*, the collection of individuals from distinct localities, the collection of a male and female in copula and the distinct gonopod differences provide confidence in identification. Specimens were found in leaf litter.

Distribution

This species is known only from the type locality, North Ryde, NSW, Australia.

Etymology

The species name, *caragoon*, is taken from the coastal Australian Aboriginal Darung dialect, *caragoon* meaning 'millipede and/or centipede'. An additional word, *cannarry*, is used for centipede/millipede, however, the word being derived from *canna*, meaning 'fire', suggests the term *cannarray* is most likely to refer to the biting or stinging centipede and the word *caragoon* is most likely used to distinguish millipedes (Kohen personal communication). The coastal Darung dialect, from the Darung people, is utilised as the specific name in respect to the original Australian Aboriginal inhabitants of the type locality.

Akamptogonus novarae (Humbert & deSaussure)

(Figs 15, 20, 21, 32, 44, 53–54, 56)

Polydesmus (*Strongylosoma*) *novarae* Humbert & deSaussure, 1869: 689. Type data: syntypes NMW, vidi. Type locality: Auckland, New Zealand.

Strongylosoma novarae (Humbert & deSaussure). – Attems, 1898: 305 (incorrect subsequent spelling).

Orthomorpha triaina Attems, 1911: 178; synonymised by Attems, 1914: 223.

Akamptogonus novarae (Humbert & deSaussure). – Attems, 1914: 223; Attems, 1937: 252 (incorrect subsequent spelling).

Zelanodesmus australianus Chamberlin, 1920: 109; synonymised by Jeekel, 1968: 23.

Zelanodesmus rotornanus Chamberlin, 1920: 108; synonymised by Jeekel, 1968: 23.

Material examined

Lectotype. ♂, **New Zealand: Auckland**: (collected by the *Novara* expedition, 1866) (NMW 3426/3).

Paralectotype. ♀, same data as lectotype, (NMW 3426/3).

Other material examined. **New Zealand: Auckland**: same data as lectotype, 2 ♂, 2 ♀, 1 juvenile ♂, (NMW 3426/1); 1 ♀, 1 juvenile ♂, (NMW 3426/2). **Australia: Western Australia**: 89 ♂, 59 ♀, Porongorups, Bolganup Rd, (AM KS15901). **Australia: NSW**: 1 ♂, Mosman, carpark on Musgrove, 15.xi.2004, coll. G. Edgecombe (AM KS92911); 2 ♂, 2 ♀, Sydney, Epping, McKay Reserve, v.2000, coll. M. Rowe (AM KS87597); 2 ♂, 1 ♀, Sydney, Epping, McKay Reserve, v.2000, coll. M. Rowe (FMMC6621).

Diagnosis

Head and trunk light or more darkly chestnut brown. Paranota, median telson, legs and antenna yellow. Antennae slim. Setae on clypeus. Collum rounded. Paranota well developed, as long as metazonite, pore-bearing and pore-less nearly of equal thickness, gradually tapering posteriorly. Pores located posteriorly on paranota. Metazonites of rings 5–17 with transverse sulcus. Pleural keels granular and

clearly visible. Sternite of fifth ring with lamella with setae, other sternites with fine setae. Legs of male thicker than female and with setal pads on tarsus. Gonopod with long femorite and three short branches; middle one, solenomere, broader, curved and unbranched; tibiotarsus and femoral process pointed and tapering towards apex (Attems 1911, 1914, 1937).

Description

The specimens generally agree with the descriptions of Attems (1911, 1914, 1937) and Chamberlin (1920). Specimens also agree with the type material and associated specimens (NMW 3426/1–3).

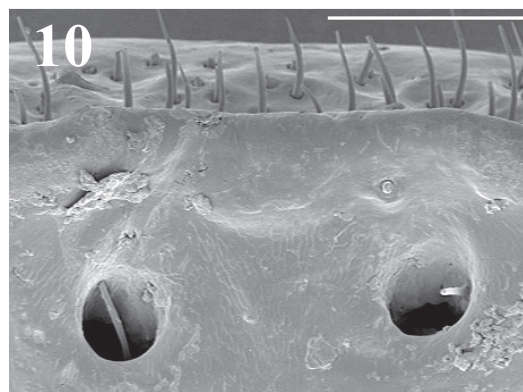
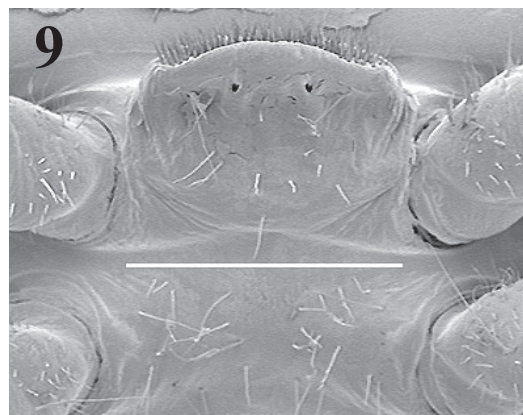
Specimens are slightly smaller than those previously noted, total length 18–21. 2.2–2.8 wide (Attems 1937).

Male

Total length 14.7; collum 0.8 long, 1.7 wide; tergite 1.5 long, 2.1 wide.

Female

Total length 16.1; collum 1.1 long, 2.1 wide; tergite 1.5 long, 2.5 wide.



Figs 9–10. Fifth sternite lamella in males, ventral view. 9, *Cladethosoma clarum*, scale bar = 1 mm; 10, pores, *Heteroclathosoma bifalcatum* illustrated here, scale bar = 100 μ m.

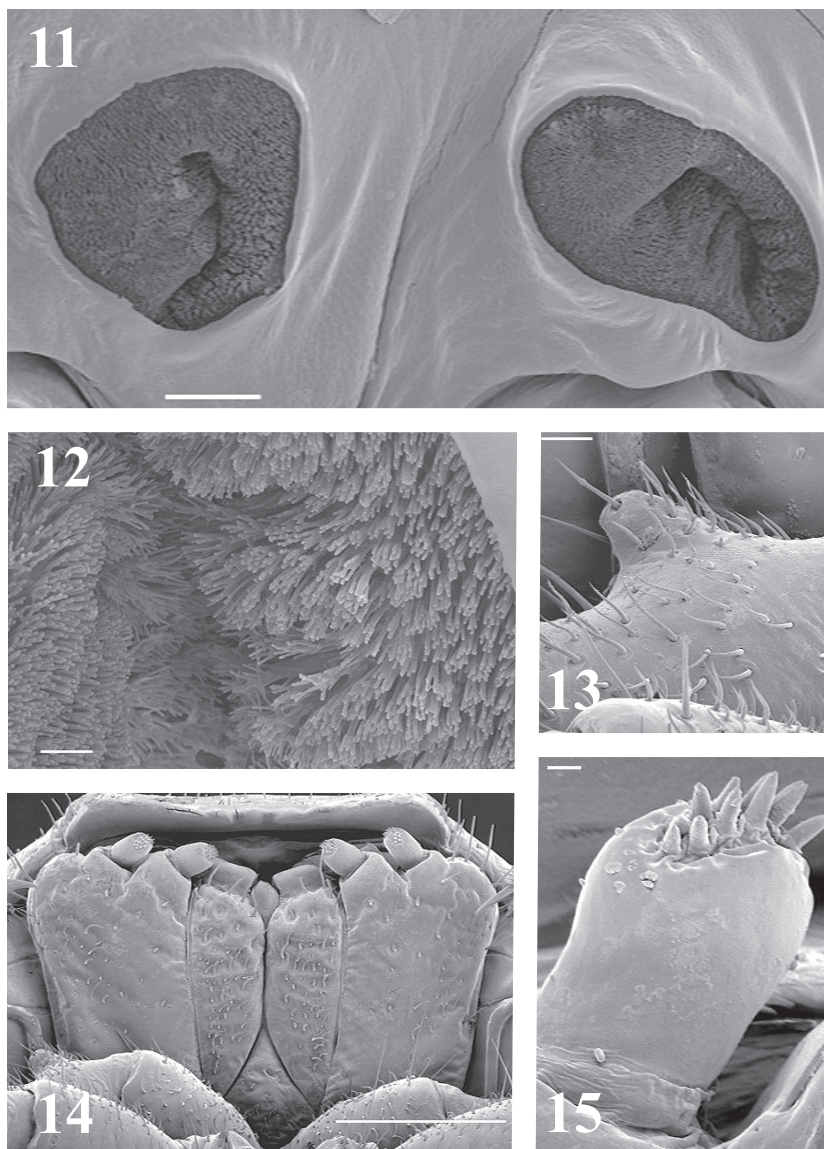
Remarks

This species has a long history of re-classification by various authors. Specimens were found in leaf litter on cool early mornings.

Distribution

The specimen collection localities indicate a wide species range extending throughout the Australian region. The subsequent discovery of this species in San Francisco, California, USA (Hoffman 1979) expanded the total range to include the Australian region (Australia: NSW, Western

Australia) and the nearctic region (United States of America, including Hawaii). With the identification of *Zelanodesmus rotornanus* as a synonym of *A. novarae* the range is expanded to include New Zealand. Although the exact origin of *A. novarae* is not clear, it is believed that this species originated in eastern Australia and was introduced into Western Australia, New Zealand, scattered Pacific island locations and the USA (Hoffman 1979).



Figs 11–15. Morphology of Australiosomatini. 11, Spiracles, *Cladethosoma clarum*, anterior spiracle at right, scale bar = 100 μ m; 12, close up view of spiracle, scale bar = 10 μ m; 13, adenostyle (tubercle), ventral surface of first femur in males, *Gigantowales chisholmi*, scale bar = 100 μ m; 14, gnathochilarium, *G. chisholmi*, scale bar = 1 mm; 15, palp of gnathochilarium, *Akamptogonus novarae*, scale bar = 10 μ m.

Genus *Cladethosoma* Chamberlin

Australiosoma (*Cladethosoma*) Chamberlin, 1920: 105.

Cladethosoma Jeekel, 1968: 26. – Jeekel, 1979: 649; Jeekel, 1982: 141; Jeekel, 1984: 32; Jeekel, 1987: 19.

Leucotessara Verhoeff, 1928b: 90, 92; Jeekel, 1968: 24; synonymised by Jeekel, 1979: 649. Type species: *Leucotessara lucida* Verhoeff, 1928b.

Walestessara Verhoeff, 1937: 137. – Jeekel, 1968: 24; synonymised by Jeekel, 1979: 649. Type species: *Hoplatessara cruciata* Verhoeff, 1937: 137.

Type species: *Australiosoma* (*Cladethosoma*) *clarum* Chamberlin, 1920.

Diagnosis

Short femorite, with acropodite of gonopod subdivided into four main branches (solenomere, femoral process and two tibiotarsal branches). Solenomere apex rounded and laminate. Femoral process, extending slightly beyond solenomere is either spine-like or broad and laminate with pronounced constriction and curved medially, or a strongly curved spine-like apex. Tibiotarsus branches deeply bifurcate, arise proximal to femoral process and are unequal in length. Both branches transversely laminate rather than rod-like. Course of the sperm groove simple, extending straight up solenomere towards apex, where it is slightly recurved.

Remarks

Jeekel (1982) suggests a close relationship between *Cladethosoma* and *Gigantowales*, without support of shared characters and notes the superficial similarity of the gonopods (due to the presence of four branches) to *Hoplatessara*. However, *Hoplatessara* is distinguished by the bilobate or trilobate apex of the solenomere and the spatulate apex of the femoral process. *Gigantowales* differs in the structure of the tibiotarsal branches and by the presence of a well developed femorite.

The genus *Cladethosoma* is relatively well known and includes seven species (Jeekel 1982, 1987; Mesibov 2002). Jeekel (1982) provides a key to six of the seven species, the seventh species described in Jeekel (1987). The species are characterised by the shape of the femoral process, the structure of the tibiotarsal branches and by minor details of size, dorsal colouration and the paranota (Jeekel 1982).

Cladethosoma clarum (Chamberlin)

(Figs 2, 5, 8, 9, 11, 18, 19, 22, 23, 30–31, 42–43, 51–52)

Australiosoma (*Cladethosoma*) *clarum* Chamberlin, 1920: 105.

Type data: holotype MCZ 4887 (collected by W. M. Wheeler).

Type locality: Hornsby, NSW. *vidi*.

Australiosoma verhoeffi Attems, 1931: 134, figs 213–216. – Attems, 1937: 240, fig. 301; synonymised by Jeekel, 1979: 649 (see below). Type data: type status unknown (ZMH). Type locality: Sydney, NSW.

Leucotessara verhoeffi (Attems). – Jeekel, 1968: 25; new combination by Jeekel.

Cladethosoma clarum (Chamberlin). – Jeekel, 1979: 649.

Material examined

Holotype. ♂, Australia: NSW: Hornsby, viii.1889, coll. W. M. Wheeler (MCZ 4887).

Paratype. ♀, **Australia: NSW:** same data as holotype (MCZ 4888).

Other material examined. **Australia: NSW:** 1 ♂, La Perouse (AM KS92914); 3 ♂, 2 ♀, Sydney, Palm Beach Headlands 33°36'3.59"S 151°19'18.22"E, v.2000, coll. M. Rowe (AM KS87595); 3 ♂, 2 ♀, data as for previous specimen (FMMC6613); 2 ♂, 1 ♀, data as for previous specimen (AMNH).

Diagnosis

Femorite short, with laminate tibiotarsal branches arising close to prefemur. Femoral process laminate, transversely flattened with an acutely angular preapical region or hook-like apex (termed the preapical process by Jeekel (1982)). Colouration also distinguishes this species from other *Cladethosoma* (Jeekel 1982). Dorsum of metatergites dark, two parallel paramedian yellowish bands bisected by narrow dark line.

*Description**Male*

Measurements. Total length 28.5; collum 1.44 (range 1.3–1.8) long, 3.17 (range 2.9–3.7) wide; tergite 2.65 (range 2.0–3.9) long, 3.82 (range 3.6–4.7) wide.

Colour. Head dark brown, paler labral region and antennal base. Antennae dark brown, whitish intersegmental tissue and terminal article tip. Gnathal lobes brown with lighter sutures. Collum dark brown, two parallel paramedian yellowish bands widening caudally, lateral margins light-brown. Body rings with dark brown dorsal surface, two parallel paramedian yellowish bands, bisected by a narrow brown line, widening on caudal portion of metazonites 1–16, straight on metazonites 17–19. Midpoint of metazonite with dark brown latitudinal suture. Lateral surface of tergites brown. Paranota yellowish. Ventral surface and sternites brown. Legs with coxae and prefemur brown, femur brown ventrally to dark brown dorsally, postfemur, tibia and tarsus dark brown. Epiproct midline with brown band tapering to a point at half of length, paramedian yellowish bands wide and merging at termination of brown midline, lateral sides and paraproct brown, hypoproct pale to light-brown. (Specimens appear to undergo some bleaching when preserved in alcohol.)

Head and antennae. Labrum with three small rounded projections medially, clypeus weakly concave. Headplate with numerous setae in clypeal region, setae denser just above labrum, fewer setae extending up between antennal sockets. Gnathal lobes with few setae. Epicranial groove deep with lateral region prominent. Top of head with distinct swellings towards lateral edges, fine transverse wrinkles between swellings and antennal sockets. Suture extending from posterior margin of headplate longitudinally down midline to point level with antennal sockets. Antennomeres

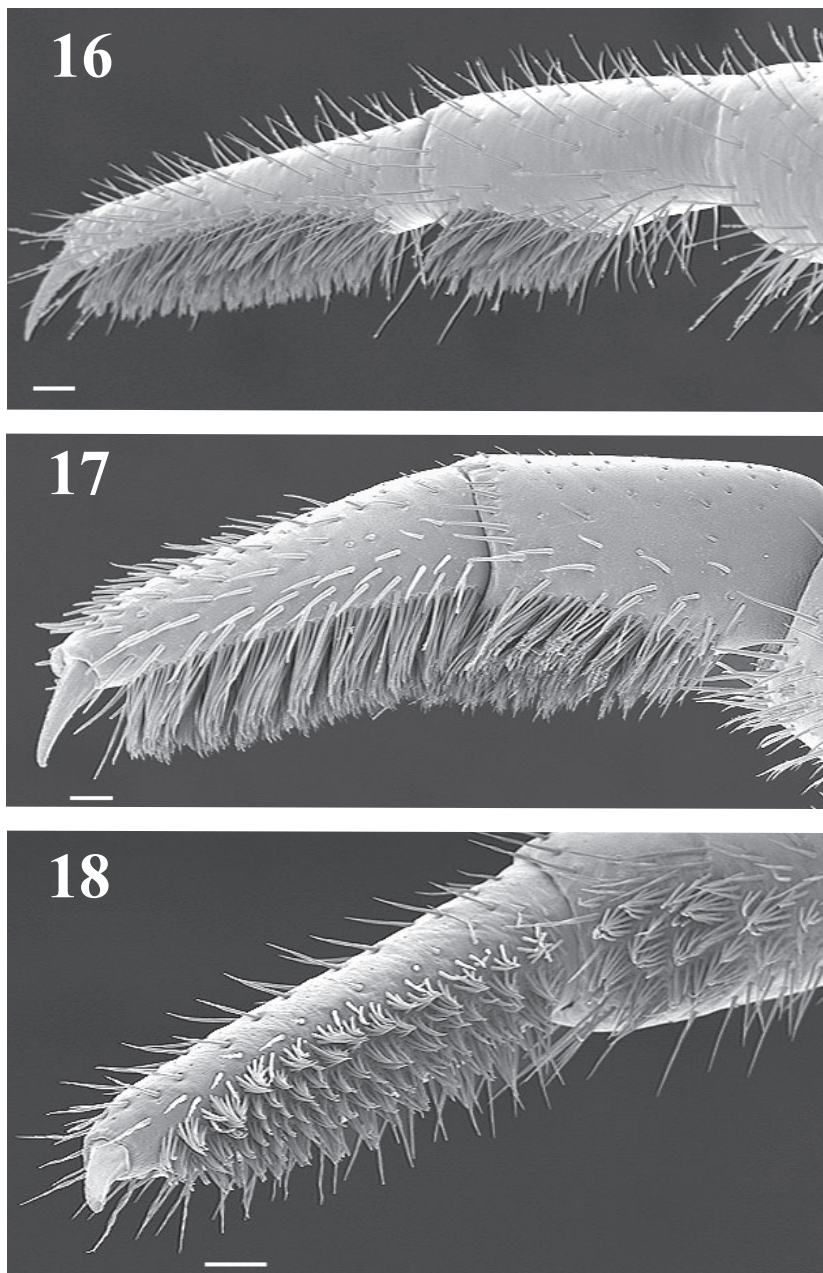
of equal length, each widening a little distally. Setae moderate with few longer setae on distal region (Fig. 19).

Collum. Surface smooth, shiny, without setae, but with typical cuticular structure (Fig. 5). Marginal rim with pre-marginal furrow on lateral border and extending halfway up anterior border. Lateral profile, top flattened with strongly convex anterior border.

Body rings. Mid-ring constriction forming a prominent sulcus on rings 4–18; laterally finely ribbed. Dorsum with median suture. Tergite surface smooth, without setae, some

small pits located laterally. Pleural keels very slight on fourth ring. Anterior spiracles with slight ridge or projection on top margin (Fig. 11). Single spiracle on fourth body ring lacking projection and larger and flatter than other spiracles.

Paranota. Paranota of second body ring strongly developed. Anterior margin relatively straight with rounded anterolateral edge, with small tooth directed downwards. Lateral margin with convexity increasing caudally. Posterolateral edge rounded and slightly extended past ring margin. Paranota of third and fourth rings small and strongly convex.



Figs 16–18. Setal 'pads' on the tarsus and apical portion of the tibia, males. 16, *Hoplatessara musgravei*; 17, *Gigantowales chisholmi*; 18, *Cladethosoma clarum*, scale bars = 100 μm .

Paranota of fifth and subsequent rings small and only narrowly laterally extended. Poriferous paranota in lateral aspect dorsoventrally wider at anterior end, gradually tapering in caudal half, with lateral projection increasing towards caudal end. Pore-less paranota dorsoventrally narrower and more strongly convex or crescent-shaped.

Sternites and legs. Well developed lamella present on sternite of fifth ring, between coxae of anterior leg pair, directed ventrally (Figs 8, 9, 51–52). Numerous short setae on anterior surface, few longer setae on posterior surface. Setae present on fourth and subsequent sternites between coxae of all segments, longer setae on fifth and sixth sternite. Femur of first leg pair with well developed adenostyle and setae. Coxae of second leg pair with small process or swelling just above gonopore opening. Legs with setae on all segments, setae denser and longer on ventral surface, single long seta at ventral apical surface of coxae and prefemur. Dense setal pads on tarsus and apical portion of tibia of legs (Fig. 18), strongest on pregonopodial legs and thinning on posterior legs until absent on final leg pairs.

Anal ring. Epiproct in dorsal aspect broad at base, sides initially straight for half of length, tapering, concave towards a blunt apex (Fig. 22). Setae not on tubercles, total of 14 setae arranged in three rows: first proximal row of six, mid row of four and posterior row of four setae at apex. Paraproct with two setae at margin with margins forming a ridge (Fig. 23), hypoproct rounded with two setae at posterior margin.

Gonopods (Figs 2, 30–31, 42–43). Cannula on mesal side of coxae forming a loop. Prefemur with numerous bunched setae on mesal region, directed up over tibiotarsus region. Tibiotarsus emerges from prefemur region initially as a single piece, splits distally into four branches. Single large branch at back (femoral process) longest, projecting past solenomere, laterally broad and laminate, transversely flattened with narrow and acutely angular preapical region recurved and forming terminal hook-like shape on mesal margin. Solenomere, forming second longest branch, emerges near base of acropodite, relatively slender with apex curving inwards. Tibiotarsus deeply bifurcate, arising close to apex of prefemur to form two branches of approximately equal length. Tibiotarsal branches laminate rather than slender or rod-like. Anterior midpoint of gonopod aperture with small triangular process, posterior midpoint with strong spine directed ventrally.

Female

Specimen colouration matches that of males as described both in the literature and observed the current study. Otherwise, similar to male but lacking dense setal pads on tibiae and tarsi of legs.

Measurements. Total length 24.04; collum 1.52 (range 1.4–1.6) long; 3.24 (range 3.1–3.5) wide; tergite 2.24 (range 2.0–2.6) long, 4.04 (range 3.9–4.3) wide.

Remarks

Specimens generally agree with the description by Attems (1931) and the holotype (MCZ 4887), with minor discrepancies. Specimens are on average smaller than those identified by Chamberlin (1920) (male: 35 long, 4 wide) but on average larger than those identified by Attems (1931, 1937) (male: 3.5 wide). (Additional measurements are taken from both males and females in this collection.)

Attems (1931) noted the presence of pleural keels on the second ring and a total of 12 setae on the epiproct. Specimens examined in this study did not show pleural keels on the second ring but on the fourth ring; individuals varied in the degree of prominence or development of these keels. Specimens exhibited the epiproct setae number and pattern typical of the family (14 in total). The collection of male and female specimens in copula supports the designation of females to this species.

Specimens were most active on overcast and/or moist early mornings at which time they were found apparently ‘grazing’ on lichen growing on exposed rock surface. At warmer and drier times specimens were much more difficult to locate, perhaps seeking refuge in rock crevices, but they could on occasion be found on logs.

Distribution

With the inclusion of specimens from the current study, the distribution of *C. clarum* includes Palm Beach Headlands, La Perouse and Hornsby, Sydney, NSW. The general distribution of the genus includes central areas of the NSW coastal region; the Sydney Basin; Gippsland, Victoria and southern Queensland.

Genus *Gigantowales* Verhoeff

Gigantowales Verhoeff, 1937: 134. – Jeekel, 1968: 24; Jeekel, 2000: 31. Type species: *Gigantowales chisholmi* Verhoeff, 1937, by monotypy.

Diagnosis

Specimens in this genus are of very large size. Straight and elongate femorite relatively long, comprising approximately half of telopodite. Acropodite consists of four main branches, plus solenomere process, total of five branches (solenomere, solenomere process, femoral process and two tibiotarsal branches). Tibiotarsal branches transversely flattened or laminate and femoral process elongate and rod-like. Females possess a strong spine on caudal side of coxae of second pair of legs.

Remarks

Attems (1940) diagnosed the genus using traits shown to be applicable at higher taxonomic levels: femur of first leg pair with adenostyle, fifth sternite with lamella, as well as the shape of the paranota and the pore formula. Diagnosis of the

genus is difficult due to a general lack of clearly defined generic characters.

The genus *Gigantowales* currently contains two species (Jeekel 2000; Mesibov 2002). Jeekel (2000) redescribed the type species from additional material from NSW and gave a description of a new species, *G. latescens*.

Jeekel (2000: 35) states, 'even after close comparison of the two species no appreciable differences between the two species could be established' and reported the gonopods to be similar to those of *G. chisholmi*. The decision to designate *G. latescens* as a species was undertaken, regardless of the morphological similarity, due to a difference in colour pattern: '*G. chisholmi* a dark species with a continuous broad light coloured median band, against *G. latescens* also with a broad median yellowish band, but medially bisected by a dark brown median stripe, which is narrowest at the waist and widens towards the caudal margin to about double that width or even a little more, the dark stripe becoming a trian-

gular spot on the metatergites' (Jeekel 2000: 36). This colour difference is believed to give the two species sufficient distinctiveness. Additionally, *G. chisholmi* is, 'known to occur at several widely separated places without appreciable variation in colouring' (Jeekel 2000: 36).

Numerous specimens from both *G. chisholmi* and *G. latescens* were examined in this study and no additional morphological differences were found. It should be noted that although the colour distinction is consistent, the additional specimens from this study do show some variation in the colouration of the yellow dorsal band in *G. chisholmi*. However, the pattern of a broad light coloured dorsal band with dark brown sides appears consistently in this species. The consistency of this colour distinction, still observable in preserved specimens of equal age (back to 1937), is striking. It may be that this represents a polymorphic species or a species complex as observed in other groups (Bond and Sierwald 2002) and requires further study and examination of additional specimens before the situation can be clarified.

Gigantowales chisholmi Verhoeff

(Figs 13, 14, 17, 34, 45–46, 55)

Gigantowales chisholmi Verhoeff, 1937: 134. – Attems, 1940: 549; Jeekel, 1968: 24; Jeekel, 2000: 31. Type data: syntypes ZMB 12653 (collected by Dr E. C. Chisholm), for ZMB holdings 'NSW', *vidi*.

Material examined

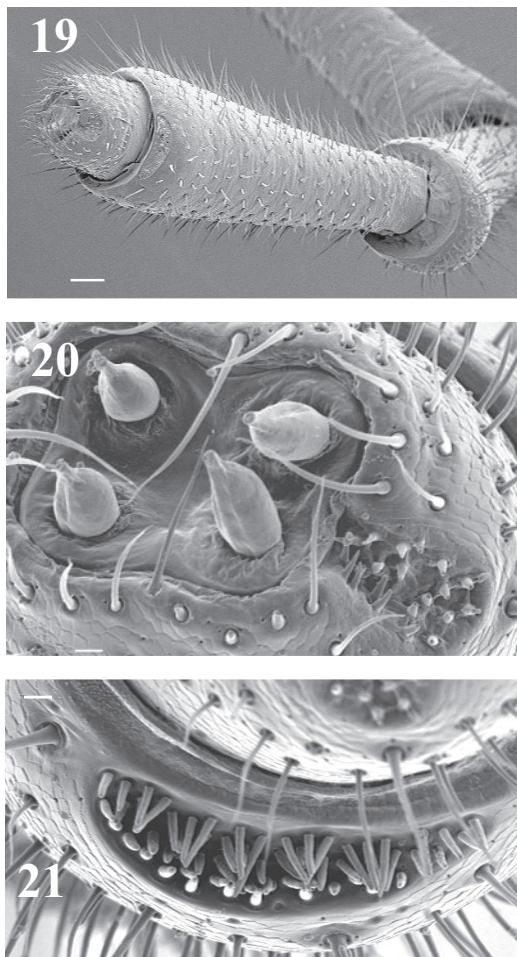
Syntypes. **Australia: NSW:** 1 ♂, 1 ♀, (ZMB 12653).

Paratypes. **Australia: NSW:** 1 ♀, 1 juvenile, Comboyne, coll. Dr E. C. Chisholm (AM KS76698); 1 ♂, 1 ♀, Comboyne (AM KS76699).

Other material examined. **Australia: NSW:** 1 ♀, 2 ♂ juveniles, ~70 km ESE of Tamworth, Branga Plains, Inglebar Ck, (map: 45.7/13.3), 4.ii.1972, coll. G. Witten (ZMA); 2 ♂, 2 ♀, Wauchope, Mt Boss SF, Easy Ck 31°11'15"S 152°22'05"E, ex pitfall trap, x.1980, coll. G. A. Webb (ZMA); 1 ♀, Mosman, Carpark on Musgrove St, 15.xi.2004, coll. G. D. E. (AM KS92912); 2 ♀, Tubrabucca, 12.i.1948, coll. W. Barnes (AM KS82779); 1 ♀, near Taree, Tinonee, Old Bar Rd, i.1932, coll. R. O. Chalmers (AM KS82778); 2 ♂, 1 ♀, Williams R., near Cutler's Pass, 28.x.1926, coll. A. Musgrave and T.G. Campbell, (AM KS82783); 1 ♂, Upper Hunter District, 10.i.1948, coll. Aust. Mus. Party (AM KS82780); 1 ♂, Jenolan, 16.iii.1932, coll. J. C. Wiburd (AM KS82785); 2 ♂, Williams R., near Cutler's Pass, 23–30.x.1926, coll. A. Musgrave and T. G. Campbell (AM KS82781); 2 ♂, 1 ♀, Tubrabucca, 4300 feet, 15.i.1948, coll. Aust. Mus. Party (AM KS82782); 1 ♂, 1 ♀, Williams R., Barrington House, 1250 ft, i.1943, coll. A. Musgrave (AM KS92913); 1 ♂, 15 ♀, 1 juvenile ♂, Narrabeen, 19.x.1983, K. Hangay (AM KS 16955); 2 ♂, 1 ♀, 1 juvenile ♂, North Ryde, Macquarie University 33°46' 28.63"S 151°4'43.75"E, v.2000, coll. M. Rowe (AM KS87596); 3 ♂, North Ryde, Macquarie University, 33°46' 28.63"S 151°4'43.75"E, v.2000, coll. M. Rowe (FMMC6618); 2 ♂, North Ryde, Macquarie University 33°46' 28.63"S 151°4'43.75"E, v.2000, coll. M. Rowe (AMNH).

Diagnosis

Dark brown colouration, with broad yellowish median dorsal band and dark brown laterally.



Figs 19–21. Antennal morphology. 19, *Cladethosoma clarum*, scale bar = 100 µm; 20, sensory cones located on antennal tip, *Akamptogonus novarae*, scale bar = 10 µm; 21, sensory fields located on the outer side of the penultimate (fourth) antennomere, *Akamptogonus novarae*, scale bar = 10 µm.

Description

Measurements. *Male:* collum 2.61 (range 2.5–2.7) long, 5.3 (range 5.2–5.4) wide; tergite 4.43 (range 4.0–4.7) long, 5.69 (range 5.5–6.0) wide. *Male (juvenile):* collum 2.1 long, 4.3 wide; tergite 3.4 long, 5.2 wide. *Female:* collum 2.6 long, 5.5 wide; tergite 4.0 long, 6.2 wide.

Remarks

Specimens generally conform to Jeekel's (2000) description, notably through the amendment of Verhoeff's (1937) original description of the presence of a small spine-like process on the solenomere. Specimens also agree with the syntype material examined. However, the specimens are smaller than those identified by Jeekel (2000).

Gigantowales chisholmi is distinguished from *G. latescens* by its colouration. In comparison to *G. chisholmi*, *G. latescens* bears a broad yellowish median band, bisected by a dark brown median stripe, narrowest at the waist and widening towards the caudal margin and light-brown laterally. Specimens were found in leaf litter.

Distribution

Gigantowales chisholmi has a fairly wide distribution including: the Sydney Basin (Mosman, Narrabeen, North Ryde), upper Hunter district (Tubrabucca), Tinonee (near Taree), Williams River, Jenolan, Comboyone district, Branga plains (near Tamworth) and Wauchope Australia.

***Gigantowales latescens* Jeekel**

Gigantowales latescens Jeekel, 2000: 35. Type data: holotype ZMA (collected by C. A. W. Jeekel). Type locality: 20 km NNE Guyra, NSW, vidi.

Material examined

Holotype. ♂, Australia: NSW: 20 km NNE of Guyra, 30.x.1980, C. A. W. & A. M. Jeekel (ZMA).

Paratypes. 2 ♂, 2 ♀, same data as holotype (ZMA).

Diagnosis

Dorsal surface with broad yellowish median band, narrowest at waist and widening towards caudal margin, approximately doubling in width. Median band bisected by dark brown stripe that becomes a triangular spot on metatergites. Laterally light brown.

Genus *Heterocladosoma* Jeekel

Heterocladosoma Jeekel, 1968: 144. – Jeekel, 1985: 19; Jeekel, 1987: 23. Type species: *Eustrongylosoma bifalcatum* Silvestri, 1898, by original designation.

Diagnosis

Short femorite, with acropodite of gonopod subdivided into four main branches (solenomere, femoral process and two

tibiotarsal branches). Basal section of solenomere and femoral process fused over half to three-quarters of its length, forming femoro-solenomere. Femoral process a simple prong. Tibiotarsus deeply bifurcate, forming two branches arising from base of acropodite, one of which is slender, one greatly enlarged (broadly laminate) and apically curved towards medial side. Sperm channel extends straight to solenomere apex.

Remarks

Jeekel (1985, 1987) grouped the genus *Heterocladosoma* with *Cladethosoma* based on the shared trait of a bifurcate tibiotarsus. He also suggests affinities to the genus *Somethus* because both possess a fused femoro-solenomere. However, *Heterocladosoma* remains distinct from *Cladethosoma*, which lacks a fused femoro-solenomere, and distinct from *Somethus*, which possesses only a single tibiotarsus branch and a sperm channel that makes a loop in a preapical process before extending to the solenomere apex.

The genus *Heterocladosoma* is relatively well known with a key to its seven species and two subspecies provided by Jeekel (1987) (see also Mesibov 2002). Species diagnoses are based on differences in gonopod structure, the femoro-solenomere apically bifurcate or trifurcate, the tibiotarsal shape and relative length of the gonopod branches. Colouration is also important in species identification. The genus was proposed for species occurring in the coastal region of Queensland, with the subsequent discovery of species in South Australia extending the range of the genus. This is the first record of the genus from NSW, connecting the previously disjunct range of the genus.

***Heterocladosoma bifalcatum* (Silvestri)**

(Figs 4, 10, 26–27, 38–39, 47–48)

Eustrongylosoma bifalcatum Silvestri, 1898: 231, figs 13, 14. Type data: type status and whereabouts unknown. Type locality: Cairns, Qld.

Australiosoma bifalcatum (Silvestri). – Brölemann, 1913: 91; Attems, 1937: 237.

Heterocladosoma bifalcatum (Silvestri). – Jeekel, 1968: 25, fig. 2; Jeekel, 1985: 19; Jeekel, 1987: 24, figs 5–8.

Material examined

Australia: NSW: 2 ♂, 2 ♀, Sydney, Epping, v.2000, coll. M. Rowe (AM KS87593); 2 ♂, 1 ♀ (FMMC6610); 2 ♂, 1 ♀ (AMNH).

Diagnosis

Femoro-solenomere not widely curved but almost straight and apically bifurcate. Smaller tibiotarsal branch approximately two-thirds of acropodite length, narrow and rod-like. Largest tibiotarsus branch projecting distad of other branches (femoral process and solenomere), tapering apically and lamellar, curving widely laterad, but not spine-like.

Colouration striking: blackish brown body with blood-red legs, antennae and sternites.

Description

Male

Measurements. Collum 1.27 (range 1.2–1.4) long, 2.45 (range 2.4–2.5) wide; tergite (10th) 2.1 (range 2.0–2.2) long, 2.88 (range 2.8–2.9) wide.

Female

Colouration dark brown-black with blood-red legs and antennae. Overall, female specimens match males in somatic characters. Small process present on caudal side of coxae of second pair of legs, but not a distinct spine. Females wider than males (10th tergite).

Measurements. Collum 1.43 (range 1.2–1.5) long, 2.73 (range 2.4–2.9) wide; tergite (10th) 2.23 (range 1.9–2.5) long, 3.3 (range 3.0–3.7) wide.

Remarks

Male specimens fit the original description by Silvestri (1898) and the more recent description provided by Jeekel (1987), including the presence of a lamella on the fifth ster-

nite and setal pads (termed ‘scopulae’ by Jeekel) on the tibiae and tarsi of the pregonopodial legs. Specimens are slightly larger than those identified by Jeekel (1987): 2.6–2.8 wide.

Heterocladosoma bifalcatum differs from the other species in the genus in the shape of the femoro-solenomere: not widely curved but almost straight and apically bifurcate. The material examined agrees well with the previous descriptions, except for the note by Jeekel (2000) that the females of this genus possess a strong spine on the caudal side of the coxae of the second pair of legs. The specimens of *H. bifalcatum* examined here possess a small peg-like process rather than a spine. Of the other species in the genus, only *H. zebratum* is confirmed to possess a strong spine (Jeekel, 1985). *Heterocladosoma galaxias* (Jeekel 1985), *H. trabeatum*, *H. asperum*, *H. transversetaeniatum perarmatum* and *H. transversetaeniatum* female specimens are either unknown or sufficient intact material is not available to reach a conclusion regarding the nature of the spine, whereas females of *H. hamuligerum* possesses distally swollen coxae but lack a clear process or spine (Jeekel 1987). This suggests that the presence of a strong caudal spine does not represent a defining genus-level character, nor does it indicate a close relationship with *Gigantowales* as suggested by Jeekel (2000) (see description of *Gigantowales* above).

At the time of Jeekel’s 1987 description, female specimens were unknown. This is the first record of female specimens, with four in the current collection. Males and females sharing the same striking colour pattern were found in copula in the field.

Specimens were located on the ground in log debris and in trees under bark and were most active and easily located during overcast conditions or during light rain and at cooler temperatures associated with early mornings.

Distribution

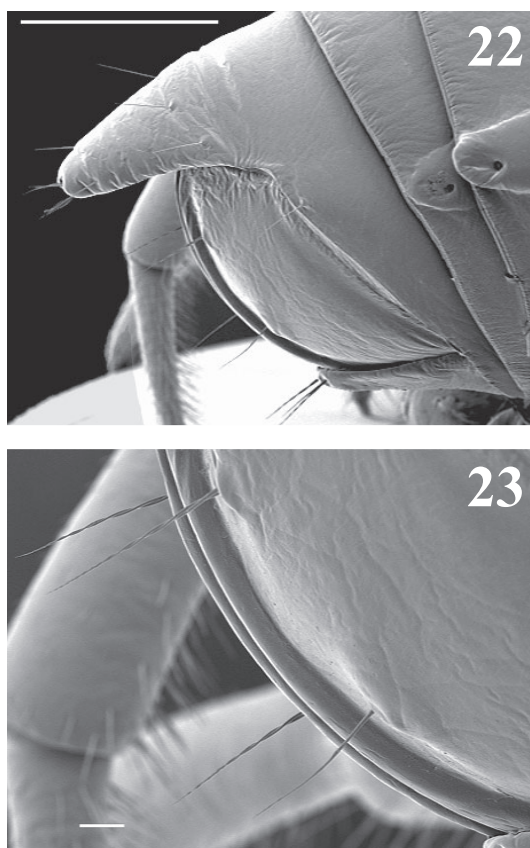
The range of the species is now known to include the Sydney region. It was formerly known only from Queensland. Of the species collected in this study, *H. bifalcatum* was the most commonly encountered and widely distributed species found within the Sydney Basin, including the site of specimen collection (Epping). It was also observed at Palm Beach headlands 33°36′3.59″S 151°19′18.22″E.

Genus *Hoplatessara* Verhoeff

Hoplatessara Verhoeff, 1928b: 89. – Jeekel, 1968: 25; Jeekel, 1984: 37; Jeekel, 2003: 28.

Hoplatessaropus (*Hoplatessaropus*) Verhoeff, 1941: 9; synonymised by Jeekel, 1968: 25. Type species: *Hoplatessara* (*Hoplatessaropus*) *pugiona* Verhoeff, 1941, by monotypy.

Type species: *Hoplatessara musgravei* Verhoeff, 1928b, by original designation.



Figs 22–23. *Cladethosoma clarum*. 22, Lateral view of the telson (epiproct), scale bar = 1 mm; 23, anal valves, scale bar = 100 μ m.

Diagnosis

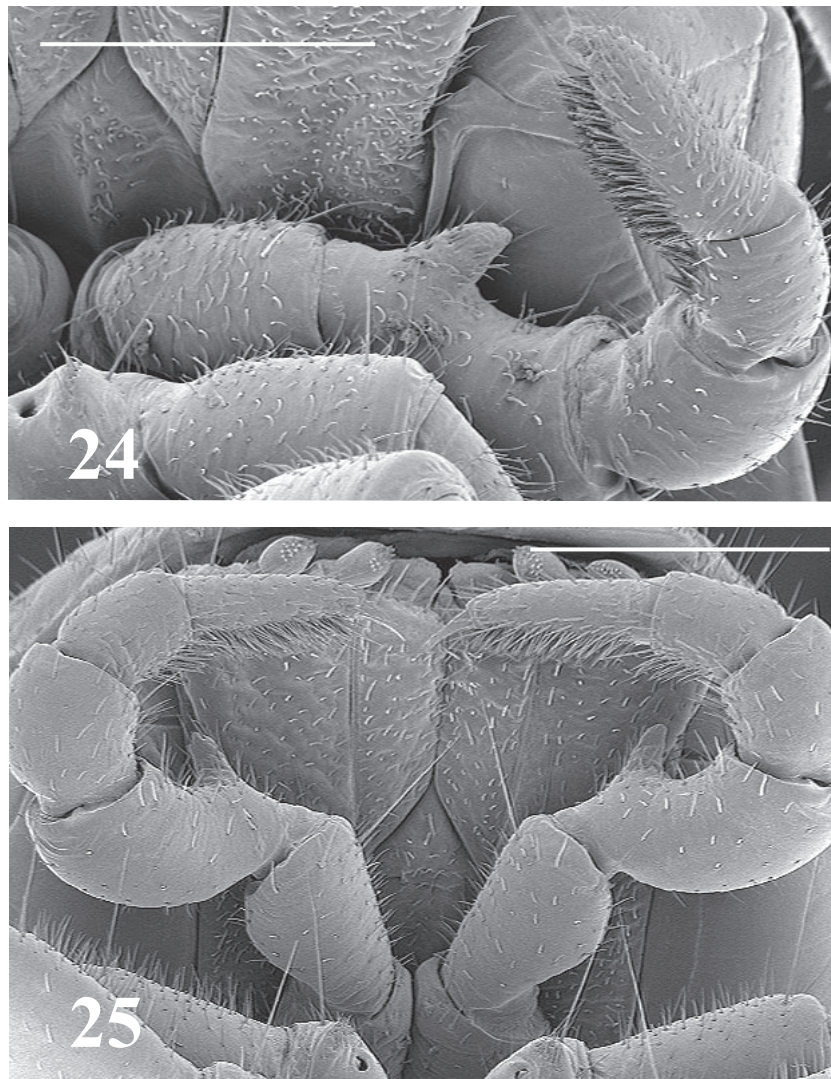
Acropodite of gonopod divided into four main branches (solenomere, femoral process and two tibiotarsal branches). Solenomere with bilobate or trilobate apex. Femoral process (longest of the branches) laminate and transversely flattened, with spatulate apex. Tibiotarsus deeply subdivided into two branches arising from base of acropodite, which form rod-like prongs and are more-or-less circular in cross section. Sperm channel extends to apex of solenomere, making a loop into middle apical lobe before terminating in proximal-most lobe.

Remarks

The genus *Hoplatessara* is relatively well known with a key to seven species provided by Jeekel (1984). An additional

species was added recently (Jeekel 2003). Species are primarily distinguished by the relative lengths of the four branches, the solenomere shape and apex and the outline of the femoral process. Jeekel (1984) compared *Hoplatessara* to the genus *Cladethosoma*, based on the shared traits of short femorite, four branches and a bifurcate tibiotarsus arising from the very base of the acropodite. The genera are distinguished by the shape of the apex of the solenomere (*Hoplatessara* with distinct bilobate or trilobate apex), and the femoral process (*Hoplatessara* less constricted pre-apically and lacking a spine-like apex).

The genus was synonymised under *Australiosoma* by Attems (1937: 233) and reinstated by Jeekel (1968). The characteristics of this genus have been revised since its initial determination with the current generic diagnosis provided by Jeekel (1984).



Figs 24–25. Adenostyle, first leg of male. 24, *Hoplatessara musgravei*; 25, *Cladethosoma clarum*, scale bar = 1 mm.

***Hoplatessara clavigera* Verhoeff**

Hoplatessara clavigera Verhoeff, 1928b: 99, figs 28–30, plate x–xi.
– Jeekel, 1968: 25 (reinstated the genus). Type data: syntype
ZMB 5712, one male, *vidi*. Type locality: NSW.

Australiosoma clavigerum (Verhoeff). – Attems, 1931: 134 (see
Remarks under genus *Australiosoma* below.)

Material examined

Syntypes. **Australia: NSW:** ♂ (ZMB 5712).

Other material examined. **Australia: Western Australia:** 3 ♂, 3 ♀, 1 juvenile (collected August 1889), *vidi*. Type locality:
Booanya, ii.1932, coll. A. E. Baesjou (AM KS92916).

Diagnosis

Solenomere apically trilobate, without preapical accessory branch. Femoral process greatly expanded in distal direction, overreaching solenomere by about one-third of total acropodite length. Tibiotarsal branches unequal in length, shorter branch about two-thirds length of longer branch (Jeekel 1984).

***Hoplatessara froggatti* (Brölemann)**

Australiosoma froggatti Brölemann, 1913: 95, figs 8–12, plate xiv.
– Attems, 1937: 237. Type data: syntypes AM KS76491, 2 ♂, 3 ♀, 1 juvenile (collected August 1889), *vidi*. Type locality:
NSW: Shoalhaven district, Mt Sassafras..

Hoplatessara froggatti (Brölemann). – Jeekel, 1968: 25; Jeekel, 1984: 38.

Material examined

Topotype. ♂, **Australia: NSW:** Sassafras, viii.1889, det. P. M. Johns (AM KS92919).

Other material examined. **Australia: NSW:** 2 ♂, 3 ♀, 1 juvenile ♂, Shoalhaven district, Mt Sassafras, viii.1889 (AM KS76491).

Diagnosis

Solenomere apically trilobate, without preapical accessory branch. Femoral process generally overreaching solenomere by less than one-third of total length of acropodite. Tibiotarsal branches with little difference in length. Femoral process spatulate, rather narrow over most of its length and widening distally in rhomboid, subquadrate, or rounded apical lamina.

Remarks

Hoplatessara froggatti is distinguished from the other species in the genus, particularly *H. musgravei*, by, ‘the solenomere not conspicuously widening in its distal half’ (Jeekel 1984: 38).

***Hoplatessara musgravei* Verhoeff**

(Figs 3, 6, 7, 16, 28–29, 40–41, 49–50)

Hoplatessara musgravei Verhoeff, 1928b: 98, figs 21–22, plate ix.
– Jeekel, 1968: 25; Jeekel, 1984: 38. Type data: AM KS76500
lectotype male; paralectotype (allotype) female (collected

24 December 1921), *vidi*. Type locality: NSW: Blue Mountains, Hazelbrook.

Australiosoma musgravei (Verhoeff). – Attems, 1931: 134; Attems, 1937: 238, fig. 298.

Material examined

Lectotype. ♂, **Australia: NSW:** Blue Mountains, Hazelbrook, 24.xii.1921, A. Musgrave (AM KS76500).

Allotype. ♀, same data as lectotype (AM KS76500).

Other material examined. **Australia: NSW:** 2 ♂, Sydney, Epping, v.2000, coll. M. Rowe (AM KS87594); 2 ♂, Sydney, Epping, v.2000, coll. M. Rowe (FMMC6624).

Diagnosis

Solenomere apically trilobate, without preapical accessory branch. Tibiotarsal branches differing little in length. Distal half of solenomere with abrupt laminate expansion on lateral side. Femoral process generally overreaching solenomere by less than one-third of total length of acropodite, stem relatively broad and widening gradually towards slightly spatulate apex, without spines or serration on margin (Jeekel, 1984).

Description**Male**

Measurements. Collum 2.55 (range 2.5–2.6) long, 4.62 (range 4.4–4.8) wide; tergite 4.45 (range 3.9–4.7) long, 5.25 (range 5.0–5.4) wide.

Remarks

The specimens mostly agree with the original description provided by Verhoeff (1928b). The species is also characterised by the setal pads on the tibia and tarsus of pregonopodial legs (pairs 1–7) (Fig. 16).

Distribution

Australia, NSW, Sydney, Epping and type recorded from Hazelbrook in the Blue Mountains, NSW.

Genus *Australiosoma* Brölemann

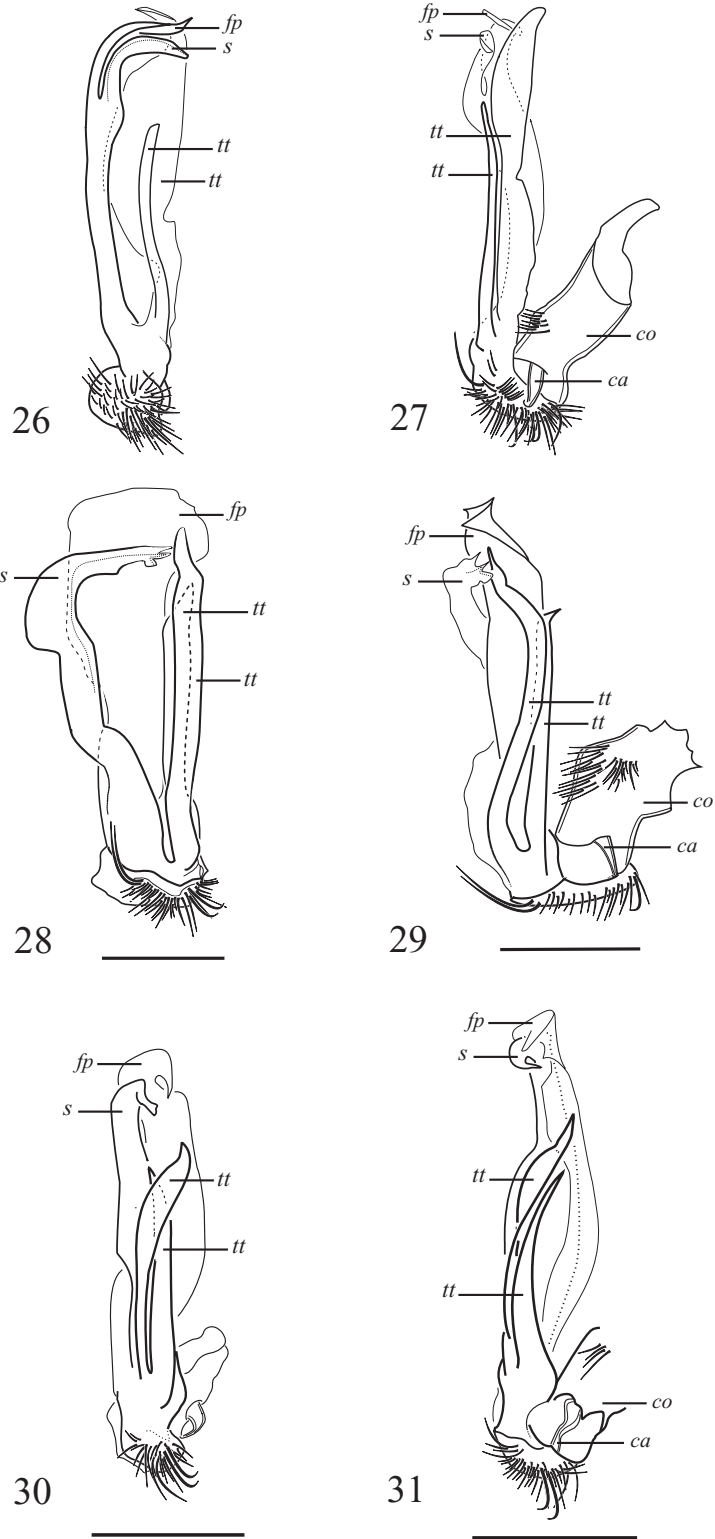
Australiosoma Brölemann, 1913: 89. – Attems, 1914: 224; Attems, 1931: 134; Attems, 1937: 233; Verhoeff, 1924: 9, 12, 23; Verhoeff, 1928b: 89; Jeekel, 1968: 25; Jeekel, 1982: 137; Jeekel, 1984: 27; Jeekel, 2003: 33.

Rhopalowales Verhoeff, 1928b: 103; synonymised by Jeekel, 1968: 24 (Jeekel ignored Attem’s (1931) earlier synonymy of *Rhopalowales* with *Leucotessara* Verhoeff, 1925). Type species: *Rhopalowales clavigera* Verhoeff, 1928b, by monotypy.

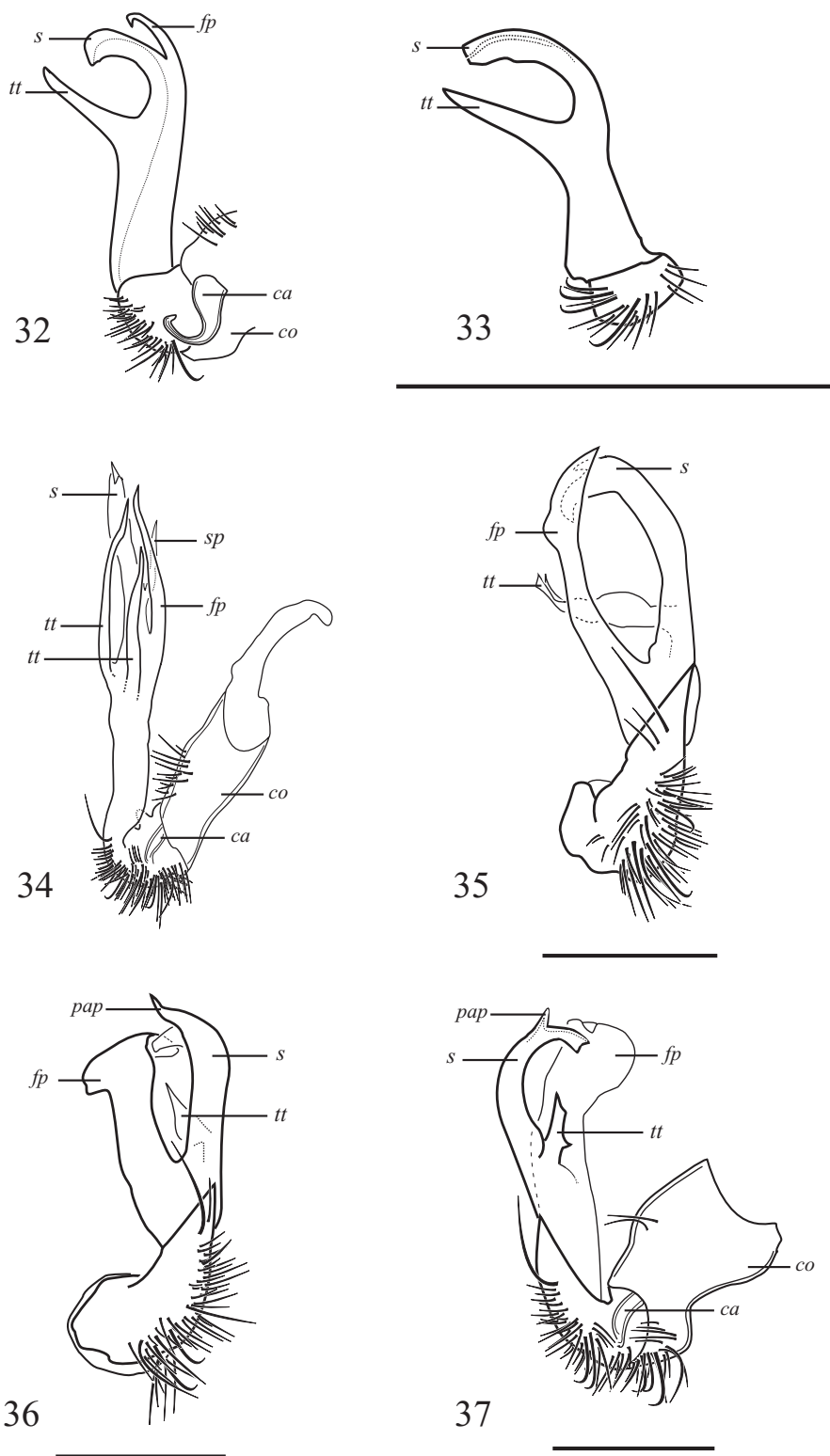
Type species: *Australiosoma rainbowi* Brölemann, 1913, by original designation.

Diagnosis

Gonopods possess relatively elongate prefemur and obvious femorite, of one-third to half length of telopodite. Acropodite deeply split into three main branches (femoral process,



Figs 26–31. Right gonopods. 26, Caudal view, *Heterocladosoma bifalcatum* (after Jeekel 1968); 27, mesal view, *H. bifalcatum* (after Jeekel 1968); 28, caudal view, *Hoplatessara musgravei*; 29, mesal view, *H. musgravei*; 30, caudal view, *Cladethosoma clarum*; 31, mesal view, *C. clarum*, scale bar = 1 mm. Abbreviations: *s*, solenomere; *fp*, femoral process; *tt*, tibiotarsus; *co*, coxae; *ca*, cannula.



Figs 32–37. Gonopods. 32, Mesal view, right gonopod, *Akamptogonus novarae* (after Attems 1911); 33, caudal view, left gonopod, *A. caragoon*; 34, mesal view, right gonopod, *Gigantowales chisholmi* (after Jeekel 1968); 35, caudal view, right gonopod, *Australiosoma combei*; 36, caudal view, right gonopod, *A. fulbrighti*; 37, mesal view, right gonopod, *A. fulbrighti*, scale bar = 1 mm. Abbreviations: *s*, solenomere; *fp*, femoral process; *tt*, tibiotarsus; *co*, coxae; *ca*, cannula; *sp*, solenomere process; *pap*, preapical process.

solenomere, tibiotarsus). Solenomere with one or more preapical processes containing a loop of sperm channel.

Remarks

Brölemann (1913: 89) first described *Australiosoma*, within the Polydesmoidea based on the following characters: 1, pore formula: 5, 7, 9, 10, 12, 13, 15–19; 2, paranota of the second tergite lower than previous or subsequent paranota; 3, paranota more-or-less reduced; 4, tarsi of male furnished below with a brush; 5, first pair of legs of male thickened, the third joint with a tooth-like process; 6, anterior part of the fifth sternite bearing a more-or-less developed lamella; 7, coxal aperture more-or-less contracted on the midline; 8, gonopods: coxal hook (= cannula) present. The femoral part of the telopodite is distinct. The telopodite is more-or-less condensed and more-or-less deeply divided into three or two branches. The type species, *Australiosoma rainbowi*, was identified along with an additional five species. The genus was split into two subgenera based upon differences in the number of acropodite branches: 1, *Australiosoma (sensu stricto)* with a total of three branches and, 2, *Dicladosoma*, with two branches. All other generic characters are identical in the two subgenera.

Since the initial description, the genus has undergone several changes of member species and the subgenera ranking has been removed, elevating *Dicladosoma* to the generic level. Further investigation into all species in *Australiosoma* has suggested that the original character traits 1, 2, 3, 5 and 6 employed by Brölemann (1913) are applicable at higher taxonomic levels. In particular, the mention of the lamella on the fifth sternite is of interest as this structure was never explicitly discussed as an apomorphy for the family Paradoxosomatidae (see discussion in the morphology section). The adenostyle on the femora of the first legs in males is an apomorphy for the subfamily Australiosomatinae.

Jeekel (1982) compared *Australiosoma* to the genus *Hoplatraria*, based on the superficial similarity of gonopod structure. *Australiosoma* was distinguished by the presence of one or more preapical processes and a loop in the sperm channel. *Australiosoma* was also compared to *Myallosoma*, based on the similarity of the solenomere structure; *Myallosoma* differs in having a shorter ovoid prefemur, with an oblique axis, a widely curved acropodite and a bifurcate tibiotarsus (Jeekel 1982).

The genus is relatively well known with six species (Jeekel 1982, 1984, 2003; Mesibov 2002). A key to three of the species is provided by Jeekel (1982) with a fourth species described by Jeekel in 1984. An additional two species descriptions and an updated key to the six nominal species is provided by Jeekel (2003). The present study includes descriptions for two new species, bringing the total number of *Australiosoma* species to eight. Species diagnoses are primarily based upon overall size and general colouration as well as the number of preapical processes on the solenomere, the length of the femoral process and tibiotarsus shape.

The genus *Australiosoma* contained two different species named *clavigerum* during its history. The species *Hoplatessara clavigera* Verhoeff, 1928b, was transferred to *Australiosoma* by Attems in 1931 and removed from *Australiosoma* in 1968 by Jeekel, when he redefined the genus *Hoplatessara*. In 1928, Verhoeff (1928b) also described the species *Rhopalowales clavigera*, which was transferred to *Leucotessara* in 1931 by Attems and to *Australiosoma* by Jeekel in 1968, when he synonymised *Rhopalowales* with *Australiosoma*. The taxonomic history is confusing, but no homonymy existed in the genus *Australiosoma*, since the two different *clavigera* species were never placed in the genus *Australiosoma* at the same time.

Australiosoma clavigerum (Verhoeff)

Rhopalowales clavigera Verhoeff, 1928b: 103, figs 14–15, plate viii (misspelled as 'clavirera' on plate viii). Type data: syntypes AM KS76504, AM KS76505 (collected 21 April 1905), vidi. Type locality: Nowra, NSW.

Leucotessara clavigera (Verhoeff). – Attems, 1931: 138. *Rhopalowales* synonymised with *Leucotessara* by Attems, 1937: 251, fig. 313.

Australiosoma clavigera (non *Hoplatessara clavigera* Verhoeff, 1928b) Jeekel, 1968: 24; Jeekel, 1982: 138 (Jeekel synonymised *Rhopalowales* with *Australiosoma*, ignoring Attem's (1931) earlier synonymy of *Rhopalowales* with *Leucotessara*).

Material examined

Lectotype. ♂, **Australia**: (P. M. Johns) Slide 1 19.xii.1967 (AM KS76504).

Other material examined. **Australia**: **NSW**: 1 ♀, Nowra, 21.iv.1905, (AM KS76505).

Australiosoma combei, sp. nov.

(Fig. 35)

Material examined

Holotype. ♂, **Australia**: **NSW**: Macquarie University, North Ryde 33°46'28.63"S 151°4'43.75"E, v.2000, coll. M. Rowe (AM KS87600).

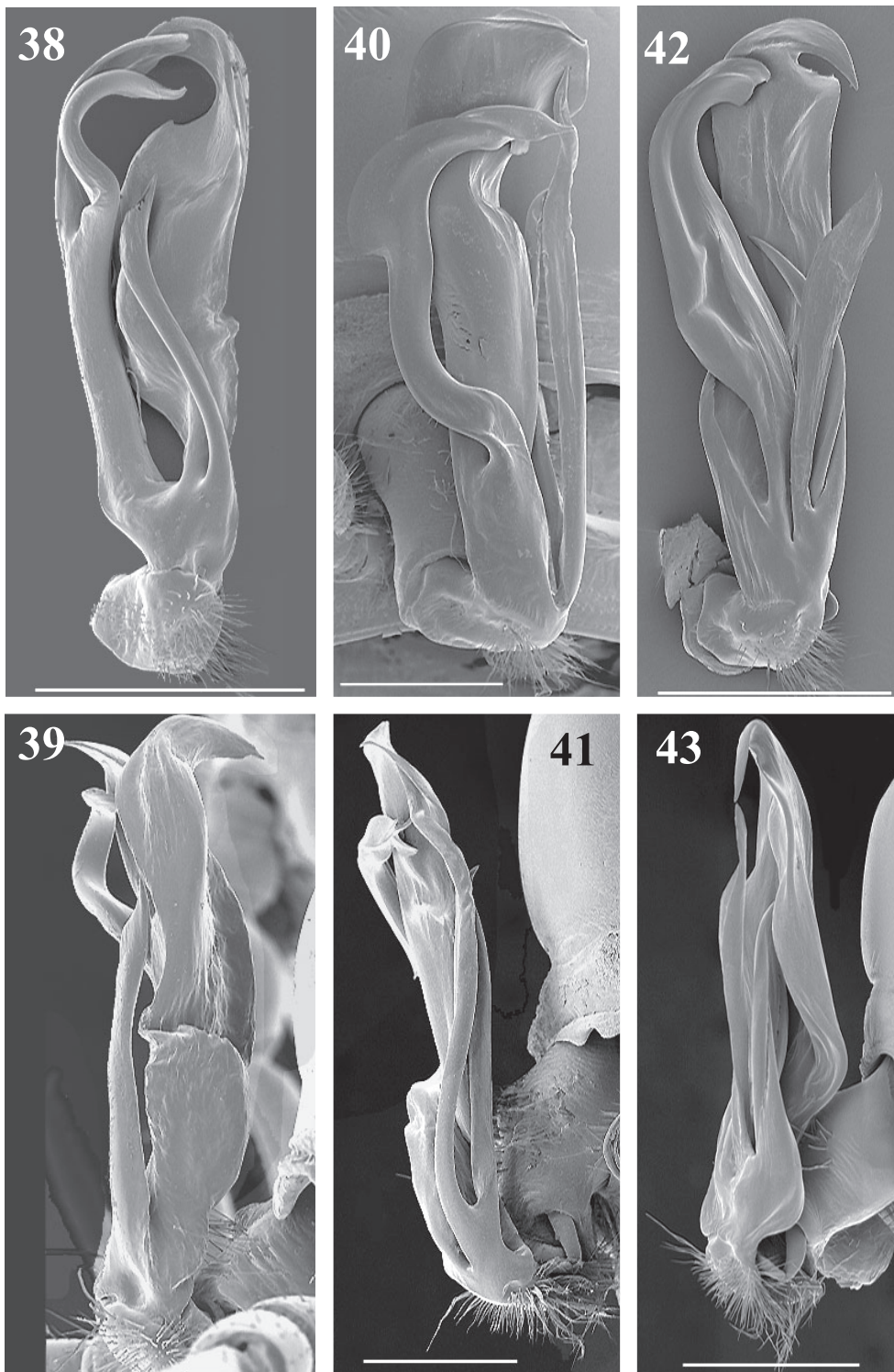
Diagnosis

Large species. Dorsum dark red-brown, lacking any paramedian bands. Femoral process and solenomere of approximately equal length, widely separated. Femoral process relatively narrow along length, not laminate, with expanded and spatulate apex. Solenomere with one preapical process, containing a loop of sperm channel. Tibiotarsus long, extending beyond outer margin of femoral process, with slight expansion at midpoint and tapering to bilobate or trilobate apex.

Description

Male (holotype)

Measurements. Collum 1.9 long, 3.5 wide; tergite 3.3 long, 4.4 wide.



Figs 38–43. Right gonopod, scanning electron micrograph (SEM). 38, Caudal view, *Heterocladosoma bifalcatum*, scale bar = 1 mm; 39, mesal view, *H. bifalcatum*, scale bar = 100 µm; 40, caudal view, *Hoplatessara musgravei*, scale bar = 1 mm; 41, mesal view, *H. musgravei*, scale bar = 1 mm; 42, caudal view, *Cladethosoma clarum*, scale bar = 1 mm; 43, mesal view, *C. clarum*, scale bars = 1 mm.

Colour. Head brown, darkest at vertex, with paler labral area and ring around antennal sockets. Antennomeres 1–4 brown, fifth and terminal article dark brown, whitish intersegmental tissue and terminal article tip. Gnathal lobes brown with paler sutures. Collum red-brown, margins and lateral ridge yellowish. Rings red-brown on dorsal surface, with faint mid-dorsal line, most noticeable at anterior of pronotite where line widens. Laterally red-brown, ventrally paler, sternite surface light-brown. Paranota red-brown to yellowish progressing anterior to posterior. Legs with light-brown coxae, prefemur ventrally light-brown, dorsally brown; femur, postfemur, tibia and tarsus red-brown, slightly darker at tarsus. Epiproct with yellowish midline band extending to tip, flanked by red-brown lateral sides. Paraproct brown with pale margins and hypoproct pale. (Specimen may have undergone some bleaching due to alcohol preservation.)

Head and antennae. Labrum midpoint with three small projections and concave clypeus. Headplate with numerous setae in clypeal region, setae denser just above labrum, fewer setae extending up between antennal sockets to bald vertex. Gnathal lobes with few setae. Epicranial groove deep with lateral region prominent. Suture extending longitudinally from vertex of headplate along midline to point level with antennal sockets. Antennomeres of equal length, each widening a little apically. Setae moderate with few longer setae on apical region. Penultimate segment with sensory field on outer apical region.

Collum. Surface smooth, shiny, without setae, but porous under high magnification. Marginal rim with pre-

marginal furrow on lateral side and extending up anterior side, fading towards middle of anterior border.

Body rings. Surface smooth, without setae, strong constriction forming prominent sulcus, dorsally finely ribbed, present on rings 5–18. Dorsum with median suture. Pleural keels small but present on second to fourth rings. Rings 5–18 with spiracles located on metazonite just anterior to each leg pair, no spiracle above gonopod. Anterior spiracles with marginal projection. Single spiracle on fourth ring lacking projection and larger and flatter than others.

Paranota. Paranota of second ring strongly developed, anterior margin relatively straight and rounded, anterolateral edge with small rounded projection or tooth. Posterolateral edge rounded and extending beyond margin of ring. Paranota of third ring well developed and relatively straight in lateral view, paranota of fourth ring strongly convex. Paranota of fifth and subsequent rings small and only narrowly laterally extended. Poriferous paranota in lateral aspect dorsoventrally wider at anterior end and gradually tapering in caudal half, with increasing lateral projection. Pore-less paranota dorsoventrally narrower and more strongly convex or crescent-shaped.

Sternites and legs. Sternite of fifth ring between coxae of anterior leg pair with well developed and prominent lamella directed ventrally, with numerous short setae on anterior surface and fewer longer setae on posterior surface. Setae present on fourth and subsequent sternites between coxae of all segments, but longer setae on fifth and sixth sternite. Femur of first leg pair with well developed adenostyle and setae. Gonopore opening on slight swelling of mesal region of coxae of second leg pair. Coxae of sixth sternite



Figs 44–46. Right gonopod (SEM). 44, Caudal view, *Akamptogonus novarae*, scale bar = 100 µm; 45, caudal view, *Gigantowales chisholmi*, scale bar = 1 mm; 46, mesal view, *Gigantowales chisholmi*, scale bars = 1 mm.

widely set, particularly on posterior leg pair. Legs with setae on all segments, sparse on dorsal surface, but dense on ventral surface and dorsal surface of tarsus, with increase in length towards apex of segment. Single long seta at ventral apical surface of coxae and prefemur and dense setal pads on apical portion of tibia and tarsus, thinning slightly on caudal leg pairs and absent on last two leg pairs.

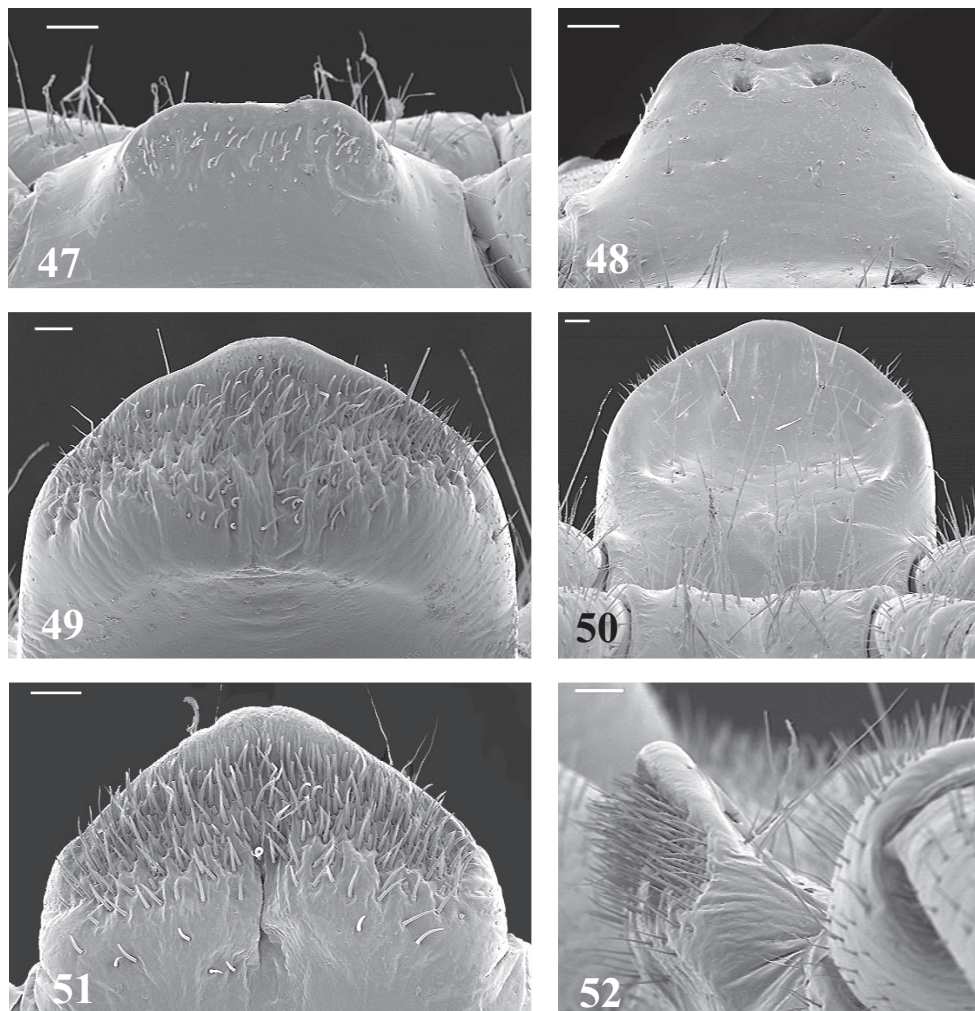
Anal ring. Epiproct in lateral aspect slightly convex, in dorsal aspect broad at base, sides initially straight, concave, tapering towards apex, apex slightly concave. Setae not on tubercles, total of 14 setae arranged in three rows, first proximal row of six, mid row of four and posterior row of four setae at apex. Hypoproct rounded with two setae at posterior margin and paraproct with two setae at ridged margins.

Gonopods (Fig. 35). Cannula on mesal side of coxae forming a loop. Prefemur elongate with distinct demarcation between prefemur and tibiotarsus and numerous bunched setae on mesal region. Femorite short and acropodite deeply

and widely bifurcate, splitting into two main branches. Mesal branch, solenomere, strongly developed and curving widely mesad, with single small preapical process, containing loop of sperm channel. Apex of solenomere laminate and slightly expanded. Femoral process strongly developed and curving widely, with expanded and spatulate apex. Femoral process and solenomere of approximately equal length. Tibiotarsus arising mesally from solenomere, just distad to bifurcation of solenomere and femoral process. Tibiotarsus lies roughly perpendicular to other branches, projecting outwards and surpassing outer margin of femoral process. Femoral process apex variable: right gonopod with distinct bilobed apex; left gonopod with distinct trilobed apex.

Remarks

As this specimen was collected as part of a study that was not intended to include species descriptions, no attempt was made to collect additional material upon which to base this



Figs 47–52. Fifth sternite lamella (SEM). 47, Anterior view, *Heterocladosoma bifalcatum*; 48, posterior view, of *H. bifalcatum*; 49, anterior view, *Hoplatessara musgravei*; 50, posterior view, *H. musgravei*; 51, anterior view, *Cladethosoma clarum*; 52, lateral view, *C. clarum*, scale bars = 100 μ m.

description. A more thorough search of the habitat may reveal additional specimens. Females of this species are unknown. The lack of specimens does not diminish our confidence in the species designation, especially due to the distinct nature of its diagnostic traits.

Etymology

The species name, *combei*, is named for Mr Andrew Combe in recognition of his support for the first author's (MR) research.

Australiosoma fulbrighti, sp. nov.

(Figs 36–37)

Material examined

Holotype. ♂, **Australia: NSW:** Sydney, Epping, v.2000, coll. M. Rowe (AM KS87599).

Paratypes. 3 ♀, same data as holotype (AM KS91584).

Diagnosis

Large species. Dorsum dark with pair of yellowish paramedian bands. Femoral process and solenomere of approximately equal length, widely separated. Femoral process relatively narrow, not laminate, with expanded and spatulate apex, particularly at mesad corner. Solenomere with one preapical process, containing a loop of the sperm channel. Tibiotarsus short, not extending beyond femoral process, with slight expansion at midpoint, tapering to single rounded tip.

Description

Male (holotype)

Measurements. Collum 1.8 long, 3.8 wide; tergite 3.1 long, 4.5 wide.

Colour. Head dark brown, darkest at vertex and paler labrum and area behind antennal sockets. Antennomeres 1–4 dark brown, fifth and terminal article slightly darker with whitish intersegmental tissue and terminal article tip. Gnathal lobes dark brown with paler sutures. Collum dark brown with margins and lateral ridge yellowish, two paramedian yellow spots at anterior margin; at posterior border, beginnings of dorsal bands, two paramedian yellow spots, widening caudally. Rings with dark brown dorsal surface, with two parallel paramedian yellowish bands separated by brown median line, band narrows slightly caudally on pronotite. Midpoint of metazonite with dark brown latitudinal suture. Lateral surface of rings brown, ventrally paler (orange-brown), sternites and underside of paranota yellow. Legs with light-brown coxae, prefemur ventrally light-brown, dorsally darker; femur, postfemur, tibia and tarsus dark brown. Epiproct with pale yellowish midline band, extending to tip, flanked by brown sides. Paraproct brown

with pale margins, hypoproct pale. (Specimen may have undergone some bleaching due to alcohol preservation.)

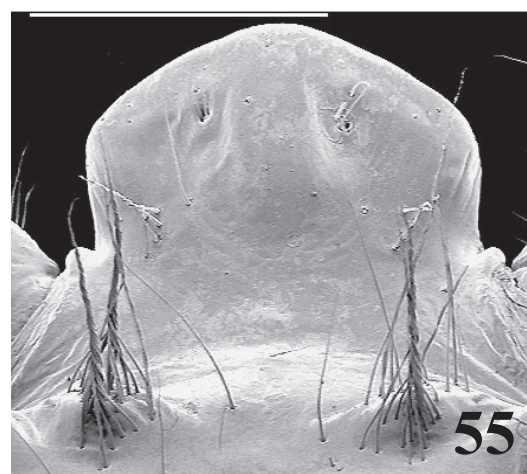
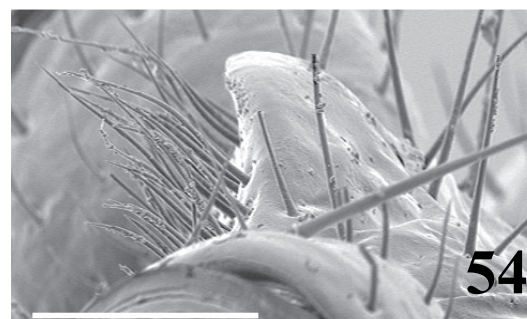
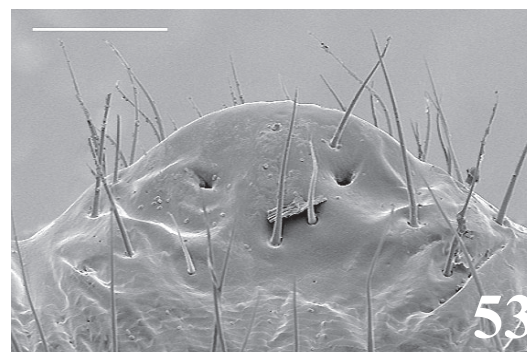
Head and antennae. As for *A. combei*. Additionally, slight transverse wrinkles behind antennal sockets above Tömösváry organs.

Collum. As for *A. combei*.

Body rings. As for *A. combei*, except slight pleural keels present on second to fifth rings, although little more than a swelling on fifth.

Paranota. As for *A. combei*.

Sternites and legs. As for *A. combei*. Additionally, sternite of seventh somite with low granular transverse ridge or



Figs 53–55. Fifth sternite lamella (SEM). 53, Anterior view, *Akamptogonus novarae*; 54, lateral view, *A. novarae*, scale bars 53–54 = 100 μ m; 55, posterior view, *Gigantowales chisholmi*, scale bar = 1 mm.

pregonopodial wall. Gonopod aperture anterior midpoint with small triangular process, posterior midpoint with strong spine directed downwards.

Anal ring. As for *A. combei*.

Gonopods (Figs 36–37). Cannula on mesal side of coxae forming a loop. Prefemur elongate, distinct demarcation between prefemur and acropodite, numerous bunched setae on mesal region. Short femorite and deeply bifurcate acropodite, forming two branches. Mesal branch, solenomere, strongly developed, curving slightly mesad, with preapical process, containing loop of sperm channel. Solenomere tapering towards slightly laminate and truncate apex. Femoral process strongly developed and curving mesad with apex expanded and spatulate. Femoral process and solenomere of approximately equal length. Tibiotarsus arising from solenomere, just distad of solenomere and femoral process bifurcation. Tibiotarsus relatively short and not extending past femoral process, widening a little distad of base, gradually tapering towards pointed apex.

Female

Specimens matching male colouration and otherwise similar to males but lacking dense setal pads on tibiae and tarsi of legs. Female exhibit greater body width than males (10th tergite).

Measurements. Collum 2.07 (range 1.9–2.2) long, 4.0 (range 3.9–4.1) wide; tergite 3.2 (range 3.1–3.3) long, 4.76 (range 4.7–4.8) wide.

Remarks

Male and female specimens were collected at the same site and in close physical contact with each other (appearing to be either pre-copulatory or post-copulatory mate guarding), allowing the collector to be confident in the identification of female specimens to this species. Specimens were located under the bark of logs of fallen trees on the ground.

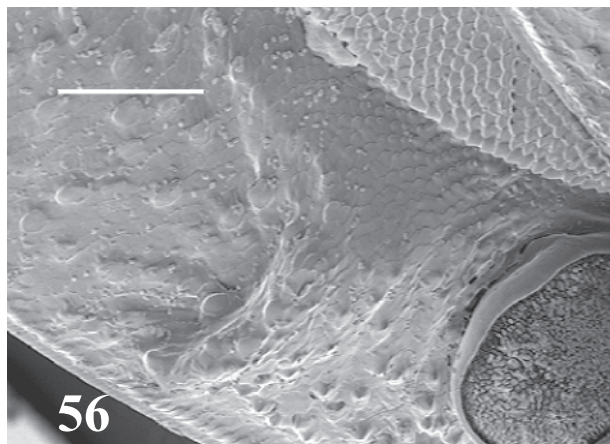


Fig. 56. Pleural keels, *Akamptogonus novarae* (SEM), scale bar = 100 μ m.

Etymology

This species name, *fulbrighti*, is derived from the word Fulbright in honour of the late Senator J. William Fulbright and the Australian-American Fulbright Commission. Senator Fulbright and the Fulbright program promote exchange between America and over 140 countries worldwide, including Australia, with the ideal that mutual understanding through international education and exchange would ‘find ways and means of living in peace’. The species name is taken in recognition of Senator Fulbright and of the support from the Australian-American Fulbright Commission by awarding a postgraduate Fulbright award to the first author (MR), without which this work would not have been possible.

Phylogenetic analysis of *Australiosoma*

With the addition of the two newly described species, *Australiosoma* now includes eight species (Jeekel 1982, 1984, 2003; Mesibov 2002): *A. rainbowi* Brölemann, 1913; *A. clavigerum* (Verhoeff, 1928); *A. michaelsoni* (Attems, 1931); *A. laminatum* Jeekel, 1984; *A. nodulosum* Jeekel, 2003; *A. inusitatum* Jeekel, 2003; *A. fulbrighti* and *A. combei*. We examined the characters of all species of the genus for a phylogenetic analysis of *Australiosoma*. Characters and character states were confirmed by comparison of actual specimens and the original species descriptions. Characters and their states for *A. clavigerum*, *A. nodulosum*, *A. inusitatum* and *Hoplatria* were taken from the literature (Jeekel 1982, 2003 and 1984 respectively).

Material examined

Australiosoma rainbowi

Holotype. ♂, Australia: NSW: Shoalhaven district, Mt Sassafras (AM KS76494).

Other material examined. 1 ♀, same data as holotype (AM KS76495); 3 ♀, same data as holotype (AM KS76496); 1 ♀, same locality as holotype, viii.1889 (AM KS92918); 1 ♂, 1 ♀, same locality as holotype, viii.1889 (AM KS92917).

A. laminatum

Holotype. ♂, Australia (AMNH).

Paratypes. 3 ♂, 1 ♀, 6 juvenile ♂; 3 juveniles, det. Jeekel, 1982, same data as holotype (AMNH).

A. michaelsoni

Syntypes. 4 ♂, 3 ♀, Australia: NSW: between Mt Victoria and Jenolan Caves (ZMH).

A. clavigerum

Lectotype. ♂ (AM KS76504). *Paralectotype.* ♀, (AM KS76505).

A. fulbrighti

Holotype. ♂, (AM KS87599).

A. combei

Holotype. ♂, (AM KS87600).

Character discussion

Character 1. *Body size, measured as width of male at the 10th tergite.* 0, medium, 2.4–3.8; 1, large, 4.3–4.8; 2, small, 1.5–1.7. Outgroup taxon *Hoplatria* falls in the medium size range. Steps, 4; *CI*, 0.500; *RI*, 0.333.

Character 2. *Colouration*. 0, dark-brown/black; 1, dark red-brown; 2, yellow-dark brown. *Hoplatria* is dark-brown/black. Steps, 3; *CI*, 0.667; *RI*, 0.000.

Character 3. *Dorsal stripes*. 0, absent; 1, present. *Hoplatria* lacks dorsal stripes. Steps, 3; *CI*, 0.333; *RI*, 0.333.

Character 4. *Lamella size*. 0, large; 1, small. Lamella size determined from the specimens, from the literature for *A. nodulosum*, *A. inusitatum* (Jeekel, 2003) and *A. clavigerum* (Jeekel 1982). *Hoplatria* possesses a large lamella. Steps, 1; *CI*, 1.000; *RI*, 0.000.

Character 5. *Solenomere shape*. 0, laminate; 1, broad and not tapering at apex; 2, broad and tapering at apex; 3, narrow and not tapering at apex; 4, narrow and tapering at apex. The solenomere in *Hoplatria* is broad and not tapering. Steps, 5; *CI*, 0.800; *RI*, 0.500.

Character 6. *Sperm channel*. 0, straight to apex; 1, with loop through preapical process. *Hoplatria* has a straight sperm channel. Steps, 1; *CI*, 1.000; *RI*, 0.000.

Character 7. *Preapical process*. 0, absent; 1, present. *Hoplatria* lacks a preapical process. Steps, 1; *CI*, 1.000; *RI*, 0.000.

Character 8. *Preapical process length*. 0, absent; 1, present, short; 2, present, long. This character is non-applicable for *Hoplatria*. Steps, 4; *CI*, 0.500; *RI*, 0.000.

Character 9. *Preapical process position*. 0, absent; 1, present, near apex; 2, present, far from apex. This character is non-applicable for *Hoplatria*. Steps, 2; *CI*, 1.000; *RI*, 1.000.

Character 10. *Shape of femoral process apex*. 0, not spatulate; 1, spatulate. The femoral process is not spatulate in *Hoplatria*. Steps, 2; *CI*, 0.500; *RI*, 0.667.

Character 11. *Overall shape of femoral process*. 0, narrow; 1, medium; 2, broad. *Hoplatria* has a narrow femoral process. Steps, 3; *CI*, 0.667; *RI*, 0.000.

Character 12. *Length of femoral process*. 0, shorter than solenomere; 1, equal with solenomere; 2, longer than

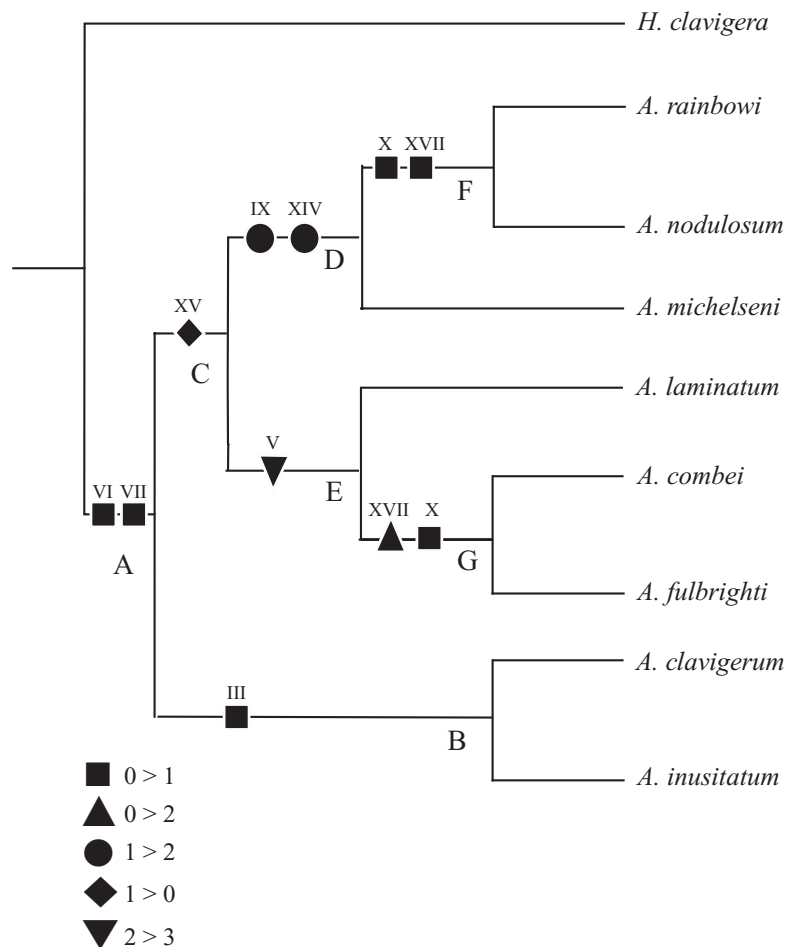


Fig. 57. Phylogenetic relationships of *Australiosoma* species. Only unambiguous, non-homoplastic character state changes are mapped on the cladogram. Roman numerals refer to supporting characters.

solenomere. In *Hoplatria* the femoral process is shorter than the solenomere. Steps, 2; *CI*, 1.000; *RI*, 0.000.

Character 13. *Length of tibiotarsus*. 0, long; 1, short. In *Hoplatria*, the tibiotarsus is long. Steps, 3; *CI*, 0.333; *RI*, 0.000.

Character 14. *Tibiotarsus shape*. 0, expanded distally; 1, expanded at midpoint; 2, uniform width. The tibiotarsus is expanded distally in *Hoplatria*. Steps, 2; *CI*, 1.000; *RI*, 1.000.

Character 15. *Shape of tibiotarsus apex*. 0, broad; 1, tapering. The apex of the tibiotarsus is broad in *Hoplatria*. Steps, 2; *CI*, 0.500; *RI*, 0.667.

Character 16. *Tibiotarsus apex*. 0, serrate; 1, single lobe; 2, multilobed. *Hoplatria* possesses a serrated tibiotarsus apex. Steps, 4; *CI*, 0.500; *RI*, 0.000.

Character 17. *Bifurcation (relative position of femoral process and solenomere)*. 0, close together; 1, diverging; 2, widely separated. In *Hoplatria* the branches are positioned closely together. Steps, 2; *CI*, 1.000; *RI*, 1.000.

Character 18. *Position of tibiotarsus branch base*. 0, equal with split in femoral process and solenomere; 1, lower than split in femoral process and solenomere. In *Hoplatria*, the tibiotarsus base is located at the same level as the split between the femoral process and the solenomere. Steps, 1; *CI*, 1.000; *RI*, 0.000.

Character 19. *Length of femorite*. 0, medium; 1, short; 2, long. The femorite is of medium length in *Hoplatria*. Steps, 2; *CI*, 1.000; *RI*, 0.000.

Discussion

We assessed primary homology-hypotheses through the standard homology criteria (Remane 1952). Comparative morphology within the class Diplopoda is plagued by gaps, as pointed out earlier. In particular, homology assessments within the male gonopod are seldom discussed within the class at all (Hoffman 1990: 40). Thus, the putative homology of the femoral process, the tibiotarsus and the preapical process may require reinvestigation among a more diverse selection of taxa within the family Paradoxosomatidae. It should be noted that the outgroup choice (*Hoplatria*) is based on a suggestion in previous work (Jeekel 1982) and not on any phylogenetic hypotheses for the large family Paradoxosomatidae.

The PAUP analysis resulted in a single most parsimonious tree (Fig. 57) with 47 steps (*CI*, 0.681 (excluding uninformative characters *CI*, 0.615); *RI*, 0.464) with a decay index of 1 for all clades. Six characters were parsimony uninformative (due to autapomorphies at various levels). The internal nodes are supported by one or two characters or character state changes, as indicated in Fig. 57.

Clade A, the ingroup *Australiosoma*, is unambiguously supported by six characters: character 6 (state 1) is non-

homoplastic and describes the trajectory of the sperm canal (with a loop in the preapical process); character 7 (state 1) is also non-homoplastic and denotes the presence of a preapical process; character 8, the preapical process length, supports the ingroup with a state change (2 to 1) in three terminal taxa (*A. michelseni*, *A. combei* and *A. inusitatum*). Character 12 exhibits a state change (1 to 2) in one terminal (*A. nodulosum*). The ingroup possesses a solenomere and femoral process of equal length with the exception of *A. nodulosum* where the femoral process is longer than the solenomere. Character 16, describing the apex of the tibiotarsus as serrate, a single lobe, or multilobed, supports the ingroup with a state change (1 to 2) in three terminals (*A. nodulosum*, *A. combei* and *A. inusitatum*). Finally, the ingroup is further supported by character 19, the length of the femorite, with a single state change (1 to 2) observed in *A. inusitatum*. *Australiosoma inusitatum* possesses a long femorite relative to the ingroup femorite.

Clade B, suggesting the sister-group relationship of *A. clavigerum* and *A. inusitatum* is supported by character 3 (state change 0 to 1) and the presence of dorsal stripes. However, this character does occur elsewhere in the tree, notably in *A. rainbowi* and *A. fulbrighti*.

Clade C is supported by character 15 (tibiotarsus tip broad or tapering), with one reversal observed in *A. nodulosum* (state change 1 to 0).

Clade D ((*A. rainbowi*, *A. nodulosum*) *A. michelseni*), is supported by their shared position of the preapical process far away from the apex (character 9, state change from 1 to 2). Additional support is gained from character 14, the overall tibiotarsus shape (state change from 1 to 2).

Clade E ((*A. combei*, *A. fulbrighti*) *A. laminatum*), is supported by character 5 (state change 2 to 3) with a further modification in *A. fulbrighti* (state change 3 to 4). However, state 3 occurs elsewhere within the tree (*A. nodulosum*).

Clade F, suggesting a sister-group relationship between *A. rainbowi* and *A. nodulosum*, is supported by the shared overall shape of the femoral process and the bifurcation of the solenomere and femoral process (character 10, state change from 0 to 1; character 17, state change from 0 to 1).

Finally, clade G, indicating a possible sister-group relationship between *A. combei* and *A. fulbrighti* is supported by character 17, the widely separated bifurcation of the solenomere and the femoral process (state change from 0 to 2) and by character 10 (overall shape of the femoral process, state change 0 to 1).

Species-level cladistic analyses are uncommon in millipedes (see Enghoff 2001 for review). In the present study we have erected a data matrix employing mainly gonopod characters, because they are used extensively for species discrimination, whereas somatic characters remain less explored. The current analysis has to be regarded as one of the first attempts at character typification and character state delineation among closely related species in this group. As

demonstrated in the section on morphology, numerous character suites await examination, which may yield a significantly larger character base for phylogenetic analyses. Testing primary homology hypotheses through cladistic analyses can promote the investigation and development of both sexual and somatic character suites.

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References

- Attems, C. (1898). System der Polydesmiden. I. Theil. *Denkschriften der Königlich-Kaiserlichen Akademie der Wissenschaften zu Wien, Mathematisch-Naturwissenschaftliche Classe* **67**, 221–482.
- Attems, C. (1911). Myriopoda exkl. Scolopendridae. In 'Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise'. (Eds W. Michaelsen and R. Hartmeyer.) *1905*, **3**(6), 147–204.
- Attems, C. (1914). Die indoaustralischen Myriapoden. *Archiv für Naturgeschichte (Abt. A)* **80**(4), 1–398.
- Attems, C. (1929). Diplopoden des Belgischen Congo. I. Polydesmoidea. *Revue de Zoologie et de Botanique Africaines* **17**(3), 253–378.
- Attems, C. (1930). Myriapoda. In 'Handbuch der Zoologie'. (Eds W. Kükenthal and T. Krumbach) **4**(1), 1–402.
- Attems, C. (1931). Die Familie Leptodesmidae und andere Polydesmiden. *Zoologica. Stuttgart* **30**(3/4), 1–150.
- Attems, C. (1937). Polydesmoidea I. Fam. Strongylosomidae. *Das Tierreich* **68**, 1–300.
- Attems, C. (1940). Polydesmoidea III. Fam. Polydesmidae, Vanhoeffeniidae, Cryptodesmidae, Oniscodesmidae, Sphaerotrhopidae, Peridotodesmidae, Rhachidesmidae, Macellolophidae, Pandirodesmidae. *Das Tierreich* **70**, 1–576.
- Bond, J. E., and Sierwald, P. (2002). Cryptic speciation in the *Anadenobolus excisus* millipede species complex on the island of Jamaica. *Evolution* **56**(6), 1123–1135.
- Brölemann, H. W. (1913). The Myriapoda in the Australian Museum. Part ii. Diplopoda. *Records of the Australian Museum* **10**(6), 77–158. [author's name also spelled Broelemann and Brolemann]
- Brölemann, H. W. (1916). Essai de classification des Polydesmiens (Myriapodes). *Annales de la Société Entomologique de France* **84**, 523–608.
- Chamberlin, R. V. (1920). The Myriopoda of the Australian region. *Bulletin of the Museum of Comparative Zoology* **64**(1), 1–269.
- Eisenbeis, G., and Wichard, W. (1985). 'Atlas on the Biology of Soil Arthropods.' (Springer Verlag: Berlin)
- Enghoff, H. (1979). Taxonomic significance of the mandibles in the millipede order Julida, In 'Myriapod Biology'. (Eds M. Camatini.) pp 27–38. (Academic Press: London.)
- Enghoff, H. G. (2001). Millipede phylogeny: how much do we know and what is it good for? In 'Progress in Studies on Myriapoda and Onychophora'. (Eds J. Wytwer and S. Golovatch.) *Fragmenta Faunistica* **43** (Suppl.), 1–17.
- Golovatch, S. I. (1984). Some new or less known Paradoxosomatidae (Diplopoda: Polydesmida) from India. *Acta Zoologica Hungarica* **30**(3–4), 327–352.
- Golovatch, S. I. (1994). Diplopoda from the Nepal Himalayas. Further Paradoxosomatidae. *Senckenbergiana Biologica* **73**(1–2), 163–182.
- Golovatch, S. I., and Enghoff, H. (1994). Review of the dragon millipedes, genus *Desmoxytes* Chamberlin, 1923 (Diplopoda, Polydesmida, Paradoxosomatidae). *Steenstrupia* **20**(2), 45–71.
- Hennings, C. (1904). Das Tömösvarysche Organ der Myriapoden. *Zeitschrift für Wissenschaftliche Zoologie* **76**, 26–52.
- Hennings, C. (1906). Das Tömösvarysche Organ der Myriapoden II. *Zeitschrift für Wissenschaftliche Zoologie* **80**, 576–641.
- Hoffman, R. F. (1965). Systematic studies in the Oxydesmidae, an African family of polydesmoid Diplopoda (Myriapoda). *Annales du Musée Royal de l'Afrique Centrale, Tervuren {Sér. Svo. Zool.}* **143**, 1–94.
- Hoffman, R. L. (1979). An Australian polydesmoid millipede in San Francisco (Paradoxosomatidae). *Wasmann Journal of Biology* **37**(1–2), 55–58.
- Hoffman, R. L. (1982). Diplopoda. In 'Synopsis and Classification of Living Organisms'. (Ed S. P. Parker) pp. 689–724. (McGraw-Hill: New York.)
- Hoffman, R. L. (1980). 'Classification of the Diplopoda.' (Muséum d'Histoire Naturelle: Genève.)
- Hoffman, R. L. (1990). Myriapoda 4. Polydesmida: Oxydesmidae. *Das Tierreich* **107**. (Eds H. Wermuth and M. Fischer.) Part 1, pp. 20–43. (Walter de Gruyter: Berlin, New York.)
- Hoffman, R.L. (1999). Checklist of the Millipeds of North and Middle America. Special Publication Number 8. Virginia Museum of Natural History, Martinsville, VA, USA.
- Humbert, A., and deSaussure, H. (1869). Description de divers Myriapodes du Musée de Vienne. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* **19**, 669–692.
- Jeekel, C. A. W. (1964). Notes on the genus *Akamptogonus* Attems, with descriptions of a new genus and species from New Guinea (Diplopoda, Polydesmida). *Nova Guinea, Zoology* **29**, 105–113.
- Jeekel, C. A. W. (1965). A new genus and a new species of the family Paradoxosomatidae from Australia (Diplopoda, Polydesmida). *Entomologische Berichten* **25**, 7–14.
- Jeekel, C. A. W. (1968). 'On the Classification and Geographical Distribution of the Family Paradoxosomatidae (Diplopoda, Polydesmida).' (C.A.W. Jeekel: Amsterdam.)
- Jeekel, C. A. W. (1979). Notes on the classification of some little-known Australian paradoxosomatid genera (Diplopoda, Polydesmida). *Journal of Natural History* **13**, 649–658.
- Jeekel, C. A. W. (1980). A new genus and two new species of the family Paradoxosomatidae from Australia (Diplopoda, Polydesmida). *Bulletin of the Zoological Museum Amsterdam* **7**(1), 1–10.
- Jeekel, C. A. W. (1982). Four new or little-known Australiosomatini from New South Wales (Diplopoda, Polydesmida, Paradoxosomatidae). (Millipedes from Australia, 3). *Bijdragen to de Dierkunde* **52**(2), 137–154.
- Jeekel, C. A. W. (1984). Millipedes from Australia, 6: Australiosomatini from Victoria (Diplopoda: Polydesmida: Paradoxosomatidae). *Records of the Australian Museum* **36**(1), 19–44.

- Jeekel, C. A. W. (1985). Millipedes from Australia, 5: Australiosomatini from South Australia, with a note on the status of *Polydesmus innotatus* Karsch, and first record of a Mediterranean julid in Australia (Diplopoda: Polydesmida, Paradoxosomatidae and Julida, Julidae). *Records of the South Australian Museum. Adelaide* **19**, 19–37.
- Jeekel, C. A. W. (1987). Millipedes from Australia, 11: Australiosomatini from Queensland (Diplopoda, Polydesmida, Paradoxosomatidae). *Beaufortia* **37**(2), 11–41.
- Jeekel, C. A. W. (2000). Millipedes from Australia, 12: Notes on the Paradoxosomatidae of New South Wales, with a key to the genera, and descriptions of a new genus and a new species (Diplopoda, Polydesmida). *Myriapod Memoranda* **2**, 31–47.
- Jeekel, C. A. W. (2002). Millipedes from Australia, 14: A third contribution to South Australian Paradoxosomatidae (Diplopoda, Polydesmida). *Myriapod Memoranda* **5**, 60–77.
- Jeekel, C. A. W. (2003). Millipedes from Australia, 16: Further notes on Australiosomatinae from New South Wales with descriptions of a new genus and four new species (Diplopoda, Polydesmida, Paradoxosomatidae). *Myriapod Memoranda* **6**, 28–45.
- Köhler, H.-R., and Alberti, G. (1990). Morphology of the mandibles in the millipedes (Diplopoda, Arthropoda). *Zoologica Scripta* **19**(2), 195–202. doi:10.1111/j.1463-6409.1990.tb00255.x
- Maddison, D. R., and Maddison, W. P. (2001). 'McClade 4.' (Sinauer Associates, Inc.: Sunderland, Massachusetts, USA.)
- Mesibov, R. (2002). <http://ea.gov.au/biodiversity/abrs/online-resources/abif/fauna/afd/frames/groups.html>
- Mesibov, R. (2004). A new genus and four new species of millipedes from Tasmania, Australia (Diplopoda: Polydesmida: Dalodesmidae), with notes on male leg setae in some Tasmanian dalodesmids. *Zootaxa* **558**, 1–19.
- Remane, A. (1952). Die Grundlagen des natürlichen Systems der vergleichenden Anatomie und der Phylogenetik. (Geest und Portig K.G.: Leipzig, Germany.)
- Schubart, O. (1944). Os Diplopodos de Pirassununga. *Acta Zoologica Lilloana* **2**, 321–440.
- Shear, W. A. (1992). A new genus and two new species of millipedes from the Cape Range, Western Australia (Diplopoda, Polydesmida, Paradoxosomatidae). *Records of the Western Australian Museum* **15**(4), 777–784.
- Shelley, R. M. (2003). A revised, annotaed, family-level classification of the Diplopoda. *Arthropoda Selecta* **11**(3), 187–207.
- Sierwald, P., and Reft, A. J. (2004). The millipede collections of the world. *Fieldiana, Zoology* (N.S.) **103** (1532), 100 pp.
- Sierwald, P., Shear, W. A., Shelley, R. M., and Bond, J. E. (2003). Millipede phylogeny revisited in the light of the enigmatic order Siphoniulida. *Journal of Zoological Systematics and Evolutionary Research* **41**, 87–99. doi:10.1046/j.1439-0469.2003.00202.x
- Silvestri, F. (1898). Note sui Chilopodi e Diplopodi conservati nel Museo Zoologico di Firenze. I. Alcuni nuovi Diplopodi de Queensland (Cairns). *Bollettino della Società Entomologica Italiana. Genova* **29**, 225–232.
- Swofford, D. (2002). 'PAUP v4.0b10: Phylogenetic Analysis using Parsimony.' (Sinauer Associates, Inc.: Sunderland, Massachusetts, USA.)
- Verhoeff, K. W. (1924). Myriapoda: Diplopoda. Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia, 1910–1913. *Arkiv för Zoologi* **16**(5), 1–142.
- Verhoeff, K. W. (1928a). Klasse Diplopoda I. In 'H. G. Bronn's Klassen und Ordnungen des Tier-Reichs'. **5.2.I**, 1–1071. (Akademische Verlagsgesellschaft: Leipzig.)
- Verhoeff, K. W. (1928b). On Diplopoda in the Australian Museum, Sydney. *Records of the Australian Museum* **16**(2), 79–115.
- Verhoeff, K. W. (1932). Klasse Diplopoda II. In 'H. G. Bronn's Klassen und Ordnungen des Tier-Reichs'. **5.2.II**, 1073–2084. (Akademische Verlagsgesellschaft: Leipzig.)
- Verhoeff, K. W. (1936). Zur Kenntnis ostasiatischer Strongylosomiden und Fontariiden. 149. Diplopodenaufsatz. *Zoologischer Anzeiger* **115**, 297–311.
- Verhoeff, K. W. (1937). Ueber einige neue Diplopoden aus Australien. *Records of the Australian Museum* **20**(2), 133–149.
- Verhoeff, K.W. (1941). Zur Kenntnis australischer Strongylosomiden und einiger anderen Diplopoden. *Lunds Universitets Årsskrift {N. F., Afdeling 2}* **36**(17), 1–25.

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