Phylogeny and biogeography of the mite harvestmen (Arachnida : Opiliones : Cyphophthalmi) of Queensland, Australia, with a description of six new species from the rainforests of the Wet Tropics

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Abstract. The Wet Tropics of Queensland, Australia, represent the largest remaining fragment of vast rainforests that once covered the entire continent. Over the past few decades the Wet Tropics bioregion has received much attention from biologists interested in the effect of climate change on diversity and distribution of rainforest animals. However, most such studies have focused on vertebrates, and despite considerable interest in the biota of the area, the diversity of many of Wet Tropics invertebrate taxa remains poorly known. Here we describe six new species of mite harvestman from the area, identified using a combination of morphological and molecular data. Our study represents the first detailed phylogenetic study of the genus *Austropurcellia*, and provides insight into the historical biogeography of these dispersal-limited arachnids.

Introduction

Mite harvestman systematics

Cyphophthalmi are tiny, cryptic arachnids, commonly known as mite harvestmen, that comprise a globally distributed suborder of Opiliones (harvestmen or daddy-long-legs). They are generally 2–5 mm long, and so morphologically conserved that species-level identifications often require scanning electron microscopy. These animals spend their entire life cycle in leaf-litter habitats (with the exception of a handful of cave-dwelling species), and are restricted to temperate and tropical forests (Giribet *et al*. 2012).

The first mite harvestman discovered in Australia, *Austropurcellia woodwardi* (Forster, 1955), was described as a member of the New Zealand genus *Rakaia* Hirst, 1925 from the Wet Tropics World Heritage Area rainforests of northern Queensland by the prolific New Zealand arachnologist Ray Forster in 1955. *Austropurcellia arcticosa* (Cantrell, 1980), was described (also in *Rakaia*) more than two decades later, and Juberthie subsequently added *Austropurcellia daviesae* (Juberthie, 1989) and *Austropurcellia forsteri* (Juberthie, 2000) from the same region. Beyond the Wet Tropics, *Austropurcellia capricornia* (Davies, 1977) from central Queensland was described in the likewise New Zealand genus *Neopurcellia* Forster, 1948 by Davies in 1977. Juberthie (1988) later described the monotypic genus *Austropurcellia* Juberthie, 1988 from Queensland, with *Austropurcellia scoparia* Juberthie, 1988 as the type species. Phylogenetic analyses of molecular data have demonstrated that the Queensland species are more closely

related to each other than they are to New Zealand taxa (Boyer and Giribet 2007; Giribet *et al*. 2012). Because the type species of *Neopurcellia* and *Rakaia* occur in New Zealand, all Queensland species from these genera have been transferred to *Austropurcellia* (Boyer and Giribet 2007). Subsequently, Boyer and Reuter (2012) described four additional species from the Wet Tropics and Popkin-Hall and Boyer (2014) described three additional species from south-east Queensland, all in *Austropurcellia;* these discoveries have broadened the range of *Austropurcellia* to include almost the entire east coast of Queensland (Fig. 1). According to our current knowledge, the southernmost limit of *Austropurcellia*'s distribution coincides with an area known as the MacPherson–Maclay Overlap (Burbidge 1960) that marks the north–south transition between the biotas of the Australian temperate zone and tropical zone.

Beyond Queensland, a second Australian genus of Cyphophthalmi, *Karripurcellia* Giribet, 2003, occurs in Western Australia (Fig. 1). Previous phylogenetic analyses indicate that *Austropurcellia* and *Karripurcellia* are each monophyletic and unequivocally members of the Pettalidae Shear, 1980, a Gondwanan lineage that also includes genera in New Zealand, Sri Lanka, South Africa, Madagascar, and Chile. However, relationships among pettalid genera are currently unresolved, and thus the relationship between *Austropurcellia* and *Karripurcellia* has not been established (Boyer and Giribet 2007; de Bivort *et al*. 2010; Giribet *et al*. 2012). It should be noted that Karaman (2012) proposed the establishment of a new Western Australian genus, *Milipurcellia*, with one species
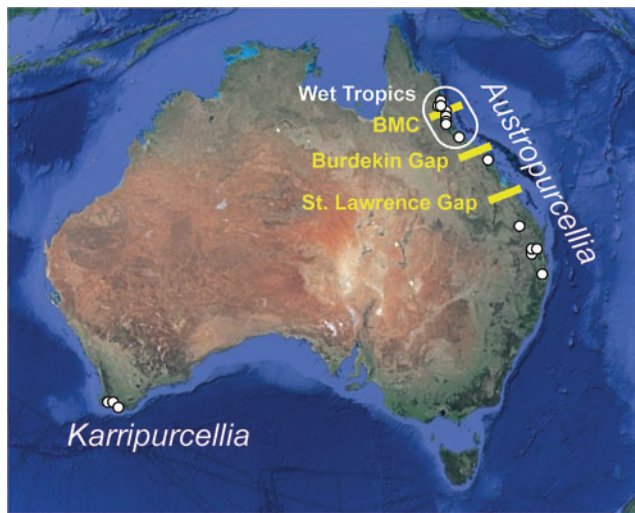
Fig. 1. Distribution of the two Australian mite harvestmen genera, *Austropurcellia* and *Karripurcellia*. The Burdekin and St Lawrence Gaps are dry areas that represent north–south faunal breaks in many taxa. The white box indicates the general location of the Wet Tropics, within which the Black Mountain Corridor (BMC) is an area from which rainforest largely disappeared during the Last Glacial Maximum.

(*Karripurcellia sierwaldi* Giribet, 2003) transferred out of *Karripurcellia*. The argument for the establishment of the genus relies on allegations of misinterpretations of anatomy by previous authors (e.g. Giribet 2003), and dismisses phylogenetic analyses that have recovered a monophyletic *Karripurcellia* (e.g. de Bivort *et al.* 2010). However, due to the absence of a compelling argument for a generic-level morphological distinction of *sierwaldi* from other *Karripurcellia* species, or a rigorous phylogenetic analysis supporting splitting of *Karripurcellia*, we do not consider *Milipurcellia* to be a valid genus.

Mite harvestmen have notoriously limited dispersal abilities, with most species known from only a handful of localities, each within a 50-km radius, even in areas that have been sampled on a very fine geographic scale (Boyer and Giribet 2009). Furthermore, no Cyphophthalmi are known from any Darwinian islands (*sensu* Gillespie and Roderick 2002), such as islands formed by volcanoes in the mid-ocean. This suggests that, unlike their vagile spider relatives, these arachnids are unable to disperse across oceanic barriers (Giribet 2000) – though, it should be noted that there are possible exceptions within the South-east Asian Stylocellidae (Clouse and Giribet 2007) and the New Caledonian Troglosironidae (Sharma and Giribet 2009). Despite their limited dispersal abilities, these animals are found in temperate and tropical forests worldwide. This biogeographical paradox can be explained by the great age of the group; their putative sister group is known from the Devonian (Dunlop *et al.* 2003; see also Sharma and Giribet 2014) and recent molecular analyses have dated the age of diversification of the suborder at ~330 million years ago (Giribet *et al.* 2012; Garwood *et al.* 2014; Sharma and Giribet 2014) (though certain methods place the age at 224 million years ago: Sharma and Giribet 2014). Cyphophthalmi also have excellent persistence; that is, they require only very small patches of suitable habitat and

therefore can withstand severe habitat contraction. The great age and high persistence of this group make them ideal for studies of historical biogeography (e.g. Boyer *et al.* 2005, 2007*b*; Clouse and Giribet 2007, 2010; Boyer and Giribet 2009; Giribet *et al.* 2012).

Wet Tropics biogeography

Australia's Wet Tropics World Heritage Area in north-east Queensland (Fig. 1) has emerged as a model system for understanding the processes that shape rainforest animal diversity (e.g. Hugall *et al.* 2002; Bell *et al.* 2004, 2007, 2012; Moussalli *et al.* 2009). Comprising 8940 km^2 of tropical rainforests stretching from Townsville to Cooktown along Queensland's coast, most of this land is protected in National Parks or other reserves. Although it represents only 0.1% of the vast land area of Australia, it is home to a huge diversity of the continent's animal life, including one-third of all Australian mammals and at least 75 regionally endemic vertebrates (Nix 1991).

The Wet Tropics represent the largest remnant of the Gondwana-derived rainforests that once dominated the entire continent of Australia, but declined throughout the Tertiary (Nix 1991; Adam 1992; Harrison and Dodson 1993; Truswell 1993). Today the Wet Tropics comprise isolated 'islands' of montane rainforest surrounded by warmer or more xeric habitats. The history of the area during the Last Glacial Maximum (LGM) through the present has been well studied by researchers working within several different disciplines. Palynological data and palaeoclimate modelling concur that these forests underwent significant contractions and expansions throughout the Pleistocene; temperature and rainfall were greatly reduced at the LGM (LGM, 18 thousand years ago), followed by an Early Holocene cool-wet phase (8–7.5 thousand years ago) and a warm-wet phase (5–3.5 thousand years ago), before the establishment of the current climate (Kershaw and Nix 1988; Hugall *et al.* 2002; Moritz *et al.* 2009). Researchers have demonstrated that rainforest has persisted throughout these climatic changes in some areas of the Wet Tropics, while in other areas it is been less stable (Graham *et al.* 2006, VanDerWal *et al.* 2009).

In vertebrate groups, major genetic divergences within the Wet Tropics coincide geographically with a feature known as the Black Mountain Corridor (BMC) (Fig. 1), which separates the northernmost Wet Tropics from more southern forests. During the LGM, the BMC was a large dry area separating the Carbine Uplands to the north from the Atherton Tablelands to the south (Winter 1984; Nix 1991; Hugall *et al.* 2002; Graham *et al.* 2006). Historically, Pleistocene climate change was invoked as a likely driver of diversification in rainforest biota (Haffer 1969); however, dating of phylogeographic breaks has demonstrated that divergences across the BMC in many of these groups predate the Pleistocene (Moritz 2005; Moritz *et al.* 2009; Bell *et al.* 2012). This finding is consistent with the hypothesis that forest habitats were subdivided not only during the LGM but throughout the Quaternary and perhaps much earlier (Joseph and Moritz 1993; Kershaw 1994; Joseph *et al.* 1995; Hugall *et al.* 2002). The influence of the history of rainforest distribution on present-day diversity within the Wet Tropics continues to be an area of active research (e.g. Moussalli *et al.* 2009; Graham *et al.* 2010; Bell *et al.* 2012).

Table 1. List of specimens used in phylogenetic analysis, with voucher specimen and GenBank information

Species	Specimen voucher	18S rRNA	28S rRNA	COI	12S	Coordinates	Locality name	Collectors
Austropurcellia absens, sp. nov.	MCZ IZ 132316	KJ767457	KJ796907	KJ796939	KJ767391	18.202°S, 145.885°E	Kirrama Ranges	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia absens, sp. nov.	MCZ IZ 132316	KJ767458	KJ796908	KJ796940	KJ767392	18.202°S, 145.885°E	Kirrama Ranges	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia acuta	MCZ IZ 134701	KJ767487	KJ796938	KJ796941	KJ767393	26.557°S, 152.866°E	Mapleton Forest Reserve	M. G. Rix, D. Harms
Austropurcellia alata	MCZ IZ 132336	KJ767459	KJ796909	KJ797009		17.685°S, 145.523°E	Charmillan Creek	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia alata	MCZ IZ 132336			KJ797010		17.685°S, 145.523°E	Charmillan Creek	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia arcticosa	MCZ IZ 132325	KJ767460	KJ796910	KJ796942	KJ767394	16.162°S, 145.417°E	Tributary to Cooper Creek	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132325			KJ796943	KJ767395	16.162°S, 145.417°E	Tributary to Cooper Creek	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132326	KJ767461	KJ796911	KJ796944	KJ767396	16.139°S, 145.449°E	Marrja Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132326			KJ796945	KJ767397	16.139°S, 145.449°E	Marrja Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132327	KJ767462	KJ796912	KJ796946	KJ767398	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132327	KJ767463	KJ796913	KJ796947	KJ767399	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132327	KJ767464	KJ796914	KJ796948	KJ767400	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132,327				KJ767401	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132,327				KJ767402	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132,327				KJ767403	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132,327				KJ767404	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132,327				KJ767405	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	MCZ IZ 132,327			KJ796949	KJ767406	16.139°S, 145.462°E	Dubuji Boardwalk	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia arcticosa	WAM T104106	KJ767465	KJ796915	KJ796950	KJ767407	16.085°S, 145.433°E	Cape Tribulation	F. Šťáhlavský
Austropurcellia arcticosa	WAM T104107			KJ796951	KJ767408	16.085°S, 145.433°E	Cape Tribulation	F. Šťáhlavský
Austropurcellia arcticosa	WAM T104108			KJ796952	KJ767409	16.085°S, 145.433°E	Cape Tribulation	F. Šťáhlavský
Austropurcellia cadens, sp. nov.	CAS ENT 9035046	KJ767466	KJ796916	KJ796953	KJ767410	17.378°S, 145.786°E	Mt Bartle Frere	H. Wood
Austropurcellia cadens, sp. nov.	CAS ENT 9035046			KJ796954	KJ767411	17.378°S, 145.786°E	Mt Bartle Frere	H. Wood
Austropurcellia cadens, sp. nov.	MCZ IZ 132319	KJ767467	KJ796917	KJ796955	KJ767412	17.573°S, 145.688°E	Malanda Falls	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia clousei, sp. nov.	MCZ IZ 132319	KJ767468	KJ796918	KJ796956	KJ767413	17.573°S, 145.688°E	Malanda Falls	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia clousei, sp. nov.	MCZ IZ 132339			KJ796957	KJ767414	19.011°S, 146.205°E	Paluma Village	R. M. Clouse, P. P. Sharma
Austropurcellia culminis	MCZ IZ 132339	KJ767469	KJ796919	KJ796958	KJ767415	19.011°S, 146.205°E	Paluma Village	R. M. Clouse, P. P. Sharma
Austropurcellia daviesae	MCZ IZ 132322	KJ767470	KJ796920	KJ796959	KJ767416	17.264°S, 145.853°E	Bellenden Ker Summit	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia daviesae	MCZ IZ 132323			KJ796960	KJ767417	17.342°S, 145.872°E	The Boulders	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia daviesae	MCZ IZ 132341	KJ767471	KJ796921	KJ796961	KJ767418	17.292°S, 145.962°E	Russell River	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132341			KJ796962	KJ767419	17.292°S, 145.962°E	Russell River	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132342	KJ767472	KJ796922	KJ796963	KJ767420	17.292°S, 145.962°E	Russell River	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132342			KJ796964	KJ767421	17.292°S, 145.962°E	Russell River	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132342			KJ796965		17.292°S, 145.962°E	Russell River	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132342			KJ796966		17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132343	KJ767473	KJ796923	KJ796967	KJ767422	17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132343			KJ796968		17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132343			KJ796969		17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132343			KJ796970	KJ767423	17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132343			KJ796971	KJ767424	17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia daviesae	MCZ IZ 132343			KJ796972	KJ767425	17.478°S, 146.073°E	Ella Bay	R. Clouse, P. Sharma
Austropurcellia despectata	MCZ IZ 132324	KJ767474	KJ796924	KJ796973	KJ767426	17.597°S, 145.756°E	Nandroya Trailhead	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia despectata	MCZ IZ 132324			KJ796974	KJ767427	17.597°S, 145.756°E	Nandroya Trailhead	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia giribeti, sp. nov.	MCZ IZ 134696	DQ517984	DQ518023	DQ518111		16.166°S, 145.416°E	Cooper Creek	C. D'Haese, G. Giribet
Austropurcellia giribeti, sp. nov.	MCZ IZ 132337	KJ767475	KJ796925	KJ796975	KJ767428	16.255°S, 145.362°E	Daintree Village	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia giribeti, sp. nov.	MCZ IZ 132344	KJ767476	KJ796926		KJ767429	16.255°S, 145.362°E	Daintree Village	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner

Table 1.   (*continued*)

Species	Specimen voucher	18S rRNA	28S rRNA	COI	12S	Coordinates	Locality name	Collectors
Austropurcellia scoparia	MCZ IZ 134700	DQ517982	DQ518021	DQ518108		16.595°S, 145.279°E	Mount Lewis State Forest	C. D'Haese, G. Giribet
Austropurcellia scoparia	MCZ IZ 132329			KJ796981	KJ767435	16.593°S, 145.275°E	Brooklyn Sanctuary	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia scoparia	MCZ IZ 132329			KJ796982	KJ767436	16.593°S, 145.275°E	Brooklyn Sanctuary	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia scoparia	MCZ IZ 132338			KJ796983	KJ767437	16.605°S, 145.436°E	Bump Track	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia sharmai, sp. nov.	MCZ IZ 134698	DQ517983	DQ518022	DQ518110		16.062°S, 145.462°E	Emmagen Creek	C. D'Haese, G. Giribet
Austropurcellia sharmai, sp. nov.	MCZ IZ 132317	KJ767477	KJ796927	KJ796976	KJ767430	16.062°S, 145.462°E	Emmagen Creek	R. Clouse, P. Sharma
Austropurcellia sharmai, sp. nov.	MCZ IZ 132317	KJ767478	KJ796928	KJ796977	KJ767431	16.062°S, 145.462°E	Emmagen Creek	R. Clouse, P. Sharma
Austropurcellia sharmai, sp. nov.	MCZ IZ 132317	KJ767479	KJ796929	KJ796978	KJ767432	16.062°S, 145.462°E	Emmagen Creek	R. Clouse, P. Sharma
Austropurcellia sharmai, sp. nov.	MCZ IZ 132328			KJ796979	KJ767433	16.239°S, 145.362°E	Old Forest Creek Road	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia sharmai, sp. nov.	MCZ IZ 132328			KJ796980	KJ767434	16.239°S, 145.362°E	Old Forest Creek Road	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia tholei, sp. nov.	MCZ IZ 134697	DQ517985	DQ518024	DQ518112		17.246°S, 145.642°E	Lake Barrine	C. D'Haese, G. Giribet
Austropurcellia tholei, sp. nov.	MCZ IZ 132330	KJ767480	KJ796930	KJ796984	KJ767437	17.177°S, 145.660°E	Cathedral Fig Tree	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132330			KJ796985	KJ767439	17.177°S, 145.660°E	Cathedral Fig Tree	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132330			KJ796986		17.177°S, 145.660°E	Cathedral Fig Tree	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 134699	KJ767481	KJ796931	KJ796987	KJ767440	17.315°S, 145.702°E	Rose Gums Wilderness Retreat	C. Griswold, D. Silva
Austropurcellia tholei, sp. nov.	MCZ IZ 134699			KJ796988		17.315°S, 145.702°E	Rose Gums Wilderness Retreat	C. Griswold, D. Silva
Austropurcellia tholei, sp. nov.	MCZ IZ 134699			KJ796989		17.315°S, 145.702°E	Rose Gums Wilderness Retreat	C. Griswold, D. Silva
Austropurcellia tholei, sp. nov.	MCZ IZ 132331	KJ767482	KJ796932	KJ796990	KJ767440	17.433°S, 145.859°E	Josephine Falls	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132331			KJ796991		17.433°S, 145.859°E	Josephine Falls	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132331			KJ796992		17.433°S, 145.859°E	Josephine Falls	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132331			KJ796993		17.433°S, 145.859°E	Josephine Falls	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132331			KJ796994	KJ767442	17.433°S, 145.859°E	Josephine Falls	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132332			KJ796995	KJ767443	17.342°S, 145.872°E	The Boulders	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132332			KJ796996	KJ767444	17.342°S, 145.872°E	The Boulders	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132332			KJ796997	KJ767445	17.286°S, 145.574°E	Curtain Fig Tree	C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia tholei, sp. nov.	MCZ IZ 132333			KJ796998	KJ767446	16.578°S, 145.312°E	Mt Lewis Rd	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia vicina	MCZ IZ 132334	KJ767483	KJ796933	KJ796999	KJ767447	16.962°S, 145.679°E	Crystal Cascades Track	C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall
Austropurcellia vicina	MCZ IZ 132318	KJ767484	KJ796934	KJ797000	KJ767449	16.882°S, 145.634°E	Speewah Trail	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia vicina	MCZ IZ 132320			KJ797001	KJ767450	16.882°S, 145.634°E	Speewah Trail	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia vicina	MCZ IZ 132320			KJ797002	KJ767451	16.469°S, 145.327°E	Mossman Circuit Track	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia vicina	MCZ IZ 132321			KJ797003	KJ767452	16.468°S, 145.327°E	Mossman Circuit Track	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia vicina	MCZ IZ 132321			KJ797004	KJ767453	16.579°S, 145.313°E	Mt Lewis Rd	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia vicina	MCZ IZ 132335		KJ796935	KJ797005	KJ767454	16.579°S, 145.313°E	Mt Lewis Rd	C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner
Austropurcellia vicina	MCZ IZ 132335	KJ767485	KJ796936	KJ797006	KJ767455	16.964°S, 145.679°E	Crystal Cascades Track	R. M. Clouse, P. P. Sharma
Austropurcellia vicina	MCZ IZ 132340	KJ767486	KJ796937	KJ797007	KJ767456	16.964°S, 145.679°E	Crystal Cascades Track	R. M. Clouse, P. P. Sharma
Austropurcellia vicina	MCZ IZ 132340			KJ797008			Crystal Cascades Track	
Aoraki longitarsa	MCZ IZ 134656	EU673613	EU673652	DQ992313		43.595°S, 170.142°E	New Zealand	S. L. Boyer, G. E. Edgecombe, G. Giribet
Chileogovea oedipus	MCZ IZ 134709	DQ517969	EU673627	EU673661			Chile	J. A. Coddington, J. Zuzko-Miller
Chileogovea sp.	MCZ IZ 134715	DQ133722	DQ518011	DQ133746			Chile	T. Cekalovic
Karripurcellia harveyi	MCZ IZ 134746	DQ517981	DQ518020	DQ518107		13.057°S, 72.439°E	Western Australia	S. H. Aktipis, G. Giribet, M. K. Nishiguchi
Neopurcellia salmoni	MCZ IZ 133839	EU673612	DQ518037	DQ825638		43.469°S, 170.018°E	New Zealand	S. L. Boyer, C. D'Haese, G. E. Edgecombe, G. Giribet
Parapurcellia monticola		DQ517973	DQ518009	DQ518098			South Africa	
Parapurcellia silvicola	MCZ IZ 134742	DQ517972	DQ518008	EU673664		28.744°S, 31.138°E	South Africa	G. Giribet, L. Prendini
Pettalus thwaitesi	MCZ IZ 78875	DQ517975	DQ518018	DQ518101		7.265°S, 80.594°E	Sri Lanka	S. L. Boyer, G. Giribet, I. Karunarathna, P. P. Sharma
Pettalus sp.	MCZ IZ 132353	DQ517976	DQ518017	DQ518102		6.925°S, 80.819° E	Sri Lanka	S. L. Boyer, G. Giribet, I. Karunarathna, P. P. Sharma
Purcellia illustrans	MCZ IZ 134752	DQ517971	DQ518010	DQ518099		33.983°S, 18.425°E	South Africa	G. Giribet, L. Prendini
Rakaia dorothea	MCZ IZ 134577	DQ517990	DQ518033	DQ992331		41.282°S, 174.910°E	New Zealand	S. L. Boyer, C. D'Haese, G. Giribet
Rakaia florensis	MCZ IZ 134588	DQ517986	DQ518025	DQ518113		40.833°S, 172.969°E	New Zealand	S. L. Boyer, G. Giribet
Rakaia lindsayi	MCZ IZ 132598	DQ517995	DQ518027	DQ518118		46.893°S, 168.104°E	New Zealand	S. L. Boyer, C. D'Haese, G. Giribet
Rakaia sorenseni digitata	MCZ IZ 134571	DQ517989	DQ518035	DQ518123		46.582°S, 169.209°E	New Zealand	S. L. Boyer, C. D'Haese, G. Giribet

It is predicted that small, dispersal-limited taxa such as mite harvestmen should display phylogenetic and/or phylogeographic structure at a finer geographic scale than large, vagile animals (Moritz *et al.* 2001), and previous studies of Wet Tropics fauna support this hypothesis. Bell *et al.* (2007, 2004), working on the Wet Tropics endemic dung beetle genus *Temnoplectron*, demonstrated that barriers between species coincide geographically with phylogeographic breaks found in

vagile vertebrates. A landmark study by Hugall *et al.* (2002) investigated the phylogeographic relationships of the terrestrial gastropod *Gnarosophia bellendenkerensis* Brazier, 1875, which is endemic to the Wet Tropics rainforests. They found that although there was a major genetic break associated with the BMC, it was only one of several deep divisions within the species (Hugall *et al.* 2002).

In recent years arachnologists have begun to map the diversity of short-range endemics (Harvey 2002) in the Wet Tropics. Rix and Harvey (2012a), working on assassin spiders, and Edward (2011), working on goblin spiders, have discovered that these rainforests are home to numerous endemic species, many of which are restricted to particular subregions or single mountaintops within the Wet Tropics. Previous work on *Austropurcellia* in our laboratory (Boyer and Reuter 2012) suggested that similarly high diversity would be found in mite harvestmen. Here, we present six new species of *Austropurcellia* endemic to the Wet Tropics. Our results highlight both the outstanding arachnid diversity of northern Queensland and the importance of integrating molecular and morphological data to the discovery of cryptic species.

Methods

Specimen collection and microscopy

Specimens collected by the authors were obtained by leaf-litter sifting and sorting *in situ* in May–June 2011 and May–June 2012.
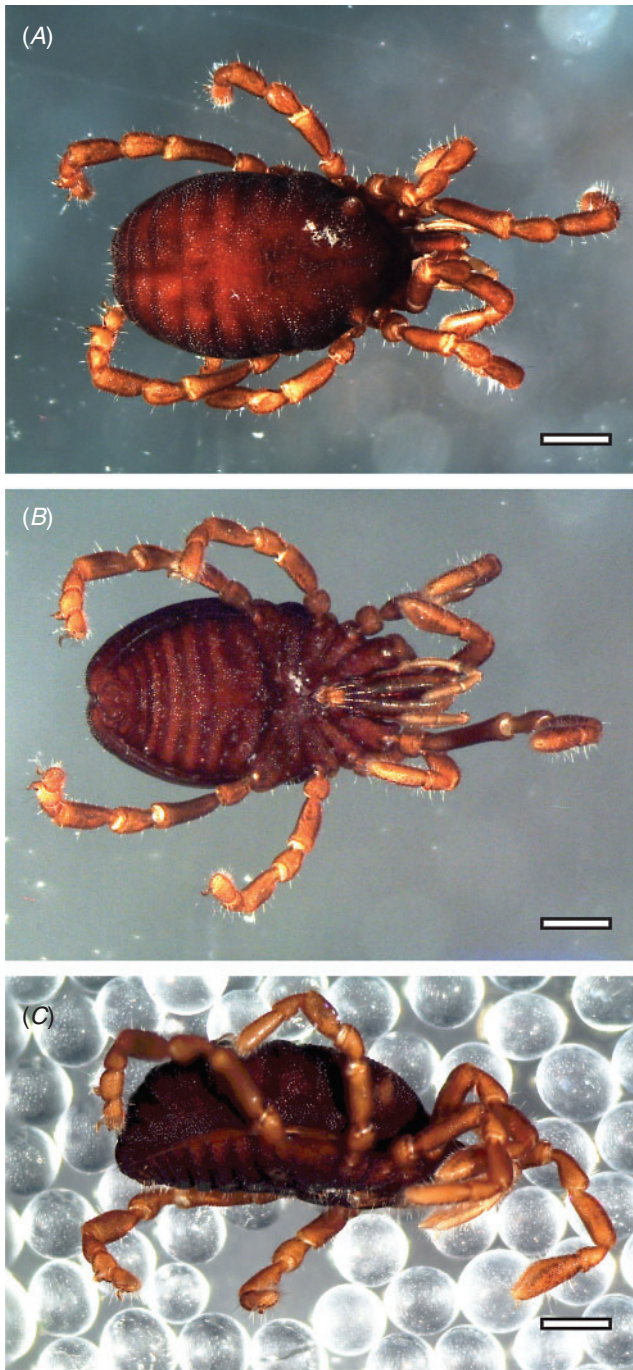
Fig. 2. *Austropurcellia absens*, sp. nov., holotype male, QM. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.
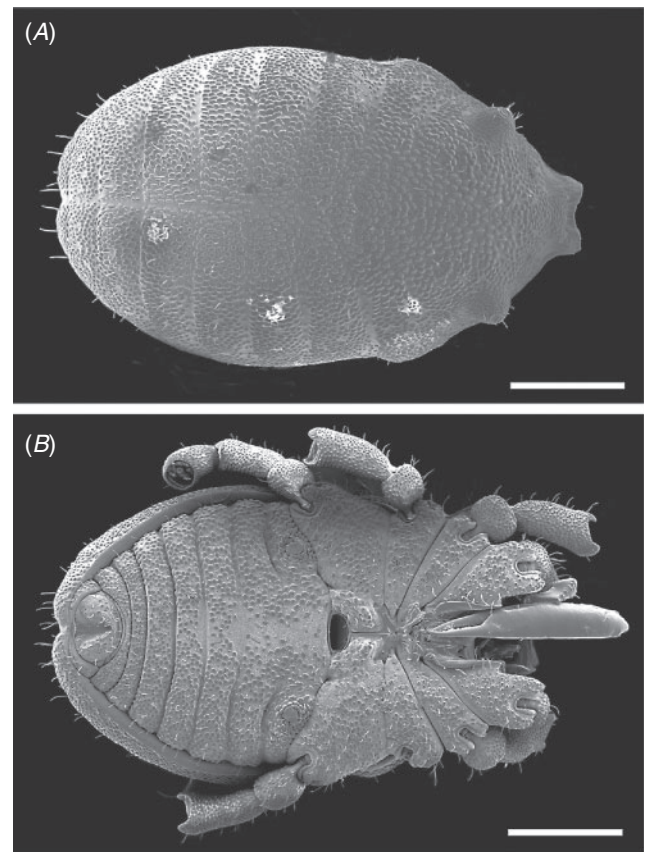
Fig. 3. *Austropurcellia absens*, sp. nov., paratype male, MCZ IZ 132316. (*A*) Dorsal view; (*B*) ventral view. Scale bars: 0.5 mm.
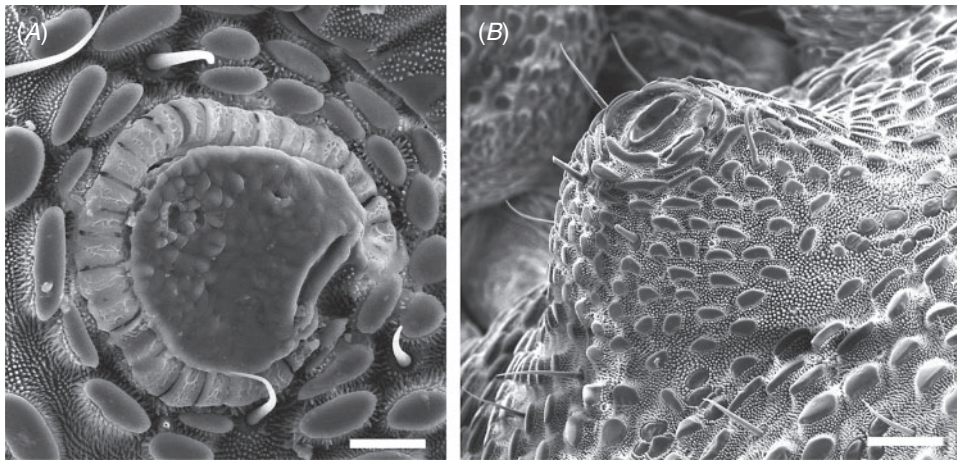
Fig. 4. *Austropurcellia absens*, sp. nov., paratype male, MCZ IZ 132316. (*A*) Spiracle, scale bar: 20 µm; (*B*) ozophore, scale bar: 50 µm.

Once collected, specimens were preserved immediately in 95% ethanol. GPS points were taken at each collecting locality. Additional collections were received from Harvard University's Museum of Comparative Zoology (MCZ), the California Academy of Sciences (CAS), the Field Museum of Natural History (FMHD), the Queensland Museum (QM), and the Western Australian Museum (WAM) (Table 1).

Initial examination of specimens was performed in an Olympus SZX10 light microscope. For holotype specimens, images were taken at multiple focal lengths using Leica Acquire software (Leica Microsystems) and integrated using Helicon Focus (Helicon Soft Limited). For lateral images, specimens were placed on a bed of glass beads.

Each individual chosen for scanning electron microscopy (SEM) imaging was dissected under a light microscope so that its appendages (legs I–IV, chelicera, and palp) were mounted on one stub, and its body was mounted in ventral view on another. Stubs were coated with gold–palladium alloy in a Denton Vacuum Desk III sputter coater for 3–5 min before imaging. Coating took place in a vacuum of 50 mTorr in all cases, and at 35% sputter power in specimens coated in the Denton machine. Specimens were imaged using a JEOL JSM-6610LV SEM. All images were taken using secondary electron imaging at 3.0 or 5.0 kV, a working distance of 10–15 mm, and a spot size of 40 or 50. Images were compiled in plates and compared against each other, type specimens of described species (when available), and specimens depicted in published literature. Species diagnoses were made primarily using the morphology of the anal plate (including the scopula), the shape and degree of division of tarsus IV, and the morphology of the adenostyle. Measurements were made using the scalar tool in the JEOL software package.

Molecular data

All specimens were given provisional identification to species level using a dissecting microscope (Olympus SZX10). For each recent collection (i.e. less than 10 years old), individuals from each locality were chosen for DNA extraction and sequencing. DNA was extracted from the right third leg of each specimen using the Qiagen DNeasy® Tissue Kit. Males were preferentially
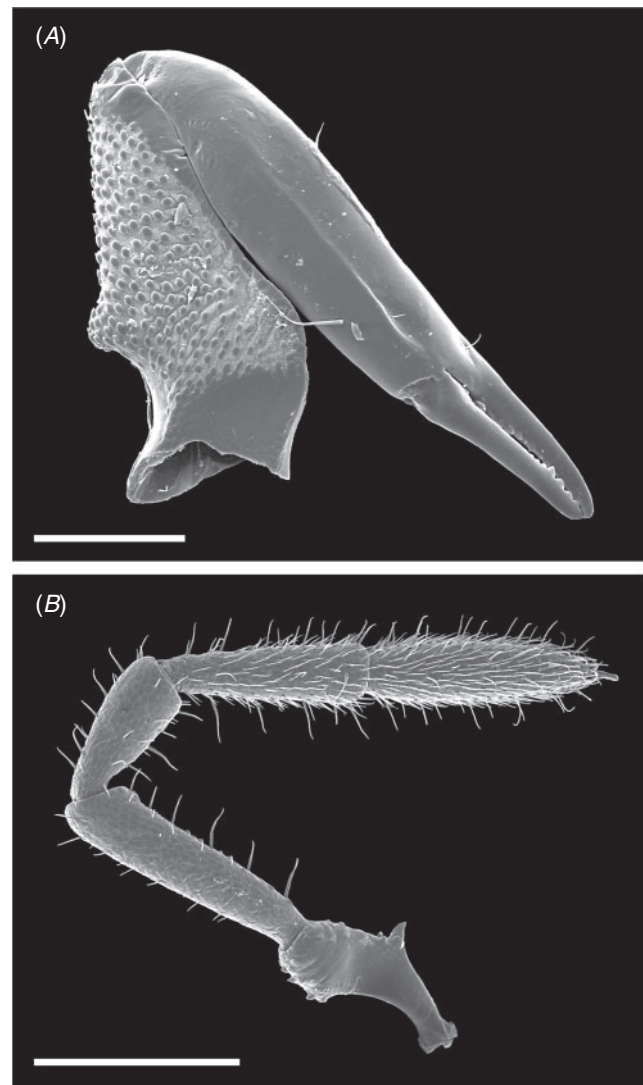
Fig. 5. *Austropurcellia absens*, sp. nov., paratype male, MCZ IZ 132316. (*A*) Chelicera; (*B*) palp. Scale bars: 200 µm.

chosen over females and juveniles, as only males are identifiable to the species level by morphology alone. By prioritising male specimens, we facilitated comparison of groups identified by morphology and groups identified by phylogenetic analysis of DNA sequence data.

We amplified and sequenced four different loci, including two more-conserved nuclear markers (18S and 28S rRNA) and two more-variable mitochondrial loci (cytochrome *c* oxidase subunit I (COI) and 12S rRNA). For each population of each species, all four loci were sequenced for one individual specimen; we sequenced many additional specimens for the more variable mitochondrial loci (Table 1). 18S and 28S rRNAs were amplified

using primers detailed by Boyer and Giribet (2007). COI was amplified using primer pair LCO1490-HCOoutout (Folmer *et al.* 1994, Schwendinger and Giribet 2005). 12S rRNA was amplified using primer pair 12Sai-degR (Kocher *et al.* 1989, R. Clouse, pers. comm.). PCR reactions (25 µL) were carried out with 6 µL DNA template, 2.5 µL of 2.5 µM primers, 2 µL of dNTPs, and 0.25 µL of PrimeStar Taq Polymerase per reaction. Amplifications were carried out in an ABI 2720 thermal cycler.

Gel electrophoresis (1.5% agarose) was used to visualise amplified DNA fragments. Successful PCR reactions were then cleaned up using Qiagen QIAquick PCR Purification Kit and sequencing was performed by either Functional Biosciences,
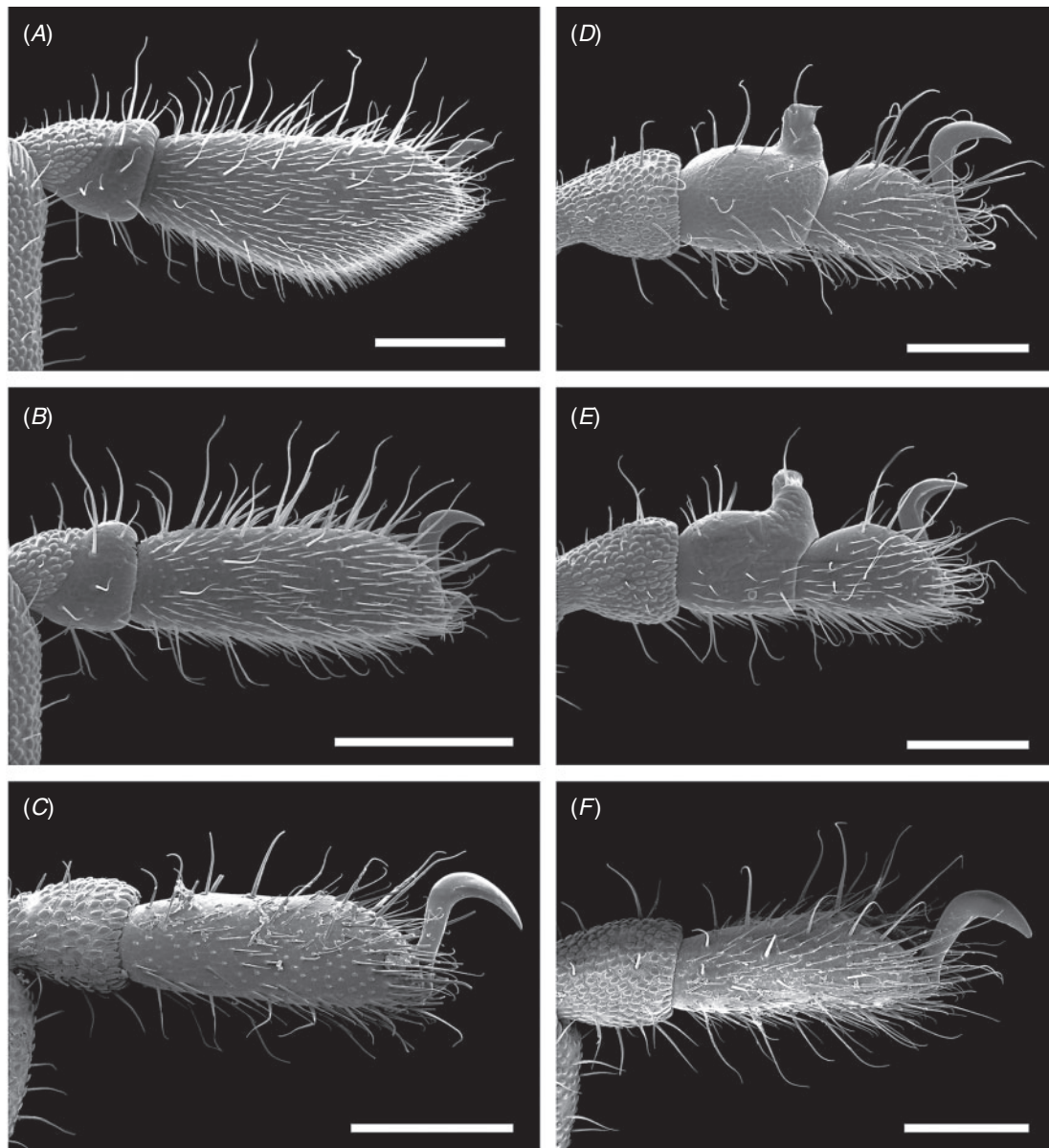
Fig. 6. *Austropurcellia absens*, sp. nov., paratype male and female, MCZ IZ 132316. (*A*) Tarsus and metatarsus I; (*B*) tarsus and metatarsus II; (*C*) tarsus and metatarsus III; (*D*) male tarsus and metatarsus IV, lateral view; (*E*) male tarsus and metatarsus IV, medial view; (*F*) female tarsus and metatarsus IV. Scale bars a, d, e, f: 200 µm; scale bars b, c: 250 µm.

Inc. (Madison, WI, USA) or the University of Minnesota DNA Sequencing Analysis Facility (St Paul, MN, USA). Forward and reverse chromatograms were assembled and edited in either CodonCode Aligner 2.0.6 (Codon Code Corporation, Dedham, MA) or Geneious 5.5 (Biomatters Ltd, Auckland, New Zealand). All new sequences have been deposited in GenBank under accession numbers KJ767391–KJ797010 (Table 1).
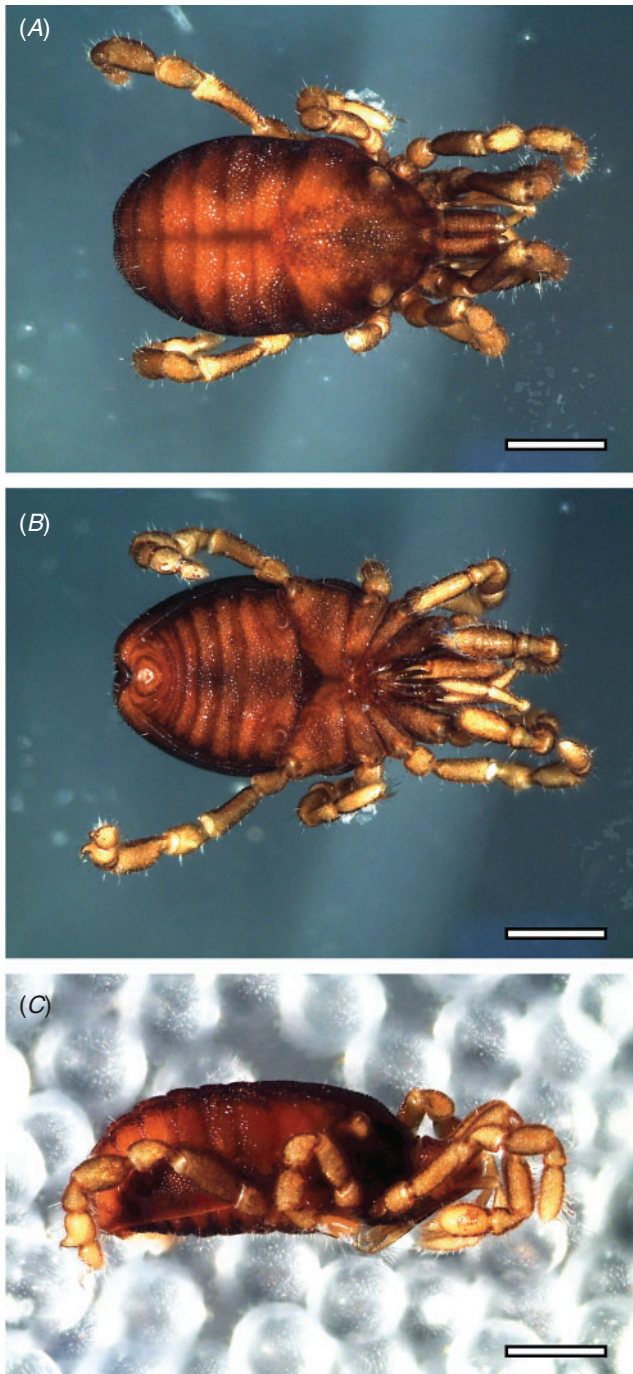
Fig. 7. *Austropurcellia cadens*, sp. nov., holotype male, QM. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.

Phylogenetic analysis

In addition to new data generated during the course of this study, we incorporated previously published sequences from *Austropurcellia* and other members of the family Pettalidae (Table 1). Our total dataset included 5192 positions. The nuclear datasets included only minor indels; areas that were non-trivial to align manually (fewer than 50 bp for each locus) were excluded from further analyses, resulting in a total of 1789 bp of data from 18S rRNA and 2106 bp of data from 28S rRNA. The COI dataset (835 bp) did not include any length variation. The 12S rRNA dataset included a large number of indels, and in this case, sequences were aligned using MUSCLE (Edgar 2004), and then treated with GBLOCKS (Castresana 2000) to cull positions of ambiguous homology, resulting in a total of 462 bp.

Data from each locus were analysed individually as well as in concatenated matrices – one containing all four loci as well as one containing the mitochondrial loci only (12S + COI). When possible, trees were rooted with *Parapurcellia* based on the results of Giribet *et al.* (2012); in the case of the 12S dataset, in which no cyphophthalmid outgroups to *Austropurcellia* have published data available, trees were rooted with individuals from *Austropurcellia acuta* Popkin-Hall & Boyer, 2014, + *A. clousei* sp. nov. based on the placement of that clade as sister to the remaining *Austropurcellia* species in analyses that included taxa outside of *Austropurcellia*.

Models of sequence evolution were selected in jModelTest (Posada 2008), using the Akaike Information Criterion. Model
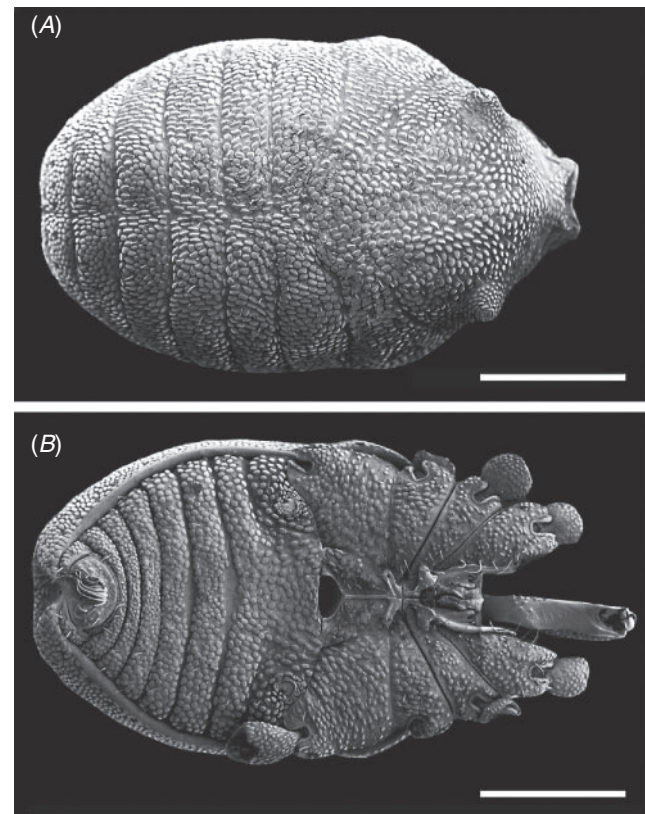
Fig. 8. *Austropurcellia cadens*, sp. nov., paratype male, CASENT 9035046. (*A*) Dorsal view, (*B*) ventral view. Scale bars: 0.5 mm.
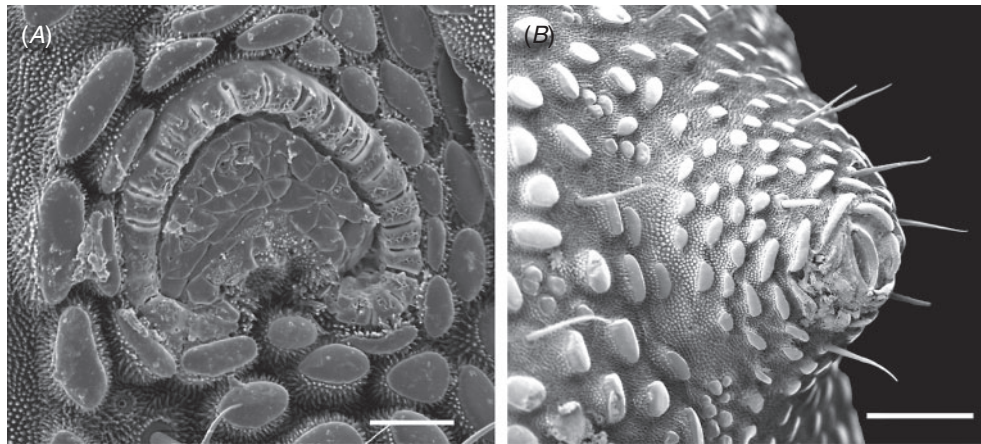
Fig. 9. *Austropurcellia cadens*, sp. nov., paratype male, CASENT 9035046. (*A*) Spiracle, scale bar: 20 µm; (*B*) ozophore, scale bar: 50 µm.

selection was performed separately for each codon position of COI. The model chosen for the 28S dataset as well as every codon position of COI was GTR+I+G. The model chosen for the 18S dataset was GTR+G. The model chosen for 12S was TPM1uf+G; the closest model that is implemented in MrBayes is GTR+G.

Bayesian analyses were performed in MrBayes (Huelsenbeck and Ronquist 2001). Concatenated datasets were partitioned and each partition was allowed its own model. Generations were added to runs until the standard deviation of split frequencies was below 0.01. The analysis of the COI dataset was run for 3 000 000 generations, the 12S dataset for 2 000 000 generations, the 28S dataset for 8 000 000 generations, the 18S dataset for 1 200 000 generations, the mtDNA dataset for 5 000 000, and the mtDNA +18S+28S dataset for 1 200 000. 10% of generations were discarded as burn-in, except in the case of COI and COI+12S, in which cases 20% of generations were discarded as burn-in on the basis of visualisation of parameters indicating a longer time to convergence.

In addition to Bayesian analyses, we performed a partitioned maximum-likelihood analysis in RAxML with bootstrap support calculated by the rapid bootstrap option (Stamatakis 2006). Finally, to include information from indels, we performed a parsimony analysis of the total combined dataset in MEGA 5 (Tamura *et al*. 2011), using all sites, with 1000 bootstrap replicates.

All mitochondrial DNA were formatted for analysis in BEAST using BEAUTi (Drummond *et al*. 2012). The data were analysed in BEAST for 10 000 000 generations, using the models selected in jModelTest. The resulting ultrametric tree was used for generalised mixed Yule-coalescent (GMYC) species delimitation (Pons *et al*. 2006) using the R package SPLITS (Ezard *et al*. 2013).

Taxonomy

Austropurcellia absens Boyer & Popkin-Hall, sp. nov.

(Figs 2–6)

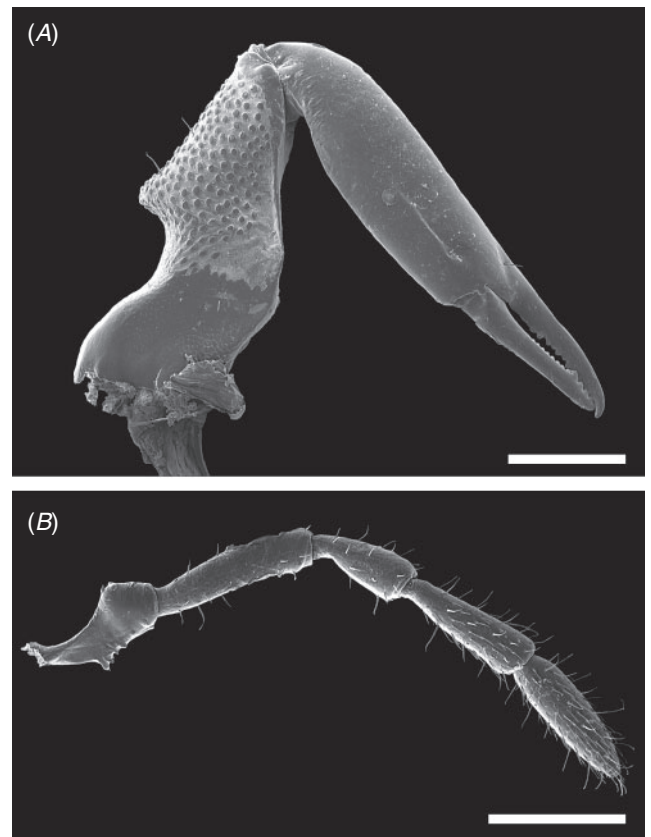urn:lsid:zoobank.org:act:7E1BFEEF-88AD-44E6-AA98-F76CE58353EB

Fig. 10. *Austropurcellia cadens*, sp. nov., males. (*A*) Chelicera, paratype CASENT 3053046; (*B*) palp, QM berlese sample 357. Scale bars: 200 µm.

Material examined

All material examined is from Queensland, Australia.

Holotype. Male (QM 61764), Range Road, Kirrama Range, primary forest, 18.202°S, 145.885°E, coll. C. M. Baker, S. L. Boyer, D. I. Laukó. H. A. Wiesner 22.v.2012 (ex MCZ 132316).

Paratypes. 2 ♂, 1 ♀, same collecting data as holotype, QM 61765 [ex MCZ IZ 132316]. 5 ♂, 2 ♀, 8 juveniles, same collecting data as holotype, MCZ IZ 132316.

Additional material studied. 3 ♂, 1 ♀, 1 juvenile, Kirrama Range, Mount Hosie, 18.183°S, 145.750°E, 930 m, coll. G. Monteith & G. Thompson 11.xii.1986, QM berlesate 733 S 1751.

Diagnosis

Distinguished from congeners by lack of scopula; anal plate strongly convex and bilobed in dorso-ventral plane with lobes separated by ungranulated triangular trough; distinct lack of

granulation in sternites immediately posterior to gonostome in area roughly the width of the gonostome and length continuing through sternite 6; tarsus IV strongly bisegmented.

Description

Pettalid with tergite VIII bilobed (Fig. 2*A*, *B*) and posterior margin of dorsal scutum curving ventrally (Fig. 2*C*). Length of male holotype ~2.1 mm, width at widest point in second opisthosomal segment ~1.0 mm, width across ozophores ~0.9 mm. Most of body surface showing tuberculate–granular microstructure (Fig. 3). Transverse and longitudinal opisthosomal sulci
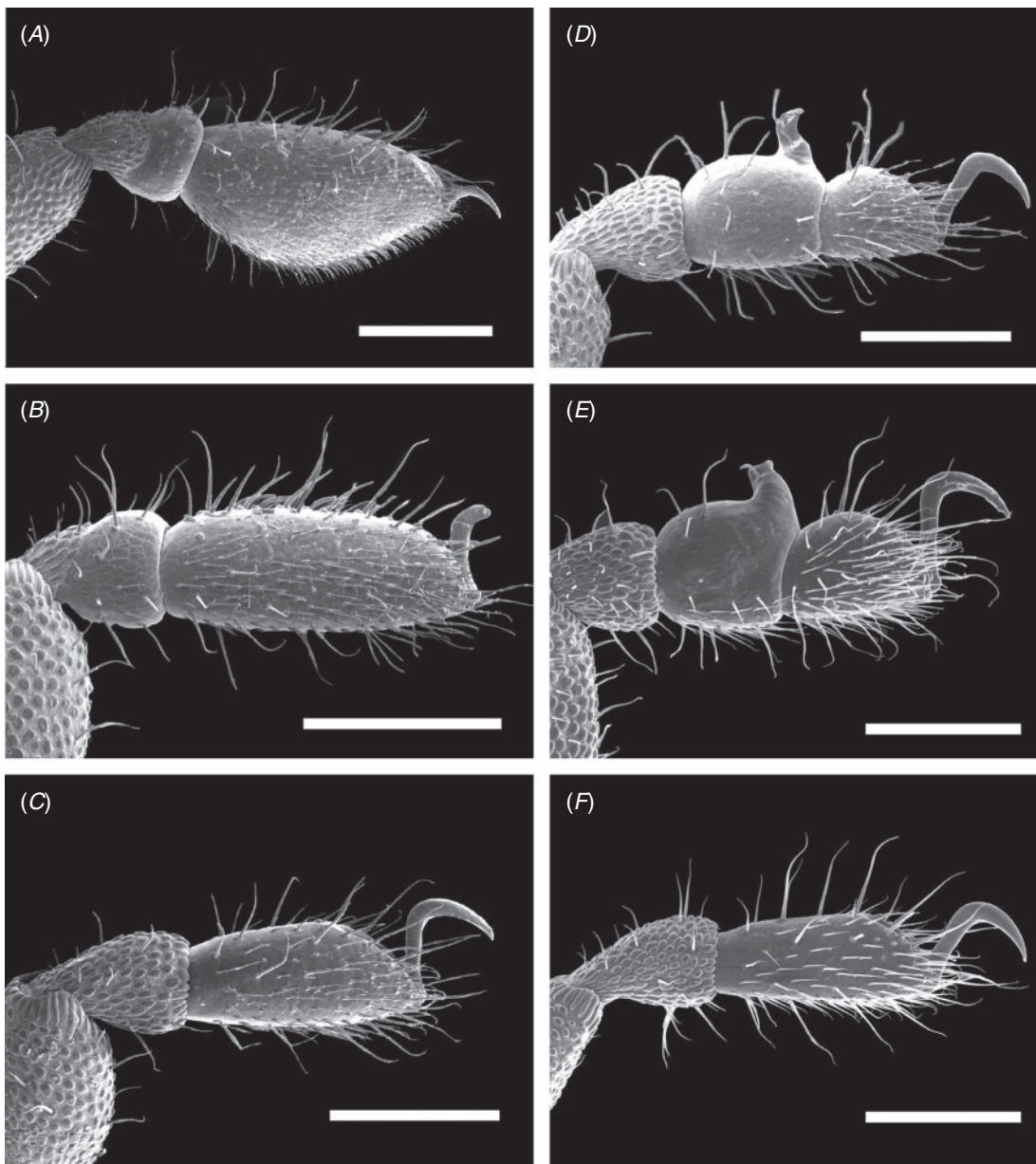
Fig. 11. *Austropurcellia cadens*, sp. nov., males and females. (*A*) Tarsus and metatarsus I, paratype male CASENT 9035046; (*B*) tarsus and metatarsus II CASENT 9035046; (*C*) tarsus and metatarsus III paratype male, CASENT 9035046; (*D*) male tarsus and metatarsus IV, lateral view paratype male, CASENT 9035046; (*E*) male tarsus and metatarsus IV, medial view, QM berlese sample 357; (*F*) female tarsus and metatarsus IV, FMHD #82–647. Scale bars: 200 μm.

distinct by lack of granulation (Fig. 3*A*). Ozophores positioned at 45° angle relative to walking plane as typical in pettalids (Fig. 2*A, C*). Coxae of legs I and II mobile. Coxae of remaining legs fixed. Male coxae II–IV meeting in the midline (Fig. 3*B*). Male gonostome small, subtriangular, wider than long, bordered on posterior margin by first opisthosomal sternite; male gonostome shorter than length of seam of contact of left and right coxae IV (Fig. 3*B*). Distinct lack of granulation ventrally in
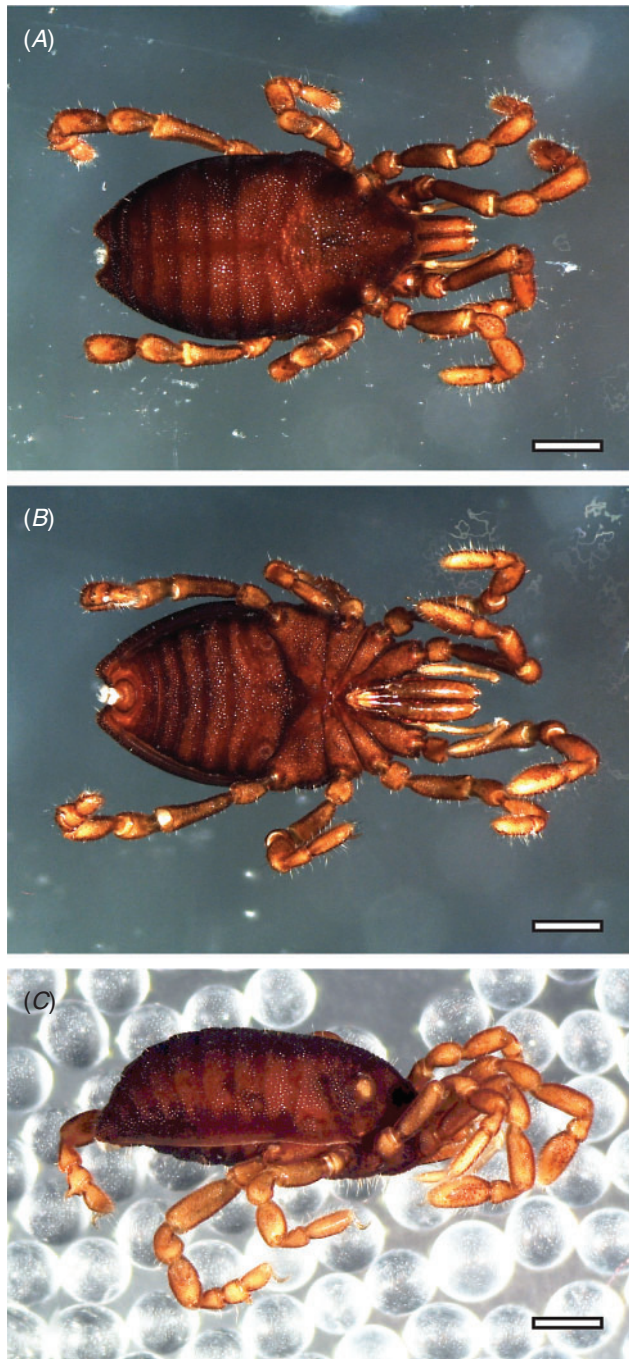
longitudinal band posterior to gonostome, and areas of contact between sternites (Fig. 3*B*). Anal region of 'pettalid type' (Giribet and Boyer 2002) with tergite IX laterally covering sternite 9, clearly meeting sternite 8. Anal plate posterior margin slightly bilobed. Anal plate smooth in posterior-medial area, granulated and strongly convex and bilobed in dorso-ventral plane in anterior-lateral areas. Anal plate convex outpocketings visible in lateral view. Distinct from other *Austropurcellia* by lack of scopula. Two anal pores visible in tergites IX and VIII close to a small point of fusion between the two tergites. Spiracle circular with slightly recurved edges, as found in 'open circle' type (Giribet and Boyer 2002) (Fig. 4*A*).

Chelicerae short and relatively robust (Fig. 5*A*). Proximal article of chelicerae with dorsal crest, without ventral process. Median article with apodeme. Two types of dentition, as typical in pettalids (Fig. 5*A*). Measurements of chelicera articles of male paratype from proximal to distal (in mm): 0.63, 0.95, 0.26. Palp (Fig. 5*B*) with prominent ventral process on trochanter. Measurements from paratype male of palp articles from proximal to distal (in mm): 024. 0.34, 0.21, 0.27, 0.31.

Legs with all claws smooth, without ventral dentition or lateral pegs (Fig. 6). Tarsi smooth (Fig. 6). Ventral side of tarsus I with distinct solea (Fig. 6*A*). Metatarsus I and metatarsus II heavily ornamented in basal half, smooth and slightly swollen in distal half, giving appearance of 'cuff' (Fig. 6*A, B*). Remaining tarsi with ornamented metatarsus (Fig. 6*C–F*). Male tarsus IV fully bisegmented (Fig. 6*D, E*). Adenostyle extremely robust and
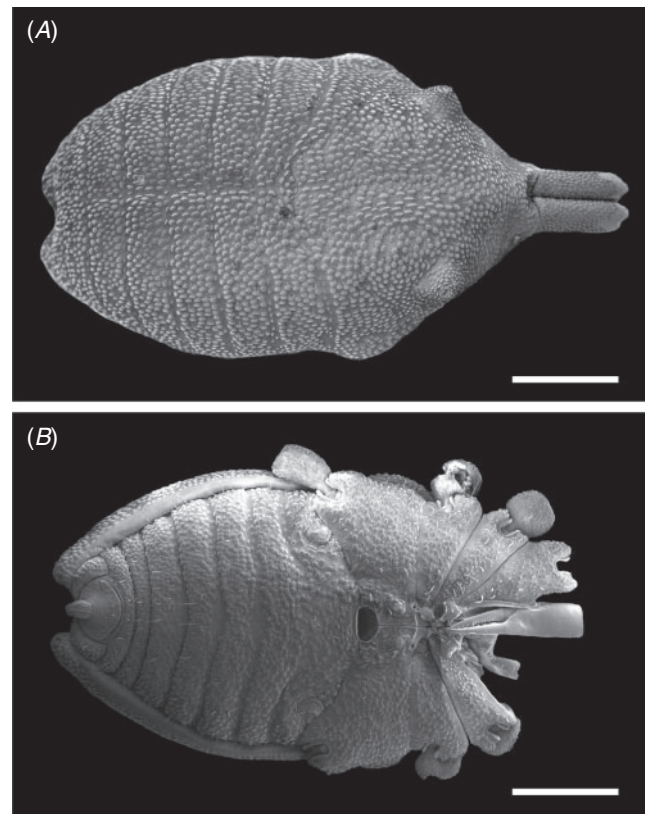

Fig. 12. *Austropurcellia clousei*, sp. nov., holotype male, QM. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.

Fig. 13. *Austropurcellia clousei*, sp. nov., paratype male, MCZ IZ 132339. (*A*) Dorsal view; (*B*) ventral view. Scale bars: 0.5 mm.
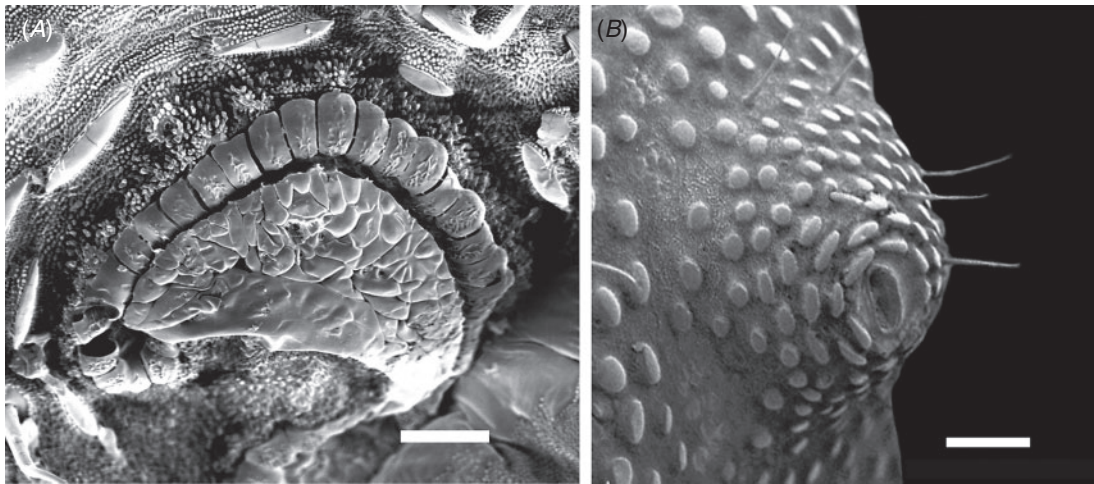
Fig. 14. *Austropurcellia clousei*, sp. nov., paratype male, MCZ IZ 132339. (*A*) Spiracle, scale bar: 20 μm; (*B*) OZOPHORE, scale bar: 50 μm.

oriented vertically, with small pore at apex on medial (internal) side (Fig. 6*D*). Long seta rising from lateral (external) face of adenostyle close to pore to well above apex (Fig. 6*E*); short seta arising from below adenostyle pore (Fig. 6*D*). Measurements from male paratype of leg articles from proximal to distal (in mm): leg I [trochanter damaged], femur 0.57, patella 0.23, tibia 0.40, metatarsus 0.17, tarsus 0.42; leg II [trochanter damaged], 0.65, 0.21, 0.43, 0.21, 0.47; leg III [trochanter damaged], 0.51, 0.21, 0.39, 0.21, 0.43; leg IV [trochanter damaged], 0.19, 0.53, 0.22, 0.44, 0.22, 0.44.

Etymology

The specific epithet refers to the absence of a scopula, which is unique among *Austropurcellia*, and also to the absence of granulation on the ventral opisthosoma posterior to the gonostome.

Austropurcellia cadens Baker & Boyer, sp. nov.

(Figs 7–11)

urn:lsid:zoobank.org:act:801E8372-DE7B-4BEE-A181-78877803A351

Material examined

All material examined is from Queensland, Australia.

Holotype. Male (QM 61766), Wooroonooran National Park, Mt Bartle Frere, HW0038, 17.378°S, 145.786°E, coll. H. Wood 23–26.iv.2009 [ex CAS ENT 9035046].

Paratypes. 1 ♂, 1 ♀, same collecting data as holotype, QM 61767 [ex CAS ENT 9035046]. 2 ♂, 2 ♀, 3 juveniles, same collecting data as holotype, CAS ENT 9035046.

Additional material studied. 4 ♂, 5 ♀, Mt Hypipamee National Park, 17.383°S, 145.767°E [estimated], coll. G. B. Monteith 5.x.1980, QM berlesate 236, S 2280. 3 ♂, 2 ♀, 2 juveniles, Mt Hypipamee National Park, 17.383°S, 145.767°E [estimated], coll. G. B. Monteith 5.x.1980, QM berlesate 237, S 2247. 2 ♂, 2 ♀, Mt Bartle Frere Summit, 17.385°S, 145.821°E [estimated], coll. G. B. & S. R. Monteith 7.x.1980, QM berlesate 239. 8 ♂, 3 ♀, 4 juveniles, 6 km E of Butcher's Creek, 17.352°S, 145.777°E [estimated], QM berlesate 245, S2249. 3 ♂, 3 ♀, 1 juvenile, Mt Bartle Frere Summit, 17.385°S, 145.821°E [estimated], QM berlesate 304, S
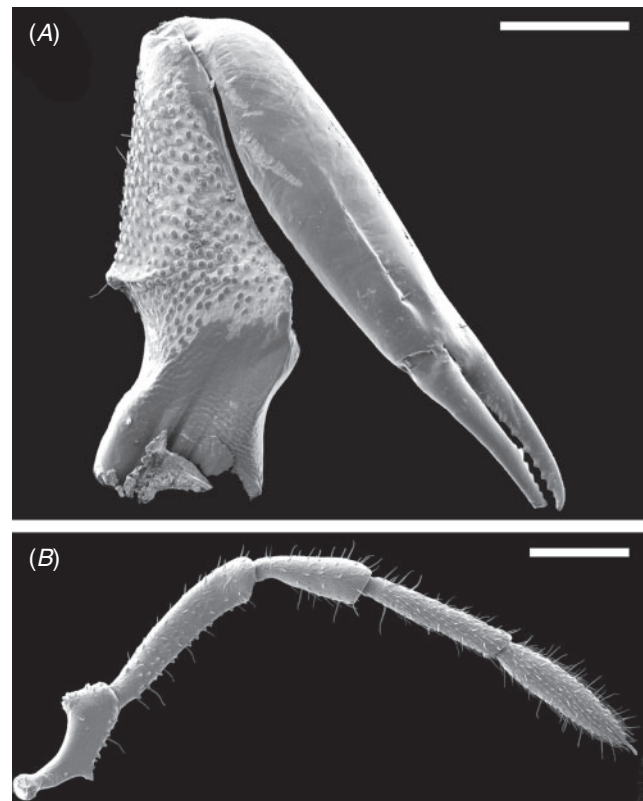

Fig. 15. *Austropurcellia clousei*, sp. nov., paratype male, MCZ IZ 132339. (*A*) Chelicera; (*B*) palp. Scale bars: 200 μm.

2276. 1 ♂, 2 ♀, 1 juvenile, 0.5 km N of Mt Bartle Frere Summit, 17.400°S, 145.817°E, coll. Earthwatch, QM berlesate 357 S 2269. 3 ♂, 1 ♀, Mt Fisher, 7 km W of Millaa Millaa, 17.567°S, 145.567°E, coll. G. B. Monteith, D. K. Yeates, D. Cook 27.iv.1982, QM berlesate 409, S 2301. 1 ♂, 1 ♀, Mt Fisher, 7 km W of Millaa Millaa, 17.567°S, 145.567°E, coll. G. Monteith, D. K. Yeates Cook 27.iv.1982, QM berlesate 412, S 2288. 4 ♂, 4 ♀, Bartle Frere Track, 17 km W of Malanda, 17.383°S, 145.767°E, coll. G. B. Monteith &
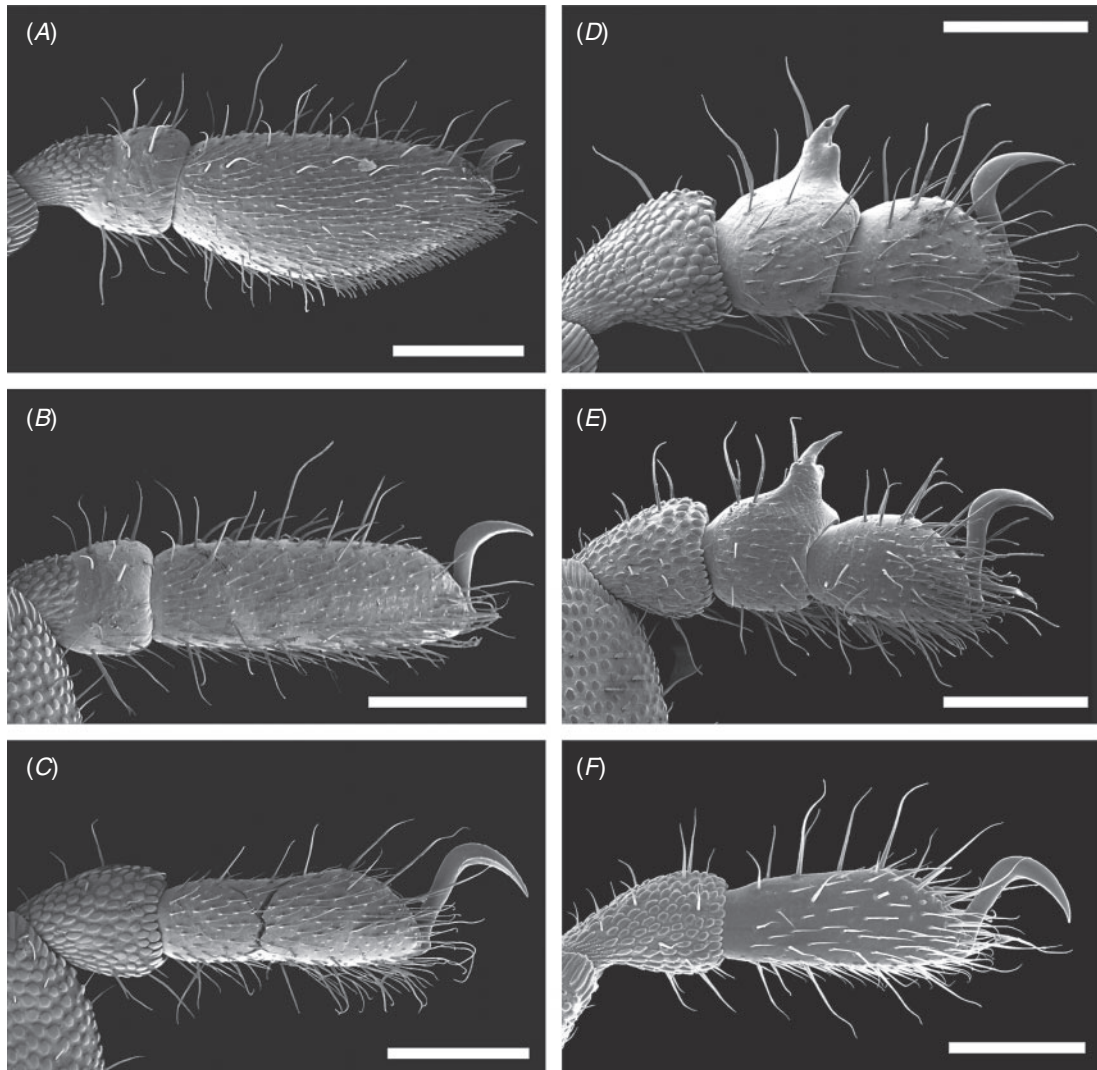
Fig. 16. *Austropurcellia clousei*, sp. nov., paratype male and female, MCZ IZ 132339. (*A*) Tarsus and metatarsus I; (*B*) tarsus and metatarsus II; (*C*) tarsus and metatarsus III; (*D*) male tarsus and metatarsus IV, lateral view; (*E*) male tarsus and metatarsus IV, medial view; (*F*) female tarsus and metatarsus IV. Scale bars: 200 µm.

G. Thompson, QM berlesate 815. 2 ♂, 2 ♀, 1 juvenile, Tower south of Crater National Park, 17.450°S, 145.483°E, coll. G. B. Monteith 16.v.1986, QM berlesate 886. 2 ♂, 2 ♀, 1 juvenile, Mt Fisher Summit, 17.567°S, 145.550°E, coll. G. B. Monteith & Cook 8.ii.1999, QM berlesate 991, S 50571. 1 ♂, 1 ♀, 21 km S of Atherton, 17.450°S, 145.483°E, coll. D. K. Yeates & G. I. Thompson 5.xi.1983, QM S 1752. 2 ♂, 2 ♀, Tower south of Crater, 17.450°S, 145.483°E, coll. G. B. Monteith 29.vi.1997, QM berlesate 965 S 35850. 2 ♂, 2 ♀, 1 juvenile, Malanda Falls Reserve, 17.355°S, 145.586°E [estimated], coll. S. & J. Peck 22.vii.1982, FMHD 82–674. 2 ♂, Malanda Falls Reserve, Aus31, 17.573°S, 145.688°E, coll. C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner 24.v.2012, MCZ IZ 132319.

Diagnosis

Distinguished from congeners by scopula approximately half the width of anal plate and half the height of the anal plate covering central area of the anal plate; distinct appearance of enlargement of sutures between sternite 5 and its neighbours in a section approximately equivalent to width of gonostome,

resulting from increase in height of area of sutures lacking granulation; male tarsus IV strongly bisegmented.

Description

Pettalid with tergite VIII bilobed (Fig. 7*A, B*) and posterior margin of dorsal scutum curving ventrally (Fig. 7*C*). Length of male holotype (Fig. 7) ~1.7 mm, width at widest point in posterior third of prosoma ~1 mm, width across ozophores ~0.7 mm. Most of body surface showing tuberculate–granular microstructure (Fig. 8). Transverse and opisthosomal sulci distinct by lack of granulation; longitudinal sulcus distinct but granulose with granules oriented longitudinally (Fig. 8*A*). First and second full sutures posterior to gonostome area lacking granulation in median area of contact (Fig. 8*B*). Ozophores positioned at 45° angle relative to walking plane (Fig. 8*A*). Coxae of legs I and II mobile. Coxae of remaining legs fixed. Male coxae II–IV meeting in midline (Fig. 8*B*). Male gonostome small, subtriangular, wider

than long, bordered on posterior margin by first opisthosomal sternite; male gonostome shorter than length of contact seam of left and right coxae IV (Fig. 8*B*). Anal region of 'pettalid type'. Anal plate flat, granulose anteriorly. Scopula emerging from ventral surface of anal plate, covering approximately half the width of anal plate and half the length of anal plate, positioned centrally such that entire margin of plate is visible. Two anal pores visible, one at suture between anal plate and tergite IX, one

between lobes of tergite VIII. Absence of granulation in meeting place between anal plate, lobes of tergite VIII, and dorsal scutum (Fig. 8*B*). Spiracle of the 'open circle' type (Fig. 9*A*).

Chelicerae (Fig. 10*A*) short and relatively robust. Proximal article of chelicerae with dorsal crest, without ventral process. Median article with apodeme. Two types of dentition, as typical in pettalids (Fig. 10*A*). Measurements of chelicera articles of male paratype from proximal to distal (in mm): 0.65, 0.88, 0.29. Palp (Fig. 10*B*) with prominent ventral process on trochanter. Measurements from paratype male of palp articles from proximal to distal (given in mm): 0.22, 0.28, 0.1, 0.21, 0.22.

Legs with all claws smooth, without ventral dentition or lateral pegs (Fig. 11). Tarsi smooth (Fig. 11). Ventral side of tarsus I with distinct solea (Fig. 11*A*). Metatarsus I and metatarsus II heavily ornamented in basal half, smooth and slightly swollen in distal half, giving appearance of 'cuff' (Fig. 11*A*, *B*). Remaining tarsi with ornamented metatarsus (Fig. 11*C–F*). Male tarsus IV fully bisegmented (Fig. 11*D*, *E*). Adenostyle extremely robust and oriented vertically, with small pore at apex on lateral (external) side (Fig. 11*D*). Seta rising from medial (internal) face of adenostyle close to pore to above apex (Fig. 11*D*, *E*); short seta arising from below adenostyle pore (Fig. 11*D*). Measurements from male paratype of leg articles from proximal to distal (in mm): leg I [trochanter damaged], 0.51, 0.20, 0.37, 0.16, 0.40; leg II [trochanter damaged], 0.42, 0.17, 0.25, 0.12, 0.33; leg III [trochanter damaged], 0.34, 0.16, 0.28, 0.15, 0.30; leg IV [trochanter damaged], 0.42, 0.24, 0.30, 0.17, 0.36.
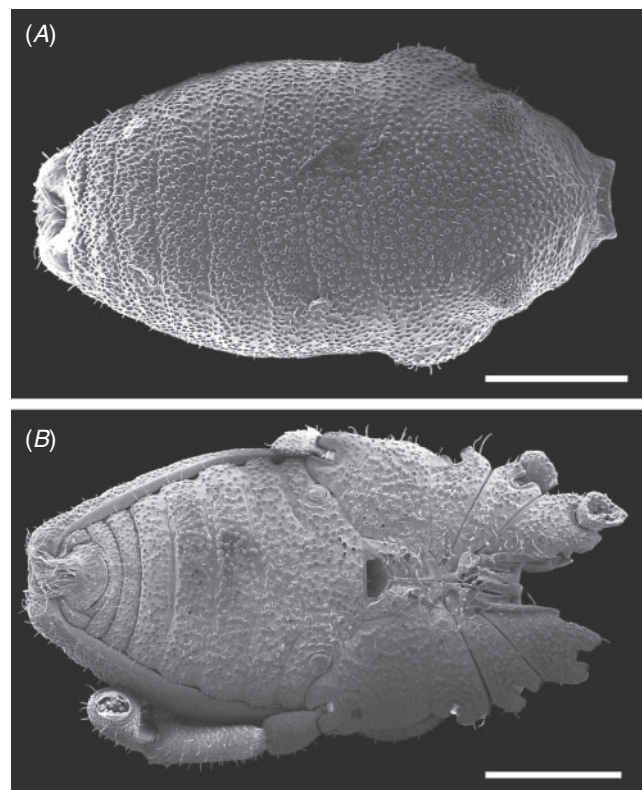

Fig. 17. *Austropurcellia giribeti*, sp. nov., holotype male, QM. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.

Fig. 18. *Austropurcellia giribeti*, sp. nov., QM berlese 252. (*A*) Dorsal view; (*B*) ventral view. Scale bars: 0.5 mm.

Etymology

The specific epithet refers to the scopula that cascades over the centre of the anal plate.

Austropurcellia clousei Boyer, Baker & Popkin-Hall, sp. nov.

(Figs 12–16)

urn:lsid:zoobank.org:act:DBDB3DAA-AFC3-4293-96A1-
2112C60743FD

Material examined

All material examined is from Queensland, Australia.

Holotype. Male (QM 61768), Paluma Range National Park, H Track, 19.011°S, 146.206°E, coll. R. M. Clouse and P. P. Sharma 14.ii.2011, QM [ex MCZ IZ 132339].

Paratypes. 1 ♀, 1 ♂, same data as holotype, QM 61769 [ex MCZ IZ 132339]. 1 ♀, 2 ♂, 1 juvenile, same data as holotype, MCZ IZ 132339.

Additional material studied. 1 ♂, 1♀, Mount Spec, Birthday Creek, 18.967°S, 146.167°E, coll. G. Monteith 18.xi.1990, QM berlesate 846.

Diagnosis

Distinguished from congeners by wide separation of lobes of tergites VIII and IX, the latter easily visible in dorsal view; anal plate smooth and relatively flat in dorso-ventral plane, with short scopula emerging from posterior margin of plate; male tarsus IV strongly bisegmented with adenostyle thin and blade-like, supported by wide and swollen base.

Description

Pettalid with tergite VIII strongly bilobed (Fig. 12*A*, *B*) and ventral margin of dorsal scutum forming straight line parallel to walking surface (Fig. 12*C*). Lobes of tergite VIII prominent in dorsal view (Fig. 12*A*). Length of male holotype (Fig. 12) ~2.2 mm, width at widest point in posterior third of prosoma ~1.3 mm, width across ozophores ~0.9 mm. Most of body surface covered in tubercles and granules (Fig. 13). Transverse sulci with very small granules present in sulcus; medial sulcus defined by band of elongated granules oriented parallel to anterior–posterior

axis of body. First three sutures between sternites posterior to gonostome with wide ungranulated area in medial zone. Ozophores positioned at 45° relative to walking plane as typical in pettalids. Coxae of legs I and II mobile. Coxae of remaining legs fixed. Male coxae II–IV meeting in the midline (Fig. 13*B*). Male gonostome small, subtriangular, wider than long, bordered on posterior margin by first opisthosomal sternite; male gonostome shorter than length of seam of contact of left and right coxae IV (Fig. 13*B*). Anal region of 'pettalid type' (Fig. 13*B*). Anal plate somewhat convex and largely ungranulated. Short scopula emerging from posterior quarter of anal plate (Fig. 13*B*). Anal pore not visible. Spiracle circular with slightly recurved edges as found in 'open circle' type (Fig. 14*A*).

Chelicerae (Fig. 15*A*) short and relatively robust. Proximal article of chelicerae with dorsal crest, without ventral process. Median article with apodeme. Two types of dentition, as typical in pettalids (Fig. 15*A*). Measurements from male holotype of chelicera articles from proximal to distal (in mm): 0.73, 0.97, 0.32. Palp (Fig. 15*B*) with prominent ventral process on trochanter. Measurements from paratype male of palp articles from proximal to distal (in mm): 0.26, 0.38, 0.24, 0.32, 0.31.

Legs with all claws smooth, without ventral dentition or lateral pegs (Fig. 16). Tarsi smooth (Fig. 16). Ventral side of tarsus I with distinct solea (Fig. 16*A*). Metatarsus I and metatarsus II heavily ornamented in basal half, smooth and slightly swollen in distal half, giving appearance of 'cuff' (Fig. 16*A, B*). Remaining tarsi with ornamented metatarsus (Fig. 16*C–F*). Male tarsus IV fully bisegmented (Fig. 16*D, E*). Adenostyle thin and blade-like but with wide, swollen base (Fig. 16*D, E*). Adenostyle with small pore at the apex on lateral (external) side (Fig. 16*D*). Long seta rising from medial (internal) face of adenostyle from below pore to well above apex (Fig. 16*D, E*); very short seta arising from adenostyle base below pore on lateral (external) face of adenostyle (Fig. 16*D*).

Measurements from male holotype of leg articles from proximal to distal (in mm): leg I 0.20, 0.61, 0.29, 0.49, 0.24,
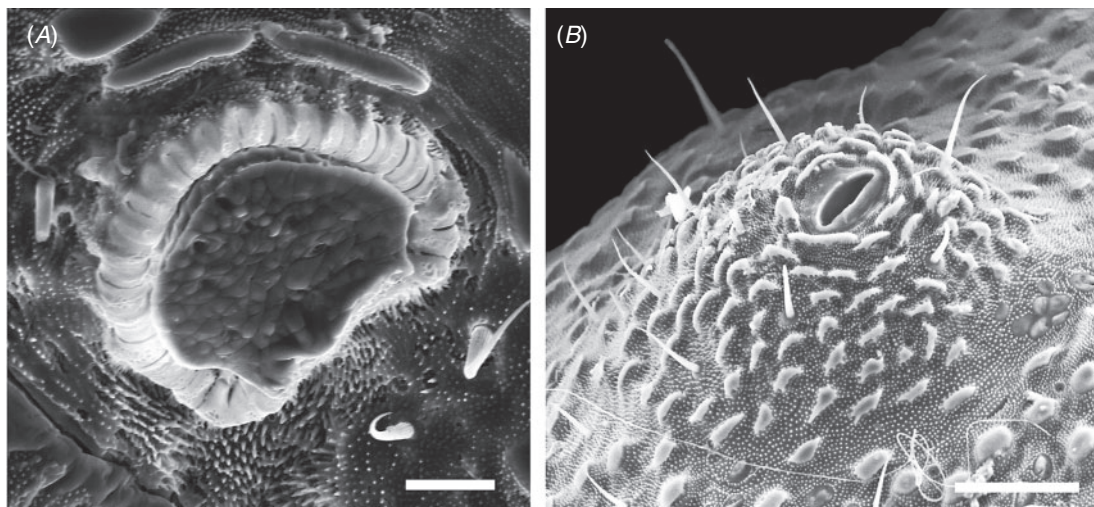

Fig. 19. *Austropurcellia giribeti*, sp. nov., males. (*A*) Spiracle, MCZ IZ 132344, Scale bar: 20 µm; (*B*) ozophore, QM berlese 252, Scale bar: 50 µm.

0.49; leg II [trochanter damaged], 0.49, 0.23, 0.38, 0.15, 0.38; leg III [trochanter damaged], 0.46, 0.20, 0.38, 0.17, 0.36; leg IV [trochanter damaged], 0.57, 0.28, 0.42, 0.23, 0.37.

Etymology

The specific epithet is a tribute to Ron Clouse, an expert on cyphophthalmid taxonomy and biogeography with a particular focus on the Pacific and South-east Asia. He collected many of the specimens used in this study, including the holotype for *A. clousei*, sp. nov., and provided valuable advice about fieldwork in Queensland.

Austropurcellia giribeti Boyer & Quay, sp. nov.

(Figs 17–21)

urn:lsid:zoobank.org:act:DA6A6735-AB9F-48F0-8635-
7C230468AD73

Material examined

All material examined is from Queensland, Australia.

Holotype. Male (QM 61770), Cooper Creek, Daintree National Park, Cape Tribulation, Loc194, 16.166°S, 145.416°E, coll. G. Giribet & C. D'Haese, 15.x.2003 [ex MCZ IZ 134696].

Paratype. ♂, Daintree Village, Aus40, 16.255°S, 145.362°E, coll. C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner 28.v.2012, MCZ IZ 132337.

Additional material studied. ♀, Daintree Village, Aus9, 16.255°S, 145.362°E, coll. C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner, 3. vi.2011, MCZ IZ 132344. 6 ♂, 5 ♀, 1 juvenile, Road Summit on Alexandra Range, Daintree, 16.250°S, 145.433°E, 250m, coll. G. Monteith, 13.x.1980, QM berlesate 252 S 2254.

Diagnosis

Distinguished from congeners by wide, rounded lobes of tergite VIII and long, wide scopula extending to posterior margin of lobes of tergite VIII, resulting in squared appearance of posterior body margin; suture dividing male tarsus IV subtle and incomplete.

Description

Pettalid with tergite VIII strongly bilobed (Fig. 17*A, B*) and ventral margin of dorsal scutum gently curving ventrally at posterior margin (Fig. 17*C*). Lobes of tergite VIII rounded, lacking granulation dorsally, and extremely prominent in dorsal view (Fig. 17*A, B*). Length of male holotype (Fig. 17) ~2.1 mm, width at widest point in posterior third of prosoma ~1.2 mm, width across ozophores ~0.8 mm. Body with most of its surface showing a tuberculate–granular microstructure (Fig. 18). Transverse sulci prominent, especially in lateral view (Fig. 17*C*); no longitudinal sulcus (Fig. 18*A*). Ozophores positioned at a 45° angle relative to walking plane, typical in pettalids (Fig. 17*C*). Coxae of legs I and II mobile. Coxae of remaining legs fixed. Male coxae II–IV meeting in the midline (Fig. 18*B*). Male gonostome small, subtriangular, wider than long, bordered on posterior margin by first opisthosomal sternite; male gonostome shorter than length of seam of contact of left and right coxae IV (Fig. 18*B*). Anal region of 'pettalid type' (Giribet and Boyer 2002) with tergite IX laterally covering sternite 9 and clearly meeting sternite 8 (Fig. 18*B*). Anal plate flat, moderately granulose with very long and wide scopula emerging from posterior third of anal plate and
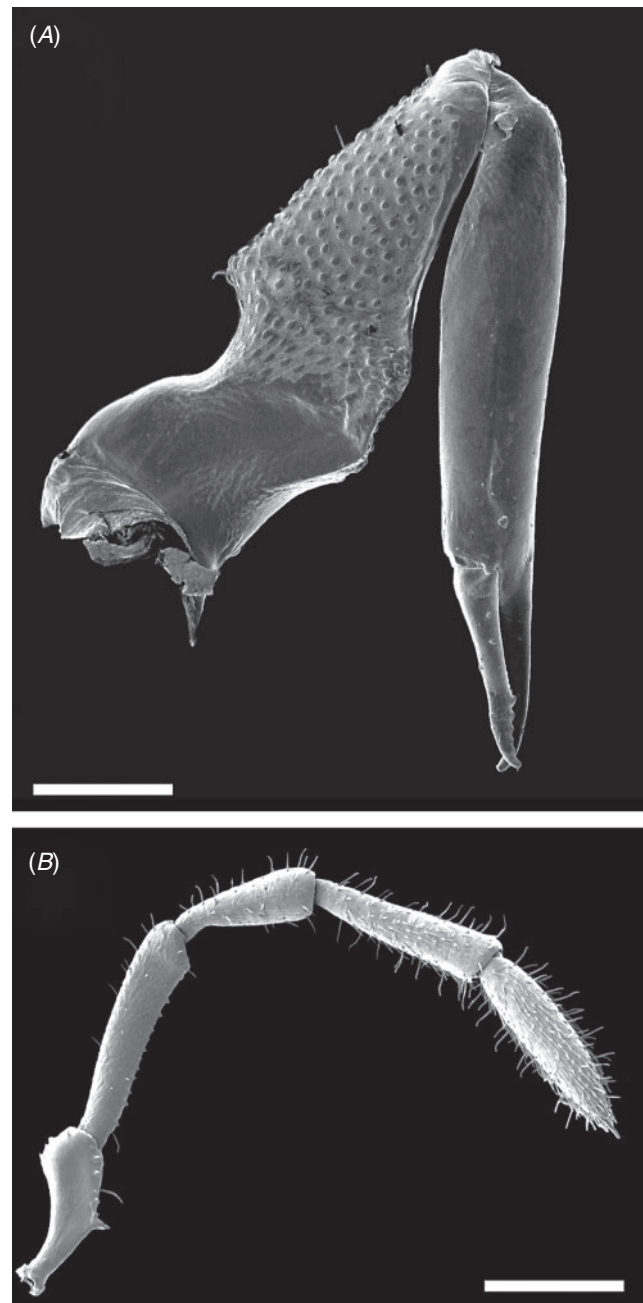
Fig. 20. *Austropurcellia giribeti*, sp. nov., males. (*A*) Chelicera, MCZ IZ 132344; (*B*) palp, QM berlese 252. Scale bars: 200 μm.

extending to posterior margin of lobes of tergite VIII (Fig. 18*B*). Scopula clearly visible in dorsal view (Figs 17*A*, 18*A*). Anal pore not visible. Spiracle circular with slightly recurved edges as found in the 'open circle' type of Giribet and Boyer (2002) (Fig. 19*A*).

Chelicerae (Fig. 20*A*) short and relatively robust. Proximal article of chelicerae with dorsal crest, without ventral process. Median article with apodeme. Two types of dentition, as typical in pettalids (Fig. 20*A*). Measurements from male paratype of chelicera articles from proximal to distal (in mm): 0.79, 0.91, 0.27. Palp (Fig. 20*B*) with prominent ventral process on
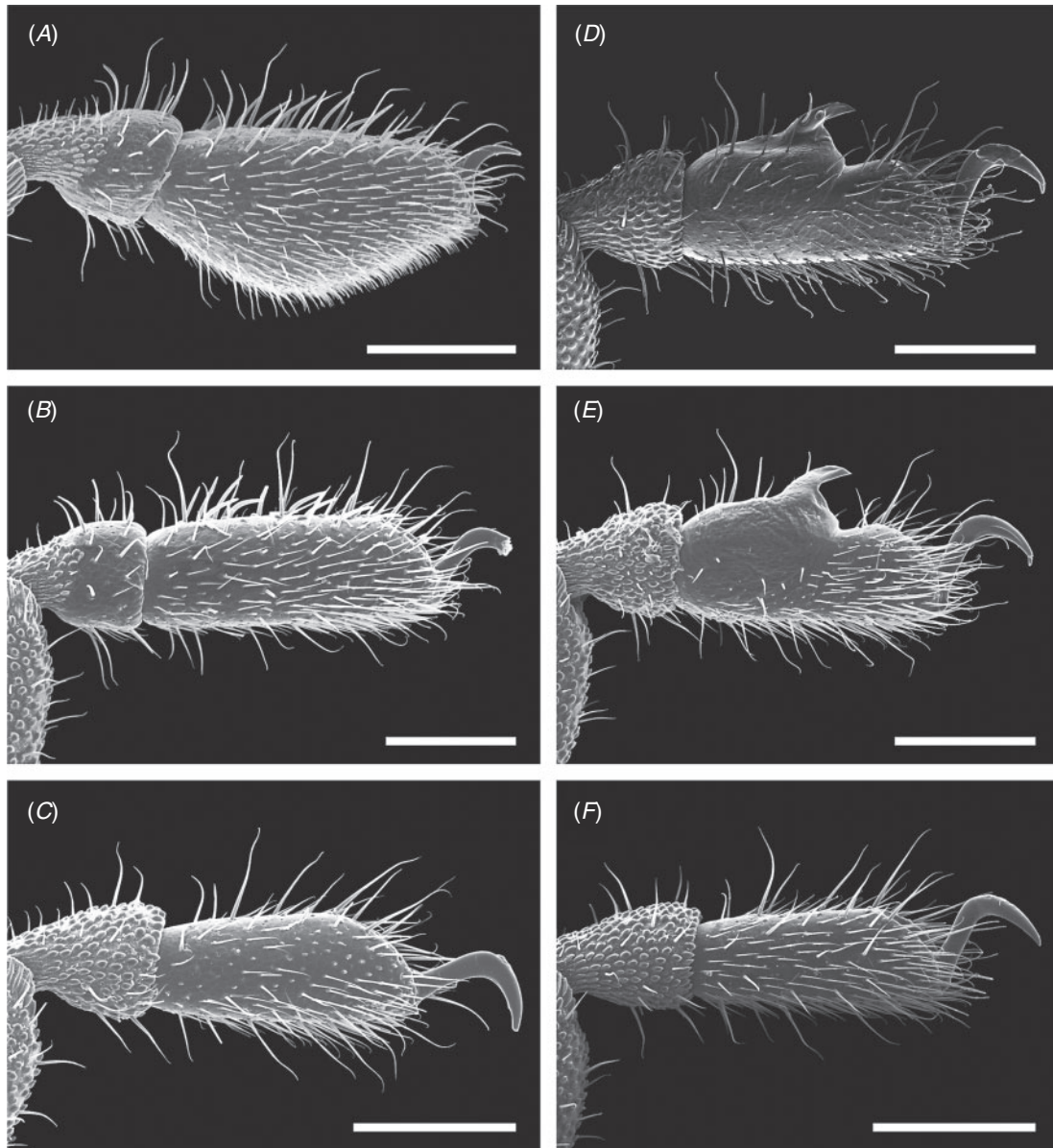
Fig. 21. *Austropurcellia giribeti*, sp. nov. (*A*) Tarsus and metatarsus I, MCZ IZ 132344; (*B*) tarsus and metatarsus II, MCZ IZ 132344; (*C*) tarsus and metatarsus III, MCZ IZ 132344; (*D*) male tarsus and metatarsus IV, lateral view, MCZ IZ 132344; (*E*) male tarsus and metatarsus IV, medial view, MCZ IZ 132344; (*F*) female tarsus and metatarsus IV, QM berlese 252. Scale bars: 200 μm.

trochanter. Measurements from paratype male of palp articles from proximal to distal (in mm): 0.24, 0.33, 0.22, 0.29, 0.29.

Legs with all claws smooth, without ventral dentition or lateral pegs (Fig. 21). Tarsi smooth (Fig. 21). Ventral side of tarsus I with distinct solea (Fig. 21*A*). Metatarsus I and metatarsus II heavily ornamented in basal half, smooth and slightly swollen in distal half, leading to appearance of 'cuff' (Fig. 21*A, B*). Remaining legs with ornamented metatarsus (Fig. 21*C–F*). Male tarsus IV partially bisegmented (Fig. 21*D, E*). Adenostyle robust and oriented distally, with small pore at apex on lateral (external) side (Fig. 21*D*). Long seta rising from medial (internal) face of adenostyle close to pore to well above apex of adenostyle (Fig. 21*D, E*). Measurements from male holotype of leg

articles from proximal to distal (in mm): leg I [trochanter damaged], 0.60, 0.25, 0.44, 0.22, 0.44; leg II [trochanter damaged], 0.49, 0.27, 0.45, 0.20, 0.42; leg III [trochanter damaged], 0.39, 0.20, 0.33, 0.17, 0.31; leg IV 0.19, 0.50, 0.21, 0.40, 0.17, 0.38.

Etymology

The specific epithet is a tribute to Gonzalo Giribet, who brought systematics of Cyphophthalmi into the modern age and continues to lead global efforts to understand the evolution of these animals. He was one of the collectors of the first specimen from this species to be sequenced, more than a decade ago.
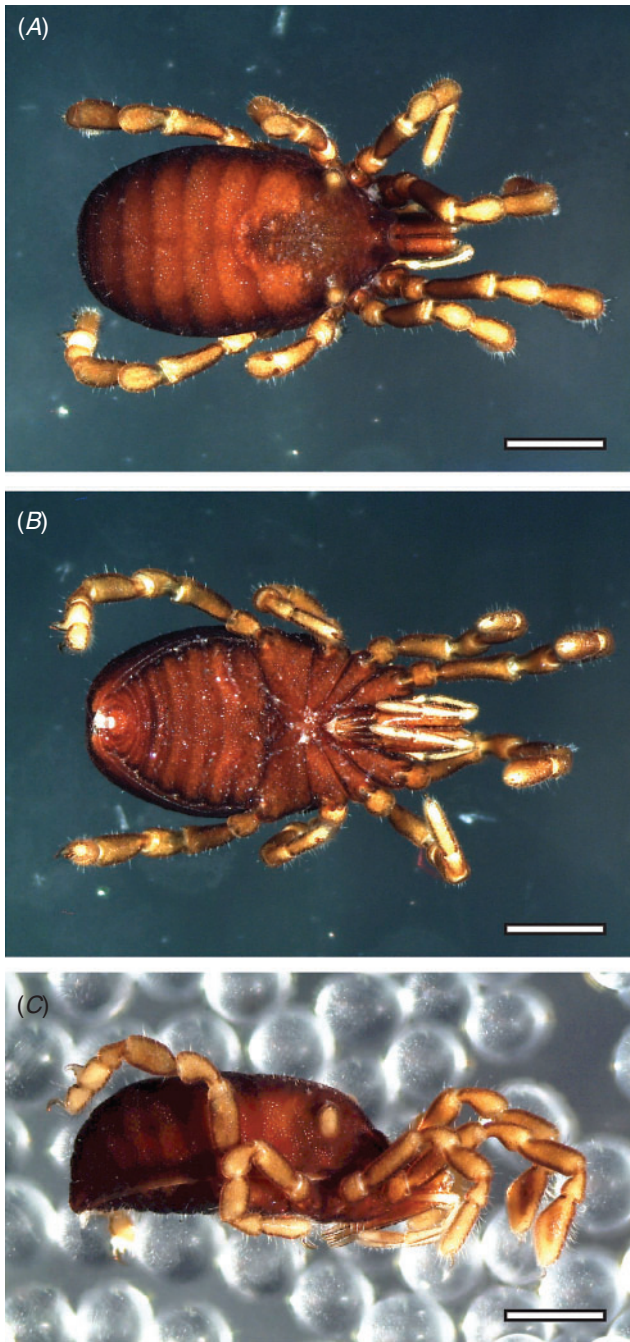
Fig. 22.   *Austropurcellia sharmai*, sp. nov., holotype male, QM. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.
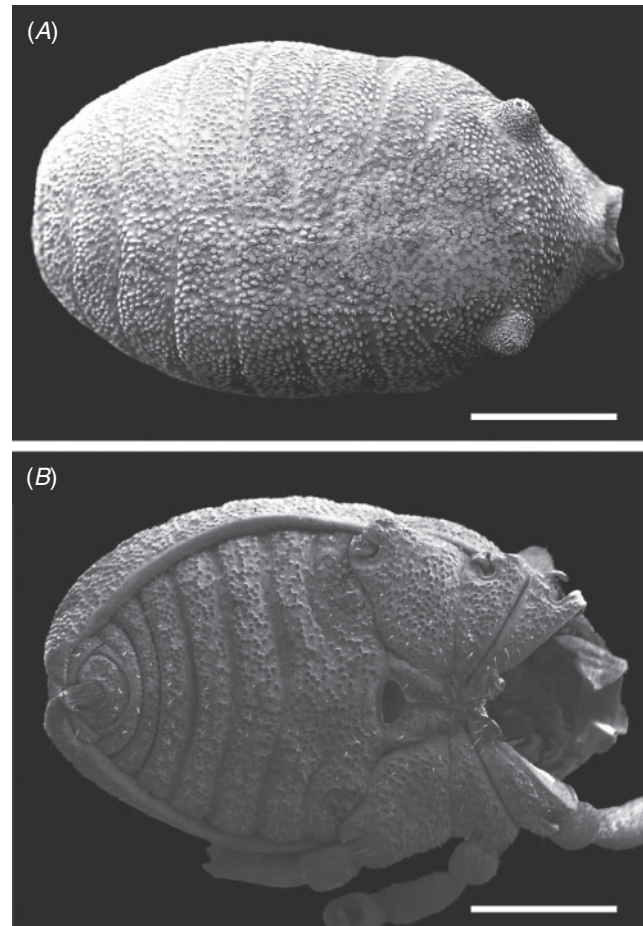
Fig. 23.   *Austropurcellia sharmai*, sp. nov., males. (*A*) Dorsal view, MCZ IZ 132317; (*B*) ventral view, MCZ IZ 134698. Scale bars: 0.5 mm.

Austropurcellia sharmai Boyer & Quay, sp. nov.

(Figs 22–26)

urn:lsid:zoobank.org:act:31B1516A-F880-45E2-8C88-
    C0CD04E91C0A

Material examined

Holotype.   Male (QM 61771), Emmagen Creek, Daintree National Park, Loc198, 16.062°S, 145.462°E, coll. G. Giribet & C. D'Haese 18.ii.2003 [ex MCZ IZ 134698].

Paratypes.   3 ♂, 4 ♀, same data as holotype, QM 61772 [ex MCZ IZ 132498]. 4 ♂, 1 ♀, same data as holotype, MCZ IZ 132698.

Additional material studied.   1 ♂, 3 ♀, 1.5 km W of Cape Tribulation Site 3, 16.083°S, 145.467°E, 150 m, coll. Monteith, Yeates and Thompson, 25.ix.1982, QM berlesate 425. 2 ♂, 2 ♀, 1.5 km W of Cape Tribulation Site 3, 16.083°S, 145.467°E, 150 m, coll. Monteith, Yeates and Thompson, 25.ix.1982, QM berlesate No. 428. 1 ♂, 3 ♀, 1.5 km W of Cape Tribulation Site 3, 16.083°S, 145.467°E, 150 m, coll. Monteith, Yeates and Thompson, 7.x.1982, QM berlesate No. 458. 1 ♂, 1 ♀, 2.0 km W of Cape Tribulation Site 4, 16.083°S, 145.467°E, 200 m, coll. Monteith, Yeates and Thompson, 7.x.1982, QM berlesate No. 454. 2 ♂, 3 ♀, 2.0 km W of Cape Tribulation Site 4, 16.083°S, 145.467°E, 200 m, coll. Monteith, Yeates and Thompson, 25.ix.1982, QM berlesate No. 429 A (sample 1 of 2). 1 ♂, 3 ♀, 2.0 km WNW of Cape Tribulation Site 2, 16.083°S, 145.467°E, 50 m, coll. Monteith, Yeates and Thompson, 23.ix–7.x.1982, QM berlesate No. 479. 3 ♂, 3 ♀, 1 juvenile, 2.0 km WNW of Cape Tribulation, Site 2 16.083°S, 145.467°E, 50 m, coll. Monteith, Yeates and Thompson 3.x.1982, QM berlesate No. 447. 1 ♂, 1 ♀, 2.5 km W of Cape Tribulation Site 5, 16.083°S, 145.450°E, 180 m, coll. Monteith, Yeates, and Thompson 2.x.1982, QM berlesate No. 481. ♂, 3.0 km W of Cape Tribulation Site 6, 16.083°S, 145.450°E, 500 m, coll. Monteith, Yeates, and Thompson 2.x.1982, QM berlesate No. B (sample 2 of 2). ♂, 4.5–5.0 km W of Cape Tribulation Top Camp, 16.083°S, 145.433°E, 760–780 m, coll. Monteith, Yeates, and Thompson 1.x.1982, QM berlesate No. 442 A (sample 1 of 2). 6 ♂, 4 ♀, 4 juveniles, Emmagen Creek, Daintree National Park, Loc859, 16.062°S, 145.462°E, coll. Clouse, Sharma
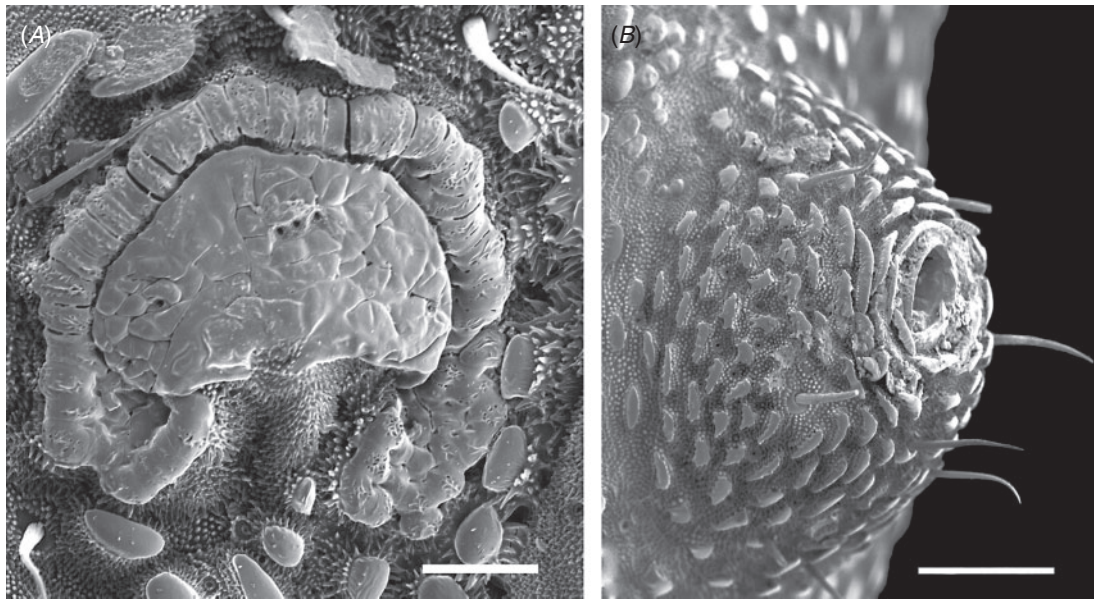
Fig. 24. _Austropurcellia sharmai_, sp. nov., male, MCZ IZ 134698. (_A_) Spiracle, scale bar: 20 µm; (_B_) ozophore, scale bar: 50 µm.
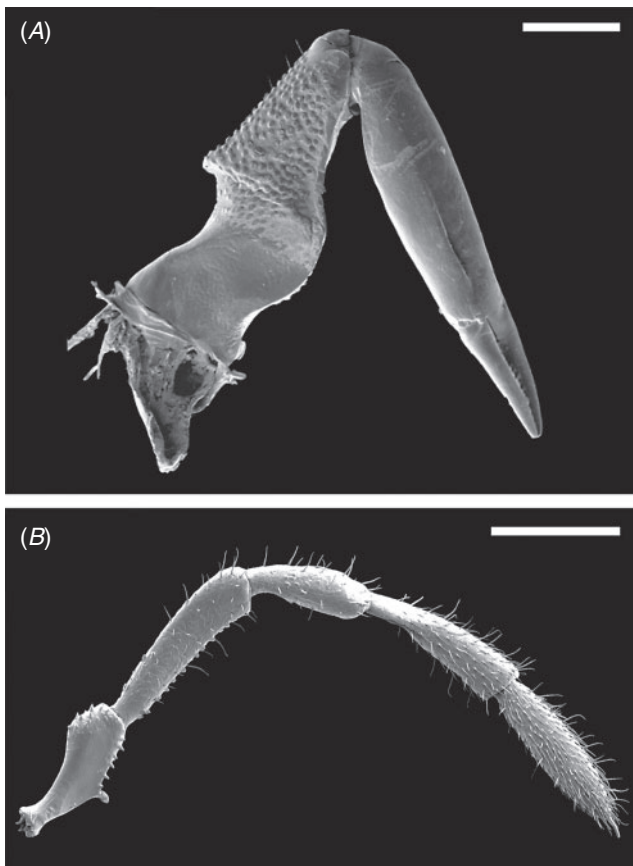

Fig. 25. _Austropurcellia sharmai_, sp. nov., males. (_A_) Chelicera, MCZ IZ 132317; (_B_) palp, MCZ IZ 134698. Scale bars: 200 µm.

26.iv.2011, MCZ IZ 132317. 15 ♂, 13 ♀, 3 juveniles, NE Mt Boolbun South, 15.950°S, 145.133°E, 850–1000 m, coll. G. B. Monteith, 6.xi.1995, QM berlesate No. 896 (2 samples). ♂, 10 ♀, 8 juveniles, NE Mt Boolbun South, 15.950°S, 145.133°E, 850–1000 m, coll. G. B. Monteith, 6.xi.1995, QM berlesate No. 897. ♂, 3 ♀, 11 juveniles, Old Forest Creek Road, 16.286°S, 145.362°E, coll. C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner, Aus41, 28.v.2012, MCZ IZ 132328.

Diagnosis

Distinguished from congeners by very rounded posterior of dorsal scutum; ozophores large and pale; scopula appearing to emerge from circular area in centre of anal plate and extending to beyond posterior margin of plate; ventral granulation sparse in central area posterior to gonostome; male tarsus IV strongly bisegmented.

Description

Pettalid with tergite VIII bilobed (Fig. 22_A, B_) and ventral margin of dorsal scutum curving ventrally in posterior margin. Lobes of tergite VIII not visible in dorsal view (Fig. 22_A_, 23_A_). Length of male holotype (Fig. 22) ~2.1 mm, width at widest point in second opisthosomal segment ~1.3 mm, width across ozophores ~0.9 mm. Most of body surface showing tuberculate–granular microstructure (Fig. 23). Transverse sulci prominent, especially in lateral view, with very small granules within sulci; longitudinal sulcus visible but granulose. Ozophores positioned at 45° angle relative to walking plane as typical in pettalids. Coxae of legs I and II mobile. Coxae of remaining legs fixed. Male coxae II–IV meeting at midline (Fig. 23_B_). Male gonostome small, subtriangular, wider than long, bordered on posterior margin by first opisthosomal sternite; male gonostome shorter than length of seam of contact of left and right coxae IV (Fig. 23_B_). Anal region of 'pettalid type' (Giribet and Boyer 2002) with tergite IX laterally covering sternite 9 and clearly meeting sternite 8 (Fig. 23_B_). Anal plate flat, granulose. Very long scopula emerging from circular area of posterior half of anal plate (Fig. 23_B_). Anal pore not visible. Spiracle circular with
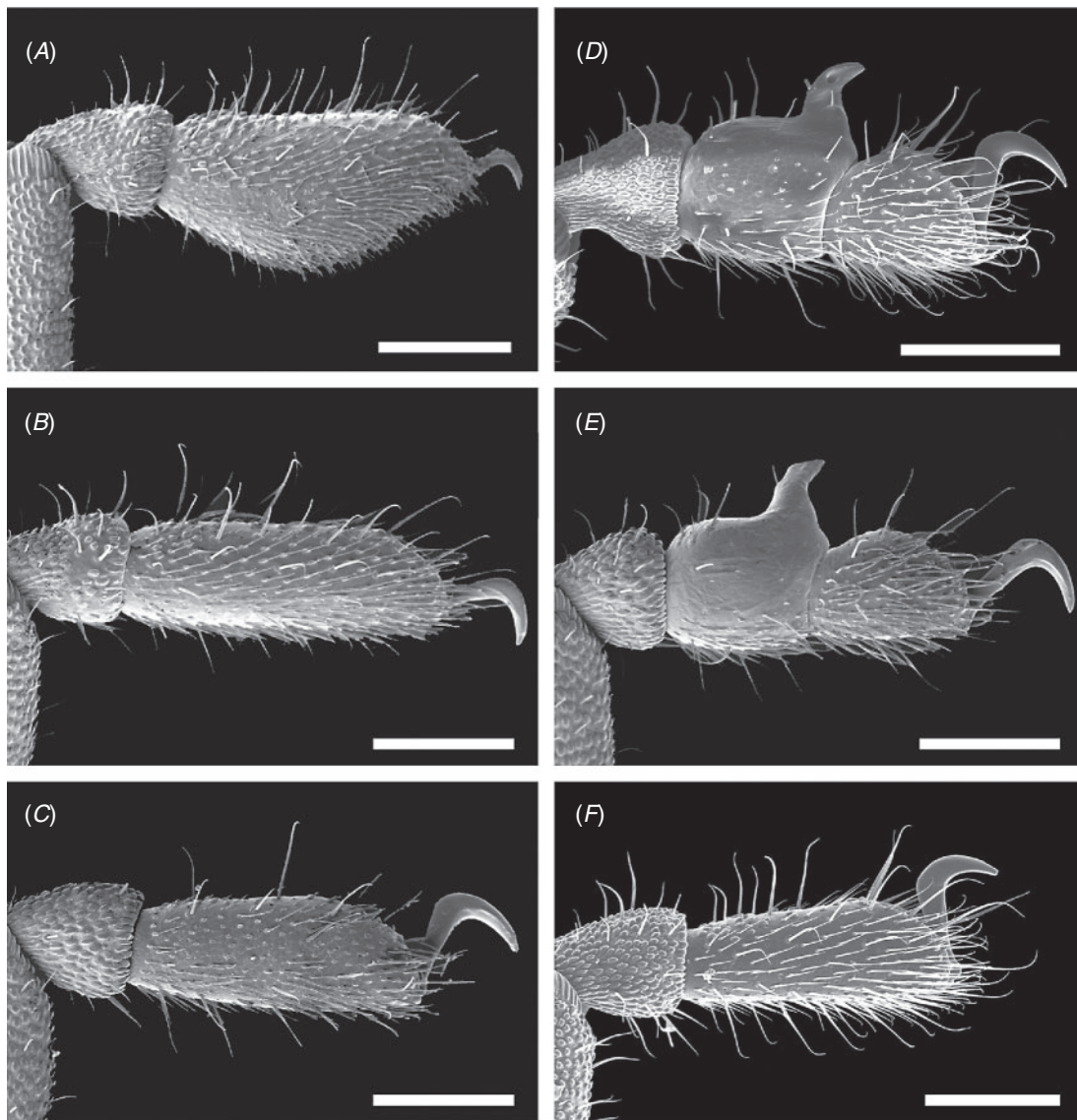
Fig. 26. *Austropurcellia sharmai*, sp. nov. (*A*) Tarsus and metatarsus I, MCZ IZ 132317; (*B*) tarsus and metatarsus II, MCZ IZ 132317; (*C*) tarsus and metatarsus III, MCZ IZ 132317; (*D*) male tarsus and metatarsus IV, lateral view, MCZ IZ 134698; (*E*) male tarsus and metatarsus IV, medial view, MCZ IZ 132317; (*F*) female tarsus and metatarsus IV, MCZ IZ 134698. Scale bars: 200 μm.

slightly recurved edges as found in 'open circle' type of Giribet and Boyer (2002) (Fig. 24*A*).

Chelicerae (Fig. 25*A*) short and relatively robust. Proximal article of chelicerae with dorsal crest, without ventral process. Median article with apodeme. Two types of dentition, as typical in pettalids (Fig. 25*A*). Measurements from male paratype of chelicera articles from proximal to distal (in mm): 0.49, 0.85, 0.21. Palp (Fig. 25*B*) with prominent ventral process on trochanter. Measurements from paratype male of palp articles from proximal to distal (in mm): 0.23, 0.32, 0.18, 0.26, 0.24.

Legs with all claws smooth, without ventral dentition or lateral pegs (Fig. 26). Tarsi smooth and metatarsi ornamented (Fig. 26). Ventral side of tarsus I with distinct solea (Fig. 26*A*). Male tarsus IV fully bisegmented (Fig. 26*D, E*). Adenostyle extremely robust and oriented vertically, with small pore at

apex on lateral (external) side (Fig. 26*D*). Short seta rising from medial (internal) face of adenostyle close to pore to below the apex (Fig. 26*D, E*); short seta arising from below adenostyle pore (Fig. 26*D*). Measurements from male paratype leg articles from proximal to distal (in mm): leg I 0.19, 0.58, 0.30, 0.39, 0.20, 0.40; leg II [trochanter damaged], 0.47, 0.23, 0.28, 0.14, 0.37; leg III [trochanter damaged], 0.40, 0.21, 0.29, 0.16, 0.34; leg IV 0.22, 0.47, 0.26, 0.30, 0.18, 0.39.

Etymology

The specific epithet is a tribute to Prashant Sharma, an expert on the systematics of Opiliones who collected many of the specimens used in this study. During his undergraduate years Sharma helped to establish an invaluable database of SEM images of morphology
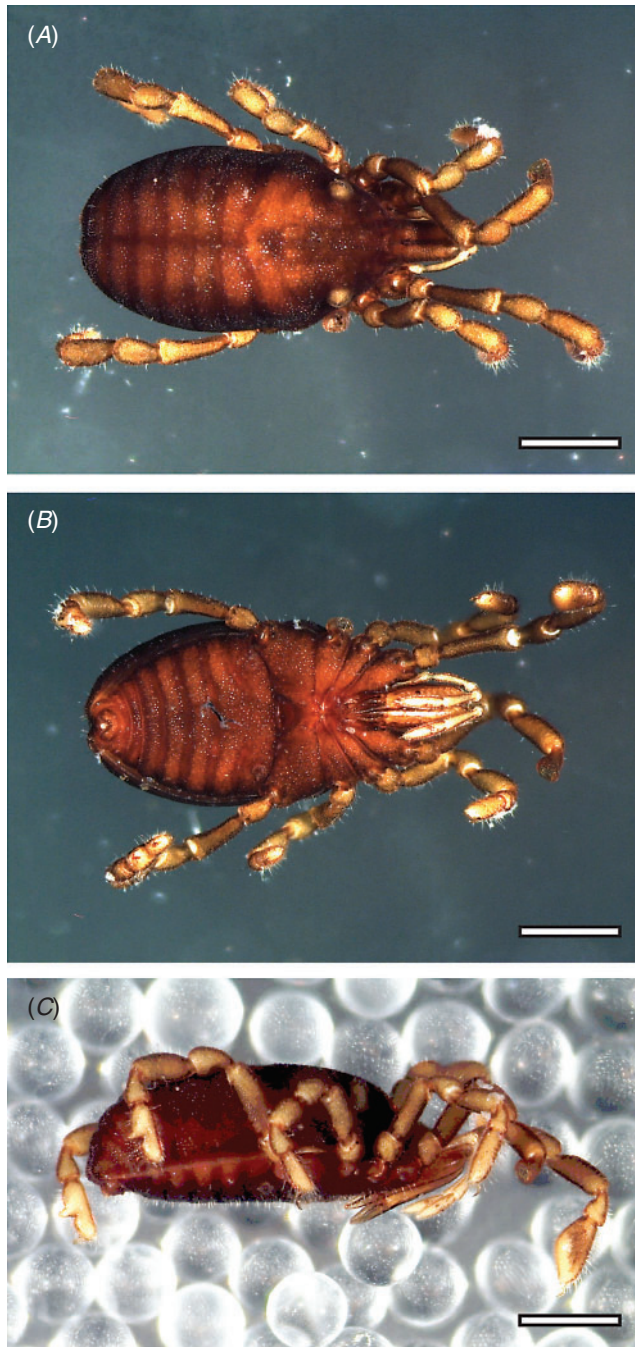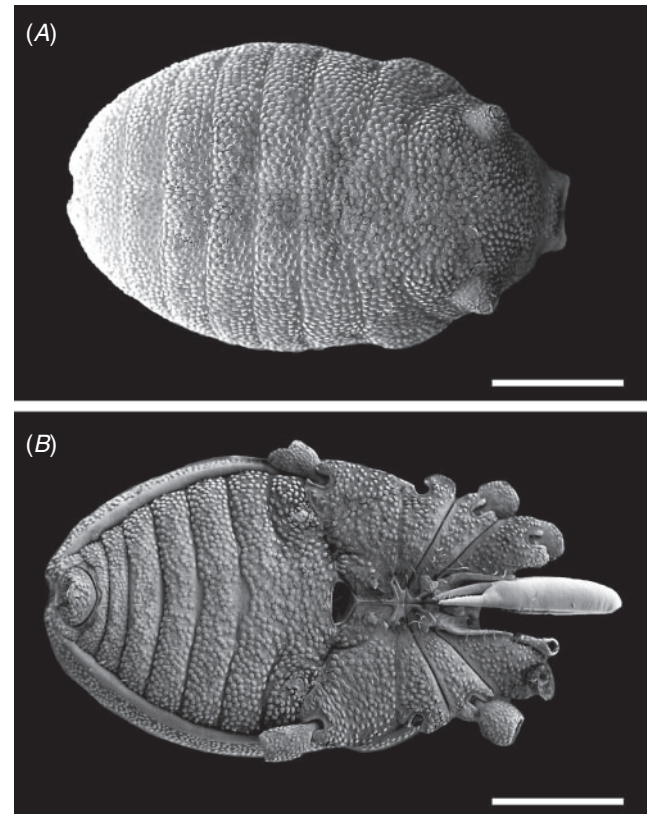
Fig. 28. *Austropurcellia tholei*, sp. nov., paratype male, MCZ IZ 132330. (*A*) Dorsal view; (*B*) ventral view. Scale bars: 0.5 mm.

Material examined

All material examined is from Queensland, Australia.

Holotype. Male (QM 61773), Josephine Falls, Wooroonooran National Park, Aus14, 17.433°S, 145.859°E, coll. C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall 5.vi.2011 [ex MCZ IZ 132331].

Paratypes. 5 ♂, 3 ♀, 6 juveniles, same data as holotype, MCZ IZ 132331.

Additional material studied. 1 ♂, 5 juveniles, 4 km E Lake Barrine, 17.267°S, 145.683°E, coll. R. W. Taylor & J. Feehan 1.vii.1971, ANIC 352. 2 ♂, 2 ♀, 3 juveniles, 4 km E Lake Barrine, 17.267°S, 145.683°E, coll. R. W. Taylor & Feehan 1.vii.1971, ANIC 352. 1 ♂, Lake Eacham, Crater Lakes National Park, 17.300°S, 145.783°E, coll. R. W. Taylor 19.ii.1973, ANIC berlesate 437. 3 ♂, 4 juveniles, Lake Eacham, Crater Lakes National Park, 17.285°S, 145.631°E [estimated], coll. I. D. Naumann & J. C. Cardale 25.v.1980, ANIC berlesate 681. 1 ♂, Josephine Falls, Wooroonooran National Park, 17.433°S, 145.852°E, coll. G. B. Monteith 19.iv.1997. 3 ♂, 2 juveniles, Rose Gums Wilderness Retreat, Atherton Plateau, OZCG-22, 17.315°S, 145.702°E, coll. C. Griswold & D. Silva 16.iii.2006, CAS ENT 9032238. 8 ♂, 4 ♀, Rose Gums Wilderness Retreat, Atherton Plateau, 17.314°S, 145.702°E, coll. G. Hormiga & L. Lopardo 15.iii.2006, MCZ IZ 134669. 1 ♂, 2 ♀, Lake Barrine, Crater Lakes National Park, Yungaburra, Locality 204, 17.245°S, 145.642°E, coll. C. D'Haese & G. Giribet 19.ii.2003, MCZ IZ 134697. 3 ♂, 12 juveniles, Cathedral Fig Tree, Danville State Forest, Aus1, 17.777°S, 145.660°E, coll. C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall 30.v.2011, MCZ IZ 132330. 2 ♀, Curtain Fig Tree, Yungaburra, Aus35, 17.286°S, 145.574°E, coll. C. M. Baker, S. L. Boyer, D. I. Laukó, H. A. Wiesner 26.v.2012, MCZ IZ 132333. 1 ♂, 1 juvenile, The Boulders, Wooroonooran National Park, Aus15, coll. C. Arango, C. M. Baker, S. L. Boyer, Z. R. Popkin-Hall 5.vi.2011, MCZ IZ 132332.
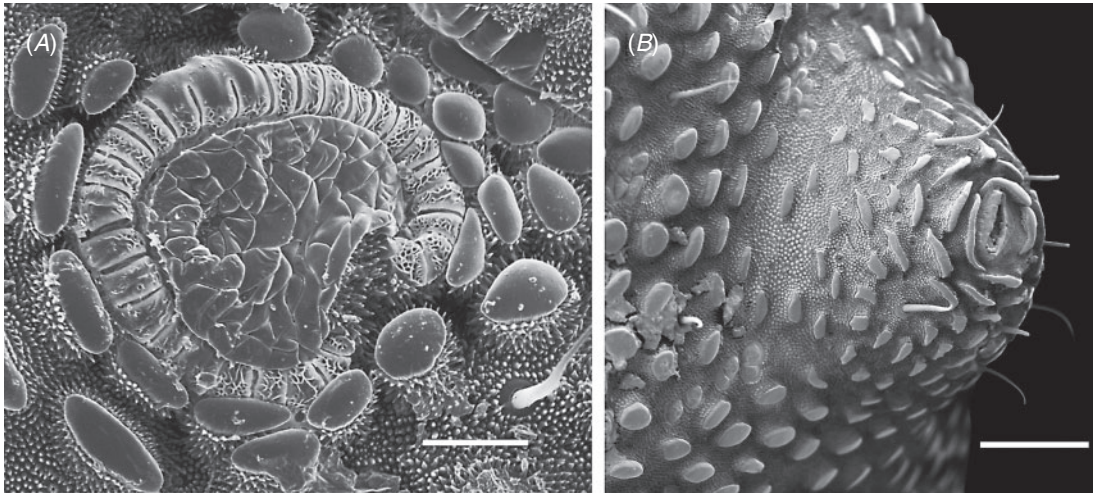

Fig. 27. *Austropurcellia tholei*, sp. nov., holotype male, QM. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.

of the Pettalidae of Australia and New Zealand, which laid the foundation for our present work.

Austropurcellia tholei Baker & Boyer, sp. nov.

(Figs 27–31)

urn:lsid:zoobank.org:act:17756093-84C5-4A59-A042-87624B85E137

Fig. 29. *Austropurcellia tholei*, sp. nov., paratype male, MCZ IZ 132330. (*A*) Spiracle, scale bar: 20 μm; (*B*) ozophore, scale bar: 50 μm.
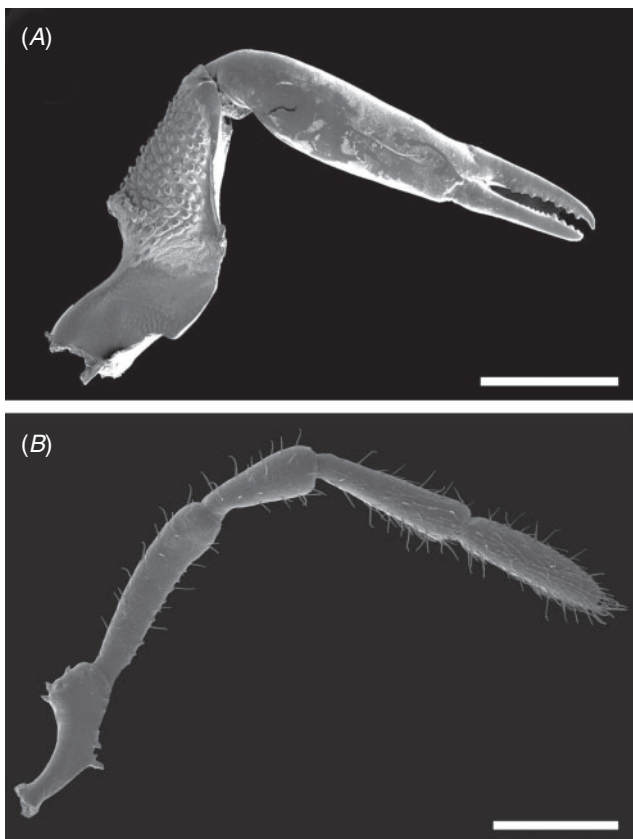

Fig. 30. *Austropurcellia tholei*, sp. nov., males. (*A*) Chelicera, MCZ IZ 132330; (*B*) palp, MCZ IZ 134699. Scale bars: 200 μm.

Diagnosis

Distinguished from congeners by anal plate convex in dorso-ventral plane in anterior half, with small and pointed scopula emerging from centre of plate; male tarsus IV partially

bisegmented; distinguished from *Austropurcellia daviesae* by consistent granulosity of anal plate throughout lateral and anterior areas.

Description

Pettalid with tergite VIII bilobed (Fig. 27*A, B*) and ventral margin of dorsal scutum forming straight edge parallel to walking plane (Fig. 27*C*). Length of male holotype (Fig. 27) ~1.8 mm, width across widest point in posterior third of prosoma ~1.0 mm, and width across ozophores ~0.7 mm. Most of body surface showing tuberculate–granular microstructure (Fig. 28). Transverse sulci distinct due to lack of granulation; no longitudinal sulcus (Fig. 28*A*). Ozophores positioned at 45° angle relative to walking plane as typical in pettalids (Fig. 28*A*). Coxae of legs I and II mobile. Coxae of remaining legs fixed. Male coxae II–IV meeting in midline (Fig. 28*B*). Male gonostome small, subtriangular, wider than long, bordered on posterior margin by first opisthosomal sternite; male gonostome shorter than length of seam of contact of left and right coxae IV (Fig. 28*B*). Anal region of 'pettalid type' (Giribet and Boyer 2002) with tergite IX laterally covering sternite 9 and clearly meeting sternite 8 (Fig. 28*B*). Anal plate convex and visible in lateral view (Fig. 27*C*) and granulose with very small scopula emerging from centre (Fig. 28*B*). Anal pore not visible. Spiracle circular with slightly recurved edges as found in 'open circle' type of Giribet and Boyer (2002) (Fig. 29*A*).

Chelicerae (Fig. 30*A*) short and relatively robust. Proximal article of chelicerae with dorsal crest, without ventral process. Median article with apodeme. Two types of dentition, as typical in pettalids (Fig. 30*A*). Measurements from male paratype of chelicera articles from proximal to distal (in mm): 0.65, 0.84, 0.27. Palp (Fig. 30*B*) with prominent ventral process on trochanter. Measurements from paratype male of palp articles from proximal to distal (in mm): 0.27, 0.31, 0.20, 0.26, 0.28.

Legs with all claws smooth, without ventral dentition or lateral pegs (Fig. 31). Tarsi smooth (Fig. 31). Ventral side of tarsus I with distinct solea (Fig. 31*A*). Metatarsus I and metatarsus II heavily ornamented in basal half but smooth and slightly swollen in distal
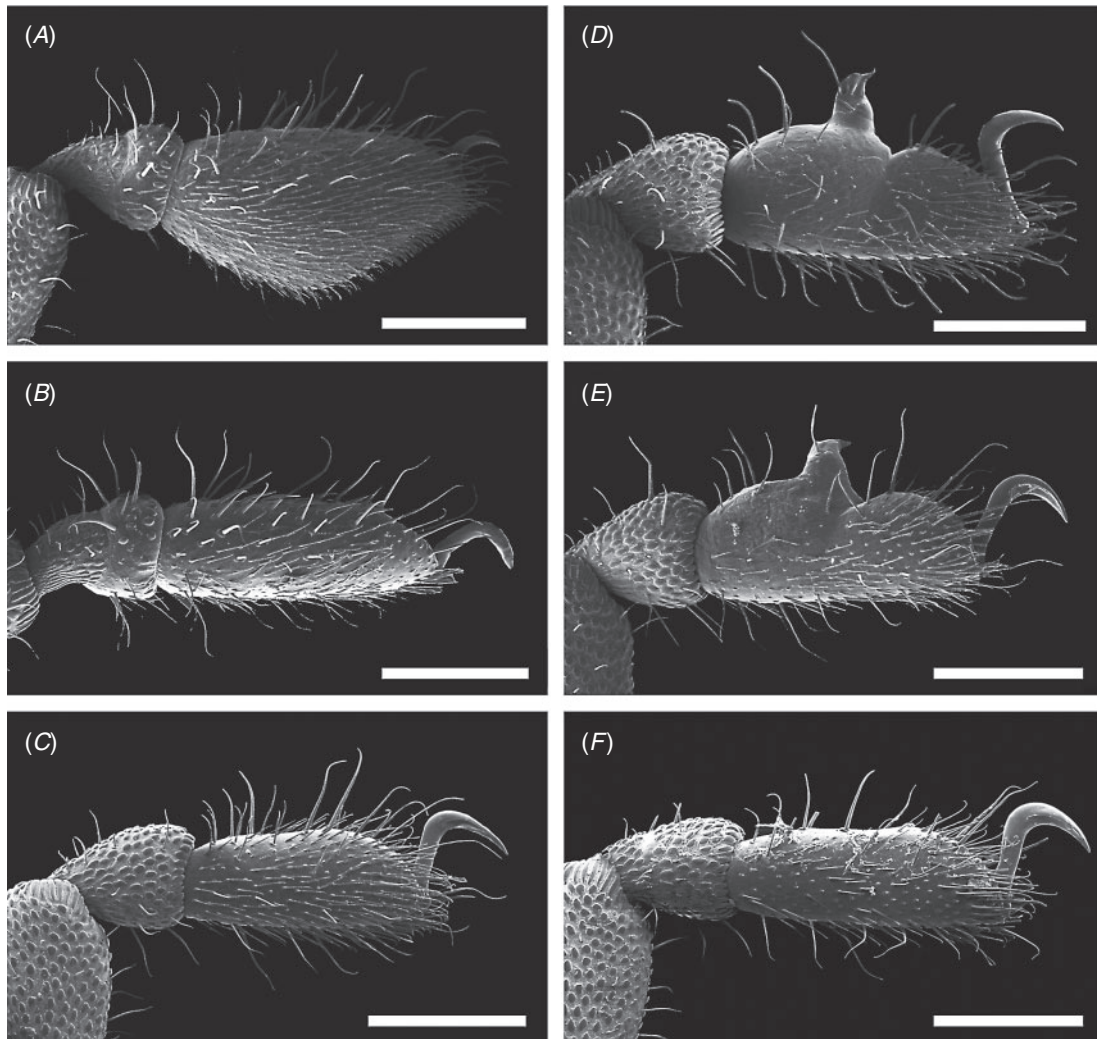
Fig. 31. *Austropurcellia tholei*, sp. nov. (*A*) Tarsus and metatarsus I, MCZ IZ 132330; (*B*) tarsus and metatarsus II, MCZ IZ 132330; (*C*) tarsus and metatarsus III, MCZ IZ 132330; (*D*) male tarsus and metatarsus IV, lateral view, MCZ IZ 132330; (*E*) male tarsus and metatarsus IV, medial view, MCZ IZ 132330; (*F*) female tarsus and metatarsus IV, MCZ IZ 132331. Scale bars: 200 μm.

half, leading to the appearance of 'cuff' (Fig. 31*A, B*). Remaining tarsi with ornamented metatarsus (Fig. 31*C–F*). Male tarsus IV partially bisegmented (Fig. 31*D, E*). Adenostyle extremely robust and oriented vertically, with small pore at apex on lateral (external) side (Fig. 31*D*). Long seta rising from medial (internal) face of adenostyle close to pore to well above apex (Fig. 31*D, E*); short seta arising from below adenostyle pore (Fig. 31*D*). Measurement of male paratype leg articles: leg I [trochanter damaged], 0.53, 0.22, 0.40, 0.19, 0.41; leg II 0.17, 0.44, 0.20, 0.32, 0.15, 0.36; leg III 0.17, 0.35, 0.19, 0.30, 0.17, 0.31; leg IV 0.25, 0.49, 0.25, 0.36, 0.16, 0.37.

Etymology

The specific epithet is a tribute to Jeff Thole, whose technical support of our scanning electron microscopy work has been invaluable to our efforts to understand the diversity, anatomy, and evolution of *Austropurcellia*.

Results

Phylogenetic analysis

Partitioned Bayesian analysis of the entire dataset resulted in a well resolved tree (Fig. 32). All morphologically distinct species were retrieved as monophyletic with high support from Bayesian, likelihood, and parsimony analyses (Fig. 32). *Austropurcellia* was retrieved as monophyletic with high support, and *A. acuta* (southern Queensland) + *A. clousei* sp. nov. (southernmost Wet Tropics) were retrieved as the sister group to the remaining clade, which we refer to as the Wet Tropics endemic clade (Fig. 33). Within the Wet Tropics endemic clade, species from the northernmost reaches of the Wet Tropics formed a paraphyletic grade with respect to a monophyletic group that includes central and north-central species (Fig. 34). Within that central + north-central group, we consistently retrieved a well supported clade composed of species from the central Wet Tropics (Fig. 35).
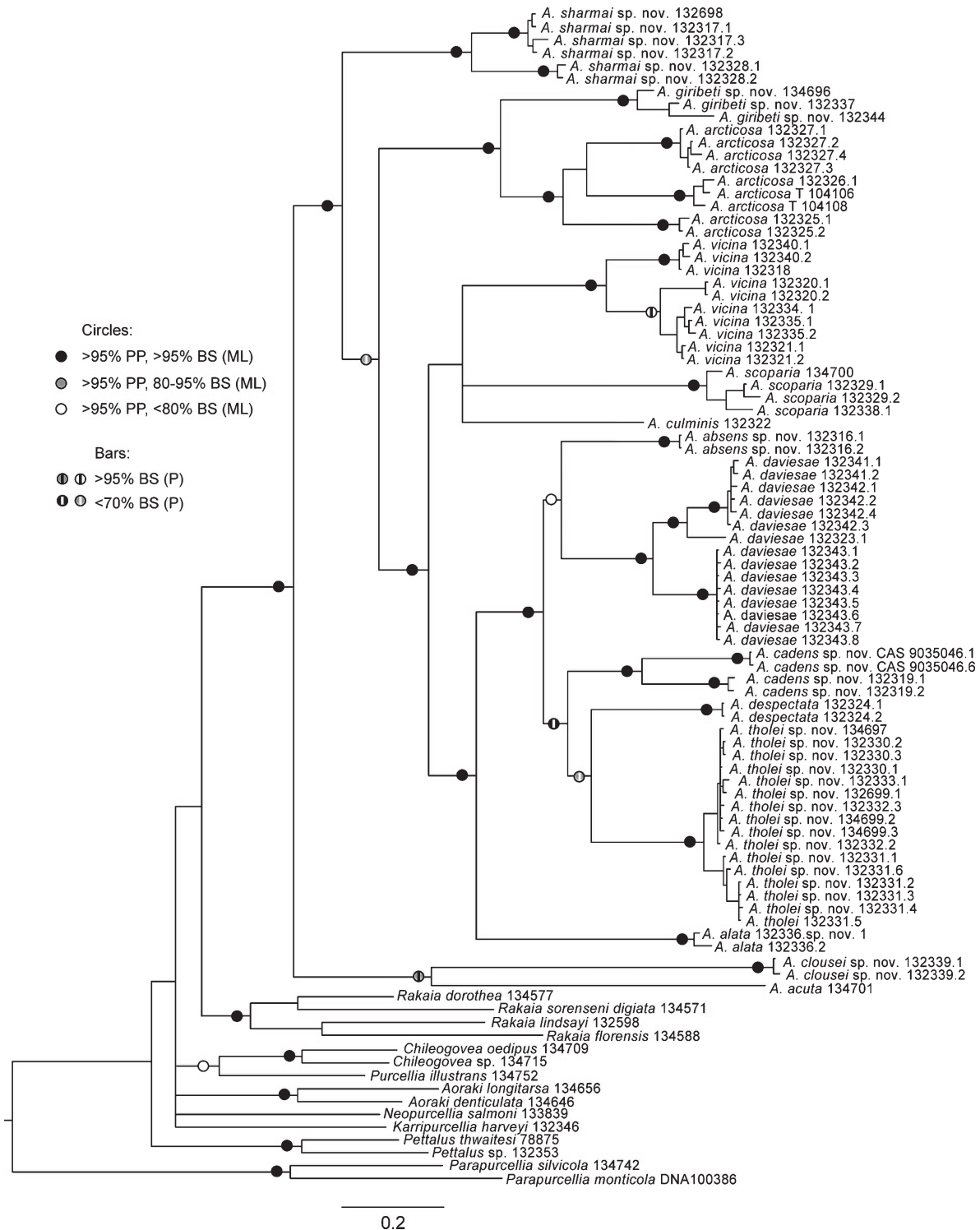
Fig. 32. Phylogeny of *Austropurcellia* based on partitioned Bayesian analysis of four loci. Circles indicate >95% posterior probability, with varying levels of bootstrap support from partitioned maximum-likelihood analysis. (BS): black indicates >95% BS; grey indicates 80–95% BS; white indicates <80% BS. Bootstrap support from parsimony analysis is above 70% for all branches indicated with circles, with a few exceptions; cases in which support from parsimony is lower than 70% are indicated by vertical white lines within circles. Black lines within circles indicate that bootstrap support from parsimony analysis is greater than 95%, and is noted only in cases in which bootstrap support from the maximum-likelihood analysis is <95%. Outgroups are other members of the family Pettalidae from New Zealand (*Aoraki*, *Neopurcellia*, *Rakaia*), Chile (*Chileogovea*), South Africa (*Parapurcellia*, *Purcellia*), Western Australia (*Karripurcellia*), and Sri Lanka (*Pettalus*).
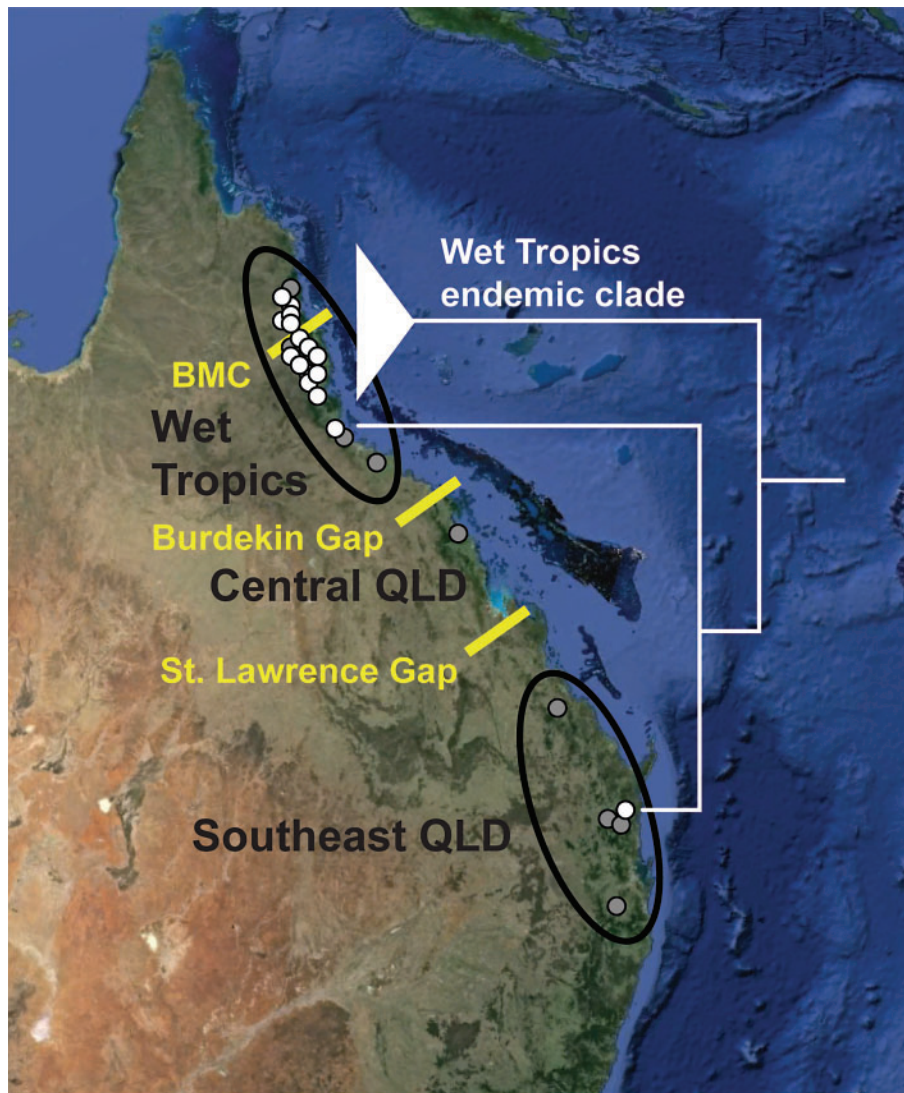
Fig. 33. Phylogeny of *Austropurcellia* in broad biogeographic context. White circles indicate localities for which molecular data has been generated; grey circles are localities for which DNA-quality specimens are not currently available. Yellow bars indicate geographic landmarks: the Black Mountain Corridor (BMC), the Burdekin Gap, and the St Lawrence Gap (see Fig. 1). Black ovals indicate major geographic areas. *A. acuta* from south-east Queensland is sister to *Austropurcellia clousei*, sp. nov. from the southernmost Wet Tropics; this clade is in turn sister to the remaining Wet Tropics species, noted as the Wet Tropics endemic clade.

GMYC retrieved every population as a species, with a small number of exceptions. In several cases, populations from localities extremely close to one another were grouped: *Austropurcellia arcticosa* from Marrja Boardwalk and a second locality on Cape Tribulation (WAM T 104106–8 MCZ IZ 132326), *Austropurcellia vicina* Boyer & Reuter, 2012 from Mt Lewis and the Mossman Circuit Track ~10 km apart from each other (MCZ IZ 132321 and MCZ IZ 132335), *A. vicina* from two collections from the Crystal Cascades trail in Barron Gorge National Park (MCZ IZ 132318 and MCZ IZ 132340), *Austropurcellia scoparia* from two collections on Mt Lewis (MCZ IZ 134700 and MCZ IZ 132329), and *A. daviesae* from two collections at Russell River (MCZ IZ 106377 and MCZ IZ 106378). More interesting is the case of *A. tholei*, sp. nov., in which specimens from several localities within ~50 km of each other were grouped together: Rose Gums Wilderness Retreat, Curtain Fig, Cathedral Fig, The Boulders, and Lake Barrine (MCZ IZ 134697, MCZ 132330, MCZ IZ 134697, MCZ IZ 134699, MCZ IZ 132322).

Discussion

The rainforests of the Wet Tropics have received considerable attention from evolutionary biologists interested in the role of historical climate change in shaping present-day biodiversity (Hugall *et al.* 2002; Graham *et al.* 2006; Bell *et al.* 2007, 2012). Biogeographic study of extremely dispersal-limited animals such as leaf litter arachnids can reveal the signature of
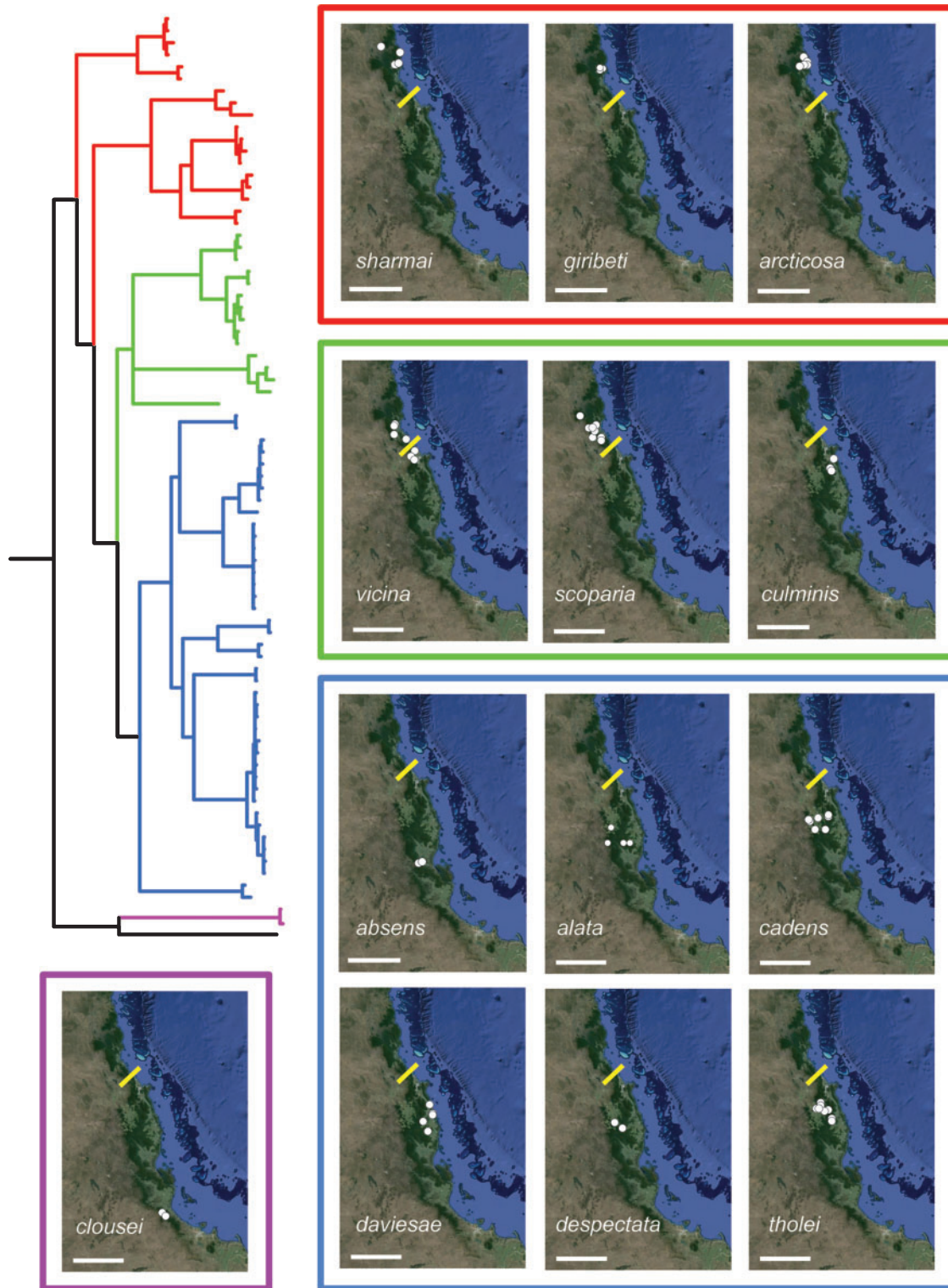
Fig. 34. Phylogeny of *Austropurcellia* highlighting biogeographic relationships. Maps include only the Wet Tropics (Figs 1, 33). Branch colours correspond to biogeographic areas; red indicates species found in the northernmost Wet Tropics, green indicates species found in north-central Wet Tropics, blue indicates species from the central Wet Tropics, and purple indicates *Austropurcellia clousei* from the southern Wet Tropics. The black branch represents *A. acuta* from southern Queensland (Fig. 33). Maps illustrate all known collections for individual species and are bordered in colours that correspond to the branch colours in the phylogeny (after Fig. 32). The yellow line on each map indicates the location of the Black Mountain Corridor. The scale bar represents 100 km.
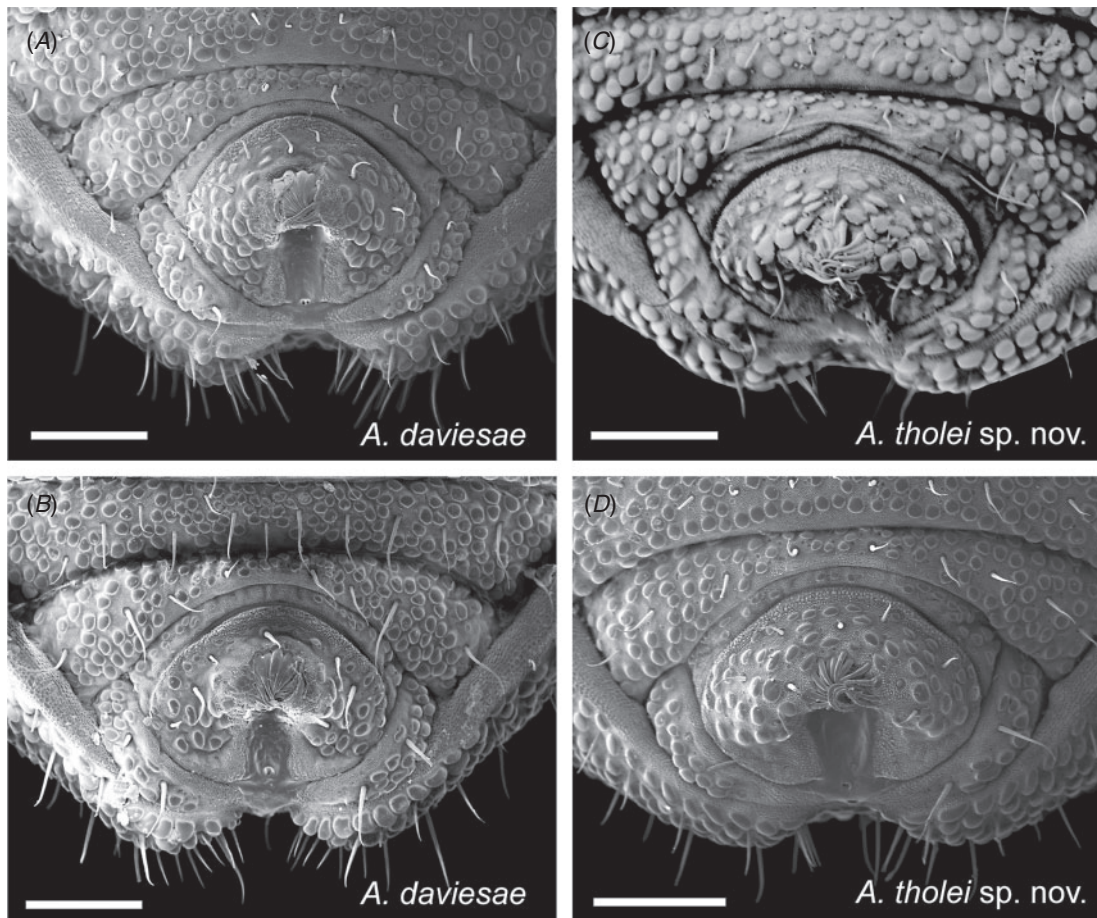
Fig. 35. Ventral posterior morphology of *A. daviesae* Juberthie, 1989 and *A. tholei*, sp. nov. These two species are distinguished by molecular data and also by the degree of ornamentation of the anal plate, which is granulated anterior to the scopula in *A. tholei*, sp. nov. but not in *A. daviesae*. (*A*) *A. daviesae* from Russell River, MCZ IZ 132341; (*B*) *A. daviesae* from Ella Bay, MCZ IZ 132343; (*C*) *A. tholei*, sp. nov. from Cathedral Fig Tree, MCZ IZ 132330; (*D*) *A. tholei*, sp. nov. from Josephine Falls, MCZ IZ 132331. Scale bars: 100 µm.

ancient events and processes (Boyer *et al.* 2007*b*; Rix and Harvey 2012*b*; Murienne *et al.* 2013), and therefore work on such groups has the potential to enrich our understanding of evolutionary dynamics within the Wet Tropics biodiversity hotspot. In order to develop *Austropurcellia* as a new study system for testing hypotheses about the evolutionary history of the Wet Tropics biota, it is first necessary to describe and map the diversity of these poorly known animals. Here, we have made progress in documenting the diversity of the Wet Tropics mite harvestmen and provide the first phylogeny for the group. Below, we discuss first our taxonomic findings, and then the biogeography and evolution of the group.

Diversity of Austropurcellia

Although researchers have known for nearly a century that mite harvestmen exist in the forests of Queensland, this group has received little taxonomic attention until very recently. The majority of *Austropurcellia* species – 13 of 19, including the six species described in the present study – have been described by

our research group since 2012 (Boyer and Reuter 2012; Popkin-Hall and Boyer 2014).

All species identified on the basis of morphology were retrieved as monophyletic with high support in phylogenetic analysis of molecular data (Fig. 32). Initially, specimens we had identified as *Austropurcellia daviesae* were retrieved in two clades that were not sister to each other; however, in re-examination of morphology using SEM, we discovered a subtle but consistent difference in the degree of ornamentation of the anal plate anterior to the scopula that separates these two clades as morphologically distinct species (Fig. 35), *A. daviesae* and *A. tholei*, sp. nov. Therefore, species identifications based on morphology and species identifications based on molecular data are fully congruent. The discovery of *A. tholei*, sp. nov., which is nearly indistinguishable from *A. daviesae*, is not surprising; Boyer *et al.* (2007*a*) performed a phylogeographic study of a widespread New Zealand mite harvestman, *Aoraki denticulata*, and found genetic divergences that likely indicate the presence of cryptic species, and Clouse and Wheeler (2014) have discovered cryptic species of mite harvestmen from Florida. Cryptic species
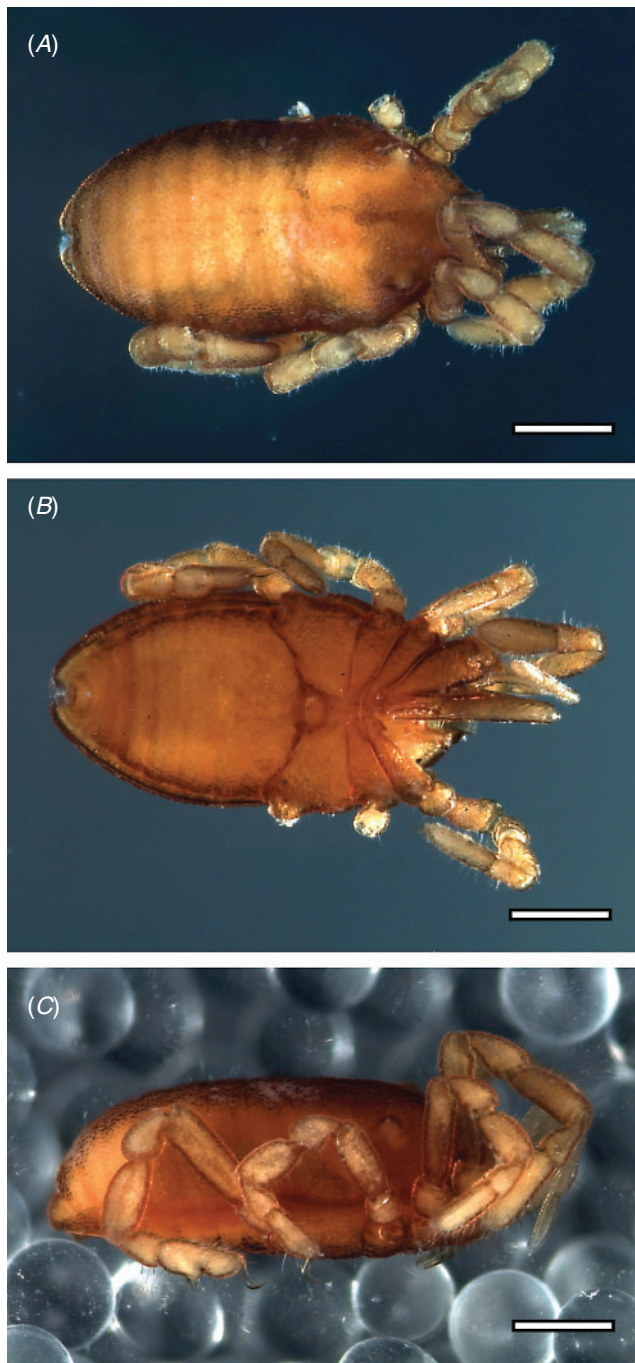
Fig. 36. *Austropurcellia arcticosa* holotype male, QM S 334. (*A*) Dorsal view; (*B*) ventral view; (*C*) lateral view. Scale bars: 0.5 mm.

have been well documented in other groups of dispersal-limited arachnids (Bond and Stockman 2008; Satler *et al.* 2013) and may be the rule rather than the exception in these taxa.

In the course of describing the new species *A. giribeti*, sp. nov. and *A. sharmai*, sp. nov. from the northern Wet Tropics, we have examined specimens from many collections of the two previously described species from the area, *A. arcticosa* and *A. forsteri* – both of whose original descriptions lack key details. The description of

A. arcticosa is illustrated with rudimentary drawings only, and includes little detail on the fourth tarsus of the male, an important character in cyphophthalmid systematics. According to Cantrell, the fourth tarsus is entire (not bisegmented), but our work reveals a more nuanced anatomy. Examination of the type specimen (Fig. 36) and others from the type locality and environs reveals that the fourth tarsus of *A. arcticosa* males bears a suture on the medial side that is closest to the animal's body (Fig. 37), while the lateral side that faces away from the body exhibits only the slightest hairline of a suture that merges with the margins of the cuticular ossicles (Fig. 38). The description of *A. forsteri*, published at the end of Juberthie's career, reveals a taxonomist in decline; in comparison with his exemplary description of *A. daviesae* (1989), which included both SEM images and beautiful drawings, this work lacks detail. Most unfortunately, the type materials of *A. forsteri* cannot be located at this time. The shortcomings of the original descriptions of *A. arcticosa* and *A. forsteri*, combined with limited sampling of *Austropurcellia* from across the Wet Tropics, hampered efforts to identify specimens used in previous phylogenetic analyses (e.g. Boyer *et al.* 2007*b*; Boyer and Giribet 2007) and specimens previously identified in the studies as *A. arcticosa* and *A. forsteri* have been reidentified as *A. giribeti*, sp. nov. and *A. sharmai*, sp. nov. respectively. SEM examination of all four of these northern species reveals characters related to the fourth tarsus (Figs 37, 38), the anal plate and scopula (Fig. 39), and the shape and ornamentation of the lobes of tergite VIII (Fig. 40) that distinguish these animals from each other.

Biogeographic patterns

The forests of eastern Queensland have been described as a 'mesotherm archipelago' consisting of 'islands' of forest habitat separated by drier areas (Nix 1991; Byrne *et al.* 2011). The most notable dry barriers are the Burdekin and St Lawrence Gaps (Fig. 1), which mark major biogeographic breaks in such diverse animal groups as birds (Kikkawa and Pearse 1969), mammals (Winter 1984), skinks (Moussalli *et al.* 2005; Dolman and Moritz 2006), beetles (Allsopp 1995), and centipedes (Giribet and Edgecombe 2006). Australian assassin spiders are also known from localities throughout eastern Queensland, and have been the subject of a recent phylogenetic analysis (Rix and Harvey 2012*b*); results of that study indicate that the Wet Tropics assassin spiders constitute a monophyletic group. Given these known barriers in other groups of animals, we expected that within *Austropurcellia* the Wet Tropics species (north of the Burdekin Gap) would form a monophyletic clade, sister to a clade of species from south of the Burdekin Gap. However, contrary to our expectations, we retrieved *A. clousei*, sp. nov. from the Paluma Range in the southern Wet Tropics as the sister taxon to *A. acuta* from south-east Queensland with high support (Figs 32, 33). This group is, in turn, sister to all other Wet Tropics species, which we henceforth refer to as the Wet Tropics endemic clade (Fig. 33). This relationship is not unexpected from the point of view of anatomy, as both *A. acuta* and *A. clousei*, sp. nov. have thin, blade-like adenostyles that are distinct from the thick robust adenostyle considered to be a diagnostic character of *Austropurcellia* by Boyer and Giribet (2007), as previously noted by Popkin-Hall and
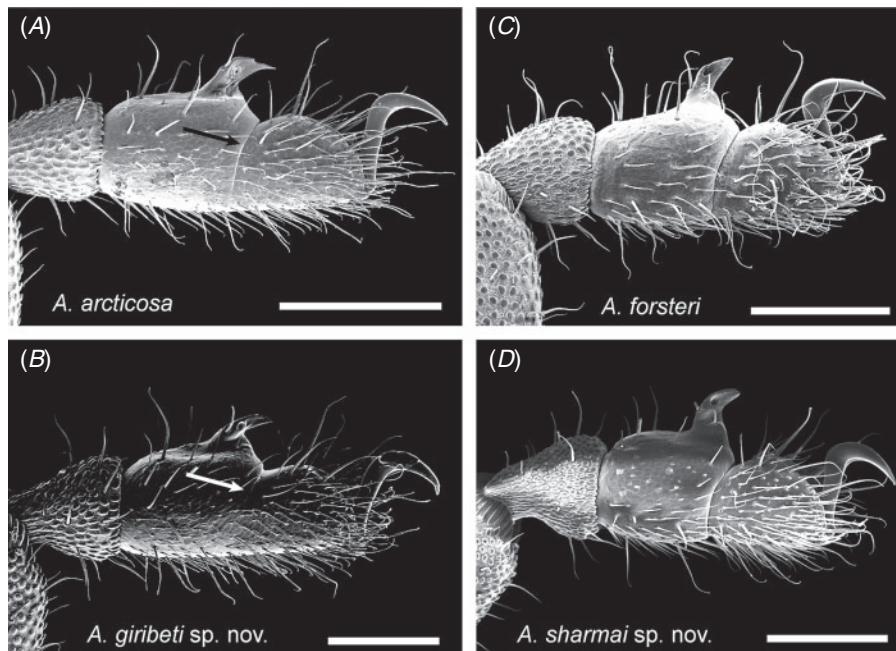
Fig. 37. Male tarsus and metatarsus IV in lateral (external) view, representing four species that occur north of the Black Mountain Barrier. The suture that divides the fourth tarsus is subtle in *A. arcticosa* (black arrow), an incomplete hairline in *A. giribeti*, sp. nov. (white arrow), and robust in the two remaining species. (*A*) *A. arcticosa* Cantrell, 1980 from Dubuji Boardwalk, MCZ IZ 132327; (*B*) *A. giribeti*, sp. nov. from Daintree Village, MCZ IZ 132344; (*C*) *A. forsteri* Juberthie, 2000 from Cape Tribulation Top Camp (type locality), QM berlese 486; (*D*) *A. sharmai*, sp. nov. from Emmagen Creek, MCZ IZ 132317. Scale bars: 200 μm.
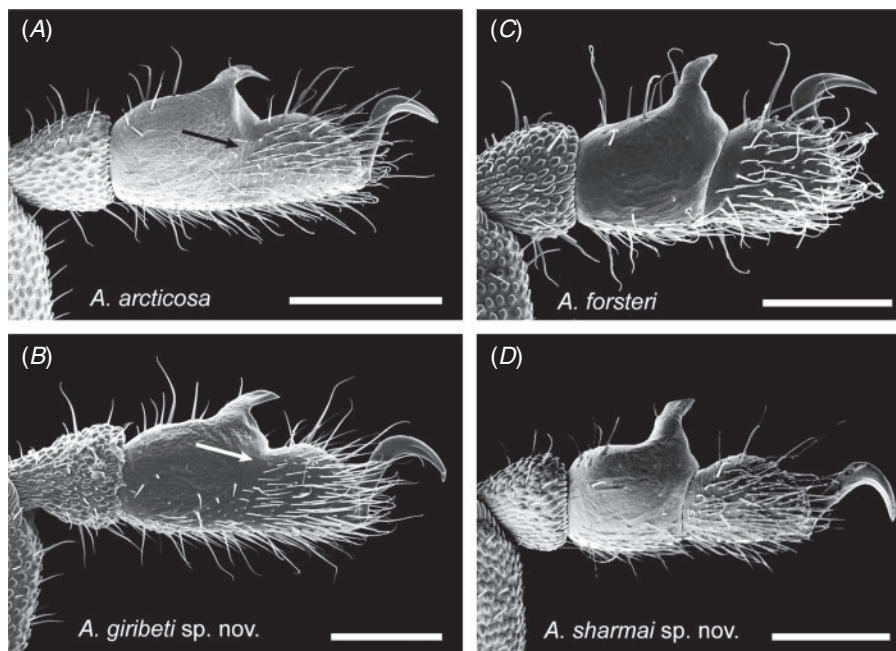

Fig. 38. Male tarsus and metatarsus IV in medial view, representing four species that occur north of the Black Mountain Barrier. The suture that divides the fourth tarsus is an incomplete hairline in *A. arcticosa* (black arrow) and *A. giribeti* (white arrow) but robust and complete in the remaining two species. (*A*) *A. arcticosa* Cantrell, 1980 from Dubuji Boardwalk, MCZ IZ 132327; (*B*) *A. giribeti*, sp. nov. from Daintree Village, MCZ IZ 132344; (*C*) *A. forsteri* Juberthie, 2000 from Cape Tribulation Top Camp (type locality), QM berlese 486; (*D*) *A. sharmai*, sp. nov. from Emmagen Creek, MCZ IZ 134698. Scale bars: 200 μm.
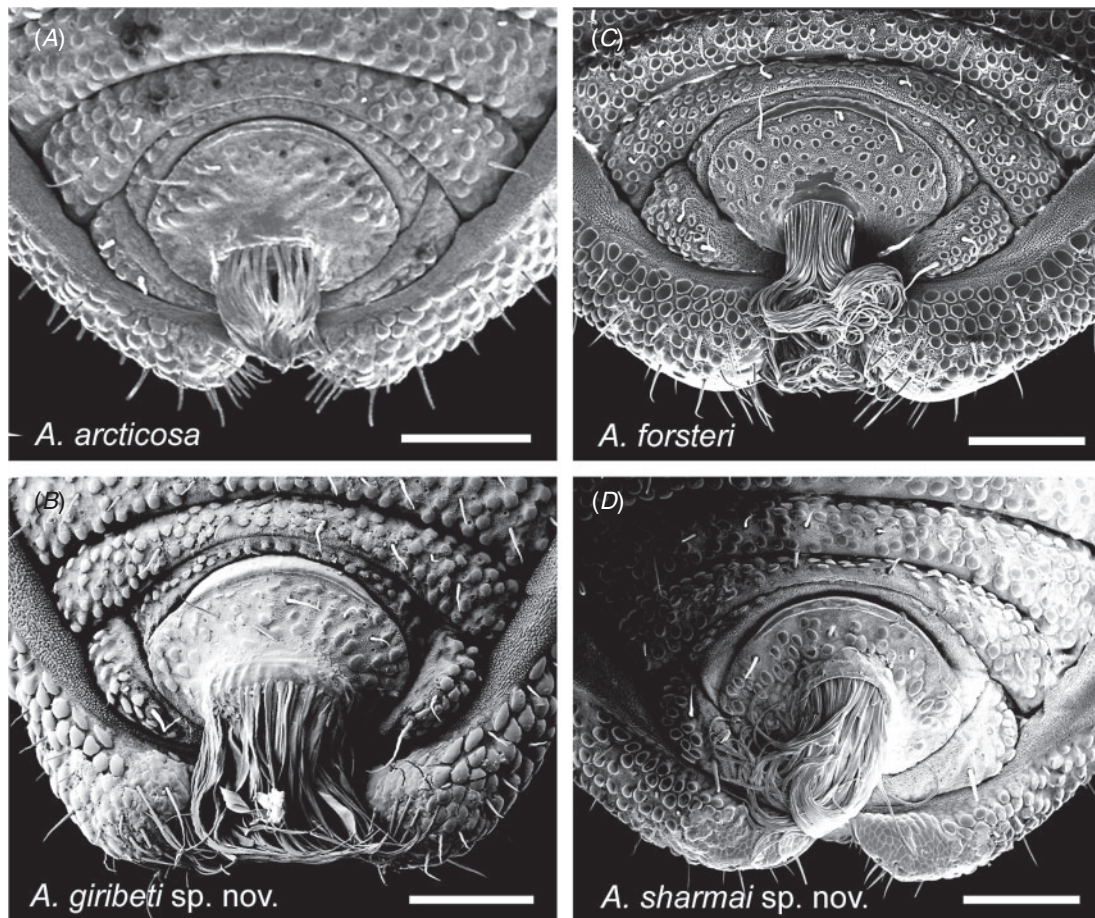
Fig. 39.   Ventral posterior morphology, representing four species that occur north of the Black Mountain Barrier. (*A*) *A. arcticosa* Cantrell, 1980 from Dubuji Boardwalk, MCZ IZ 132327; (*B*) *A. giribeti*, sp. nov. from Alexandra Range, QM berlese 252; (*C*) *A. forsteri* Juberthie, 2000 from Cape Tribulation Top Camp (type locality), QM berlese 486; (*D*) *A. sharmai*, sp. nov. from Emmagen Creek, MCZ IZ 132317. Scale bars: 100 μm.

Boyer (2014). Although this finding is surprising from a biogeographical point of view, mite harvestmen are known for defying breaks such as Wallace's Line and Lydekker's Line in South-east Asia, possibly due to the ancient age of the suborder in comparison to vertebrate groups, as well as the potential for relictual lineages of Cyphophthalmi to persist in tiny patches of suitable habitat across millennia (Clouse and Giribet 2007, 2010; Stelbrink *et al.* 2012).

In more vagile animals with larger species ranges, the Black Mountain Corridor (BMC) (Figs 1, 33, 34), an area from which rainforest vanished during the Last Glacial Maximum, marks a phylogeographic break within species. Endemism occurs on a much finer spatial scale within *Austropurcellia* than it does in Wet Tropics vertebrates, or even dung beetles or gastropods (with some notable exceptions within microhylid frogs: Hoskin 2004). Species ranges, even within areas that have been thoroughly sampled, do not exceed 100 km in any dimension and most are much smaller (Fig. 34). There is one species, *A. vicina*, whose distribution does span the BMC (Fig. 34; however, although we find two well supported and genetically divergent clades within this species, they do not correspond to populations from north

and south of the BMC. One lineage comprises specimens from a locality north of the BMC (MCZ IZ 132340 and 132318), and the other includes specimens from both north and south of the BMC (MCZ IZ 132321, 132334, and 132335). Likewise, we do not find a phylogenetic break centred around the BMC within the genus (Fig. 34). Again, the great age of the genus and the potential for mite harvestmen to persist in refugia too small to harbor vertebrates may explain a biogeographic pattern that runs contrary to expectations established through study of vertebrates.

Despite the lack of a major phylogenetic or phylogeographic break corresponding to the BMC, north–south biogeographic structure is evident within the genus. To begin with the most basal lineages, we find that the species from north of the BMC (*A. arcticosa*, *A. giribeti*, sp. nov., and *A. sharmai*, sp. nov.) form a paraphyletic grade that is sister to the remainder of the Wet Tropics endemic clade. Within the central Wet Tropics we find a well supported clade that includes six species from the Atherton Tablelands, the Malbon–Thompson Uplands, the Kirrama Range, Mount Bellenden Ker, and Mount Bartle Frere (indicated by blue in Fig. 34). The sister taxon of this group is uncertain; however, there is high support for the
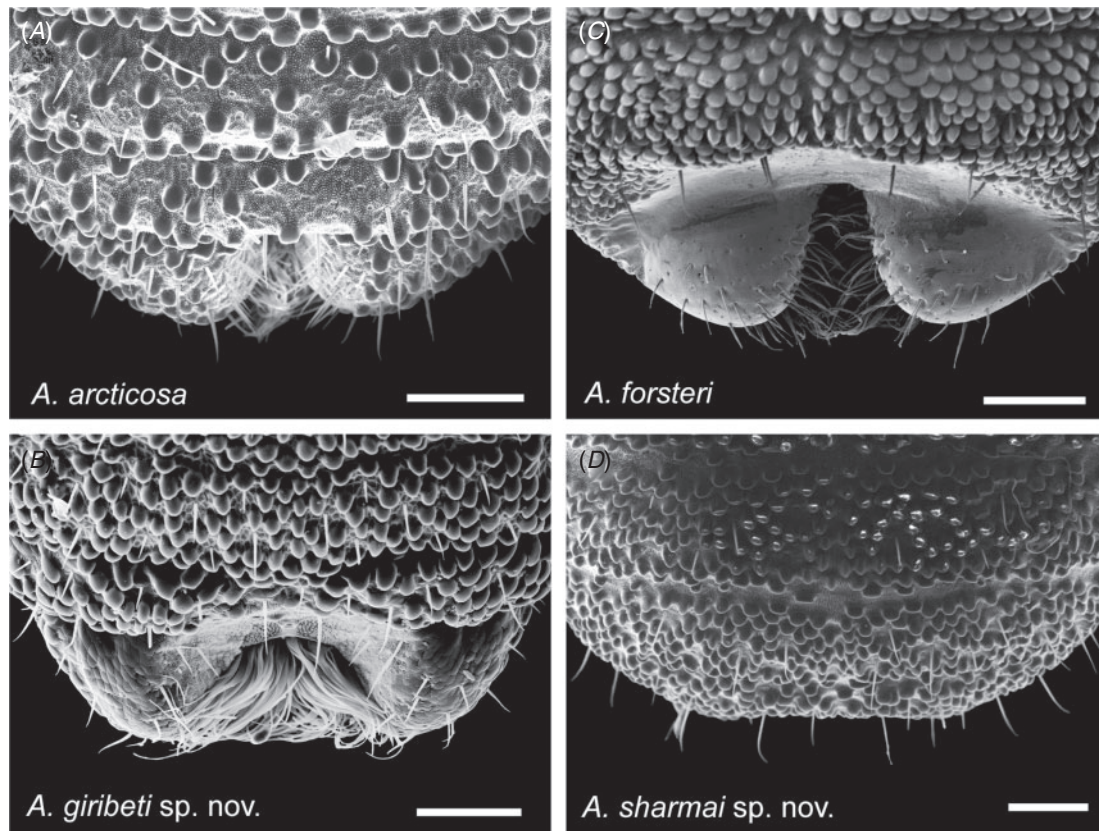
Fig. 40. Dorsal posterior morphology, representing four species that occur north of the Black Mountain Barrier. (*A*) *A. arcticosa* Cantrell, 1980 from Marrja Boardwalk, MCZ IZ 132326; (*B*) *A. giribeti*, sp. nov. from Alexandra Range, QM berlese 252; (*C*) *A. forsteri* Juberthie, 2000 from Mt. Pieter Botte summit, QM 872; (*D*) *A. sharmai*, sp. nov. from Emmagen Creek, MCZ IZ 132317. Scale bars: 100 µm.

north-central species *A. culminis* Boyer & Reuter, 2012, *A. scoparia*, and *A. vicina* as closely related to the central Wet Tropics group (Figs 32, 34).

It has been suggested that the Wet Tropics region could have sustained rainforests continuously since the Late Cretaceous (Morley 2000). It is possible that *Austropurcellia* has inhabited the area for just as long, as the age of earliest diversification of the genus has been dated to the Late Cretaceous (Giribet *et al*. 2010). Although these forests are ancient, there is ample abundance that their connectivity and extent have changed, based on models that go back to the LGM (VanDerWal *et al*. 2009) – and this history has shaped the diversity of rainforest animals across the region. Using maps of rainforest stability based on such models, Graham *et al*. (2006) found that relative stability of rainforest habitat from the LGM through the present was a predictor of relative diversity in Wet Tropics vertebrates, supporting a 'museum' model of biodiversity preservation within refugia. This effect was strongest in dispersal-limited microhylid frogs, and weaker in the most vagile group considered, birds. Likewise, Edward (2011) noted that areas of highest endemism in goblin spiders corresponded with the areas of high rainforest stability found by Graham *et al*. (2006). Does such a pattern hold for *Austropurcellia*? We note that there seems to be more range overlap between the

northernmost species of this genus, in comparison with species from other areas of the Wet Tropics (Fig. 34). And, it is interesting to note a contrast between two of the *Austropurcellia* species represented by multiple populations in the current study, *A. arcticosa* and *A. tholei*, sp. nov.: *A. tholei*, sp. nov. exhibits shallow divergences between several populations (Fig. 32) and our GMYC analysis grouped multiple populations into a single species. On the other hand, *A. arcticosa*, sampled from a smaller geographic area, appears to be more highly structured (Fig. 32) and GMYC analysis did not recognise any species composed of specimens from multiple locations. It is possible that such contrasts in range overlap and genetic diversity in different subregions of the Wet Tropics could reflect differences in relative habitat stability over time in different areas, with a greater number of lineages preserved in areas of higher stability.

At present, several more undescribed *Austropurcellia* species from the Wet Tropics, known only from older museum material, still await description (authors' unpublished data). Description and mapping of these taxa will result in a more complete picture of the distribution of mite harvestman diversity across the Wet Tropics. In addition, it is likely that intentional collecting efforts will uncover additional diversity in the undersampled forests of central and south-east Queensland (Popkin-Hall and Boyer 2014). Future phylogenetic work incorporating wider

geographic and taxonomic sampling will help to clarify biogeographical patterns within this genus and permit tests of the hypothesis that Miocene aridification drove evolutionary divergences within this group as it did in other dispersal-limited arachnids of Queensland (Rix and Harvey 2012*b*). We have made considerable progress in documenting the diversity of this once-neglected cryptic group and reconstructing evolutionary relationships among its species, paving the way for historical biogeographic study of *Austropurcellia* within the Wet Tropics and beyond.

Acknowledgements

References

Adam, P. (1992). 'Australian Rainforests.' (Clarendon Press: Oxford.)

Allsopp, P. G. (1995). Biogeography of the Australian Dynastinae, Rutelinae, Scarabaeinae, Melolonthini, Scitalini and Geotrupidae (Coleoptera: Scarabaeoidea). *Journal of Biogeography* **22**, 31–48. doi:10.2307/2846071

Bell, K., Yeates, D., Moritz, C., and Monteith, G. (2004). Molecular phylogeny and biogeography of the dung beetle genus *Temnoplectron* Westwood (Scarabaeidae: Scarabaeinae) from Australia's wet tropics. *Molecular Phylogenetics and Evolution* **31**, 741–753. doi:10.1016/j.ympev.2003.09.010

Bell, K. L., Moritz, C., Moussalli, A., and Yeates, D. K. (2007). Comparative phylogeography and speciation of dung beetles from the Australian Wet Tropics rainforest. *Molecular Ecology* **16**, 4984–4998. doi:10.1111/j.1365-294X.2007.03533.x

Bell, R. C., MacKenzie, J. B., Hickerson, M. J., Chavarria, K. L., Cunningham, M., Williams, S., and Moritz, C. (2012). Comparative multi-locus phylogeography confirms multiple vicariance events in co-distributed rainforest frogs. *Proceedings. Biological Sciences* **279**, 991–999. doi:10.1098/rspb.2011.1229

Bond, J. E., and Stockman, A. K. (2008). An integrative method for delimiting cohesion species: finding the population–species interface in a group of Californian trapdoor spiders with extreme genetic divergence and geographic structuring. *Systematic Biology* **57**, 628–646. doi:10.1080/10635150802302443

Boyer, S. L., and Giribet, G. (2007). A new model Gondwanan taxon: systematics and biogeography of the harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand. *Cladistics* **23**, 337–361. doi:10.1111/j.1096-0031.2007.00149.x

Boyer, S. L., and Giribet, G. (2009). Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography* **36**, 1084–1099. doi:10.1111/j.1365-2699.2009.02092.x

Boyer, S. L., and Reuter, C. N. (2012). New species of mite harvestmen from Australia's Wet Tropics, with commentary on historical biogeography of the genus *Austropurcellia* (Opiliones, Cyphophthalmi, Pettalidae). *The Journal of Arachnology* **40**, 96–112. doi:10.1636/Ha11-44.1

Boyer, S., Karaman, I., and Giribet, G. (2005). The genus *Cyphophthalmus* (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. *Molecular Phylogenetics and Evolution* **36**, 554–567. doi:10.1016/j.ympev.2005.04.004

Boyer, S. L., Baker, J. M., and Giribet, G. (2007*a*). Deep genetic divergences in *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi): a widespread 'mite harvestman' defies DNA taxonomy. *Molecular Ecology* **16**, 4999–5016. doi:10.1111/j.1365-294X.2007.03555.x

Boyer, S. L., Clouse, R. M., Benavides, L. R., Sharma, P., Schwendinger, P. J., Karunarathna, I., and Giribet, G. (2007*b*). Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *Journal of Biogeography* **34**, 2070–2085. doi:10.1111/j.1365-2699.2007.01755.x

Brazier, J. (1875). Descriptions of ten new species of shells from the collection of Mr C. Coxen, of Brisbane, Queensland. *Proceedings of the Zoological Society of London* **1875**, 31–34.

Burbidge, N. T. (1960). The phytogeography of the Australian Region. *Australian Journal of Botany* **8**, 75–211. doi:10.1071/BT9600075

Byrne, M., Steane, D. A., Joseph, L., Yeates, D. K., Jordan, G. L., Crayn, D., Aplin, K., Cantrill, D. J., Cook, L. G., Crisp, M. D., Keogh, J. S., Melville, J., Moritz, C., Porch, N., Sniderman, J. M. K., Sunnucks, P., and Weston, P. H. (2011). Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* **38**, 1635–1656. doi:10.1111/j.1365-2699.2011.02535.x

Cantrell, B. K. (1980). Additional Australian harvestmen (Arachnida: Opiliones). *Journal of the Australian Entomological Society* **19**, 241–253. doi:10.1111/j.1440-6055.1980.tb00980.x

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**, 540–552. doi:10.1093/oxfordjournals.molbev.a026334

Clouse, R. M., and Giribet, G. (2007). Across Lydekker's Line – first report of mite harvestmen (Opiliones: Cyphophthalmi: Stylocellidae) from New Guinea. *Invertebrate Systematics* **21**, 207–227. doi:10.1071/IS06046

Clouse, R. M., and Giribet, G. (2010). When Thailand was an island – the phylogeny and biogeography of mite harvestmen (Opiliones, Cyphophthalmi, Stylocellidae) in Southeast Asia. *Journal of Biogeography* **37**, 1114–1130. doi:10.1111/j.1365-2699.2010.02274.x

Clouse, R. M., and Wheeler, W. C. (2014). Descriptions of two new, cryptic species of *Metasiro* (Arachnida: Opiliones: Cyphophthalmi: Neogoveidae) from South Carolina, USA including a discussion of mitochondrial mutation rates. *Zootaxa* **3814**, 177–201. doi:10.11646/zootaxa.3814.2.2

Davies, V. T. (1977). *Neopurcellia capricornia*, a new opilionid (Opiliones: Cyphophthalmi: Sironidae: Sironinae) from Queensland Australia. *Memoirs of the Queensland Museum* **18**, 61–63.

de Bivort, B. L., Clouse, R. M., and Giribet, G. (2010). A morphometrics-based phylogeny of the temperate Gondwanan mite harvestmen (Opiliones, Cyphophthalmi, Pettalidae). *Journal of Zoological Systematics and Evolutionary Research* **48**, 294–309. doi:10.1111/j.1439-0469.2009.00562.x

Dolman, G., and Moritz, C. (2006). A multilocus perspective on refugial isolation and divergence in rainforest skinks (*Carlia*). *Evolution* **60**, 573–582. doi:10.1111/j.0014-3820.2006.tb01138.x

Drummond, A. J., Suchard, M. A., Xie, D., and Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**, 1969–1973. doi:10.1093/molbev/mss075

Dunlop, J., Anderson, L., Kerp, H., and Hass, H. (2003). Preserved organs of Devonian harvestmen. *Nature* **425**, 916. doi:10.1038/425916a

Edgar, R. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**, 1792–1797. doi:10.1093/nar/gkh340

Edward, K. (2011). 'Systematics and biogeography of the goblin spider genus *Ischnothyreus* (Oonopidae) in the Australian Wet Tropics Bioregion.' Ph.D. Thesis, University of Western Australia, Perth.

Ezard, T., Fujisawa, T., and Barraclough, T. G. (2013). SPLITS: SPecies' LImits by Threshold Statistics. R package version 1.0–18/r45. Available at http://r-forge.r-project.org/projects/splits/

Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Forster, R. R. (1955). Further Australian harvestmen (Arachnida: Opiliones). *Australian Journal of Zoology* **3**, 354–411. doi:10.1071/ZO9550354

Garwood, R. J., Sharma, P. P., Dunlop, J. A., and Giribet, G. (2014). A Paleozoic stem group to mite harvestmen revealed through integration of phylogenetics and development. *Current Biology* **24**, 1017–1023. doi:10.1016/j.cub.2014.03.039

Gillespie, R., and Roderick, G. (2002). Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* **47**, 595–632. doi:10.1146/annurev.ento.47.091201.145244

Giribet, G. (2000). Catalogue of the Cyphophthalmi of the world (Arachnida, Opiliones). *Revista Ibérica de Aracnología* **2**, 49–76.

Giribet, G. (2003). *Karripurcellia*, a new pettalid genus (Arachnida: Opiliones: Cyphophthalmi) from Western Australia, with a cladistic analysis of the family Pettalidae. *Invertebrate Systematics* **17**, 387–406. doi:10.1071/IS02014

Giribet, G., and Boyer, S. (2002). A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). *The Journal of Arachnology* **30**, 110–128. doi:10.1636/0161-8202(2002)030[0110:ACAOTC]2.0.CO;2

Giribet, G., and Edgecombe, G. D. (2006). The importance of looking at small-scale patterns when inferring Gondwanan biogeography: a case study of the centipede *Paralamyctes* (Chilopoda, Lithobiomorpha, Henicopidae). *Biological Journal of the Linnaean Society* **89**, 65–78. doi:10.1111/j.1095-8312.2006.00658.x

Giribet, G., Vogt, L., Perez Gonzalez, A., Sharma, P. P., and Kury, A. B. (2010). A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics* **26**, 408–437.

Giribet, G., Sharma, P. P., Benavides, L. R., Boyer, S. L., Clouse, R. M., De Bivort, B. L., Dimitrov, D., Kawauchi, G. Y., Murienne, J., and Schwendinger, P. J. (2012). Evolutionary and biogeographical history of an ancient and global group of arachnids (Arachnida: Opiliones: Cyphophthalmi) with a new taxonomic arrangement. *Biological Journal of the Linnean Society. Linnean Society of London* **105**, 92–130. doi:10.1111/j.1095-8312.2011.01774.x

Graham, C., Moritz, C., and Williams, S. (2006). Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 632–636. doi:10.1073/pnas.0505754103

Graham, C. H., VanDerWal, J., Phillips, S. J., Moritz, C., and Williams, S. E. (2010). Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography* **33**, 1062–1069. doi:10.1111/j.1600-0587.2010.06430.x

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science* **165**, 131–137. doi:10.1126/science.165.3889.131

Harrison, S. P., and Dodson, J. (1993). Climates of Australia and New Guinea since 18,000 yr. In 'Global Climates Since the Last Glacial Maximum'. (Eds H. E. Wright Jr, J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrot, and P. J. Bartlein.) pp. 265–293. (University of Minnesota Press: Minneapolis, MN.)

Harvey, M. S. (2002). Short-range endemism among the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics* **16**, 555–570. doi:10.1071/IS02009

Hoskin, C. J. (2004). Australian microhylid frogs (*Cophixalus* and *Austrochaperina*): phylogeny, taxonomy, calls, distributions and breeding biology. *Australian Journal of Zoology* **52**, 237–269. doi:10.1071/ZO03056

Huelsenbeck, J., and Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755. doi:10.1093/bioinformatics/17.8.754

Hugall, A., Moritz, C., Moussalli, A., and Stanisic, J. (2002). Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). *Proceedings of the National Academy of Sciences of the United States of America* **99**, 6112–6117. doi:10.1073/pnas.092538699

Joseph, L., and Moritz, C. (1993). Phylogeny and historical aspects of the ecology of eastern Australian scrubwrens *Sericornis* spp. – evidence from mitochondrial DNA. *Molecular Ecology* **2**, 161–170. doi:10.1111/j.1365-294X.1993.tb00105.x

Joseph, L., Moritz, C., and Hugall, A. (1995). Molecular support for vicariance as a source of diversity in rainforest. *Proceedings. Biological Sciences* **260**, 177–182. doi:10.1098/rspb.1995.0077

Juberthie, C. (1988). Un nouvel opilion cyphophthalmie aveugle d'Australie: *Austropurcellia* gen. nov., *scoparia* n. sp. *Memoires de Biospeologie* **15**, 133–140.

Juberthie, C. (1989). *Rakaia daviesae* sp. nov. (Opiliones, Cyphophthalmi, Pettalidae) from Australia. *Memoirs of the Queensland Museum* **27**, 499–507.

Juberthie, C. (2000). A new blind Cyphophthalmi (Opiliones) from Queensland (Australia). *Memoires de Biospeologie* **27**, 149–154.

Karaman, I. (2012). Revision of the genus *Karripurcellia* Giribet 2003 (Opiliones: Cyphophthalmi: Pettalidae). *Biologia Serbica* **34**, 89–99.

Kershaw, A. (1994). Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**, 399–412. doi:10.1016/0031-0182(94)90188-0

Kershaw, A., and Nix, H. (1988). Quantitative paleoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. *Journal of Biogeography* **15**, 589–602. doi:10.2307/2845438

Kikkawa, J., and Pearse, K. (1969). Geographical distribution of land birds in Australia – a numerical analysis. *Australian Journal of Zoology* **17**, 821–840. doi:10.1071/ZO9690821

Kocher, T., Thomas, W., Meyer, A., Edwards, S., Pääbo, S., Villablanca, F., and Wilson, A. (1989). Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America* **86**, 6196–6200. doi:10.1073/pnas.86.16.6196

Moritz, C. (2005). Overview: Rainforest history and dynamics in the Australian Wet Tropics. In 'Tropical Rainforests: Past, Present and Future'. (Eds C. W. Dick and C. Moritz.) pp. 313–321. (The University of Chicago Press: Chicago, IL.)

Moritz, C., Richardson, K. S., Ferrier, S., Monteith, G. B., Stanisic, J., Williams, S. E., and Whiffin, T. (2001). Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London B: Biology* **268**, 1875–1881.

Moritz, C., Hoskin, C. J., MacKenzie, J. B., Phillips, B. L., Tonione, M., Silva, N., VanDerWal, J., Williams, S. E., and Graham, C. H. (2009). Identification and dynamics of a cryptic suture zone in tropical rainforest. *Proceedings. Biological Sciences* **276**, 1235–1244. doi:10.1098/rspb.2008.1622

Morley, R. J. (2000). 'Origin and Evolution of Tropical Rain Forests.' (John Wiley and Sons: Chichester, UK.)

Moussalli, A., Hugall, A. F., and Moritz, C. (2005). A mitochondrial phylogeny of the rainforest skink group *Saproscincus*, Wells and Wellington (1984). *Molecular Phylogenetics and Evolution* **34**, 190–202. doi:10.1016/j.ympev.2004.08.022

Moussalli, A., Moritz, C., Williams, S. E., and Carnaval, A. C. (2009). Variable responses of skinks to a common history of rainforest fluctuation: concordance between phylogeography and palaeo-distribution models. *Molecular Ecology* **18**, 483–499. doi:10.1111/j.1365-294X.2008.04035.x

Murienne, J., Benavides, L. R., Prendini, L., Hormiga, G., and Giribet, G. (2013). Forest refugia in Western and Central Africa as 'museums' of Mesozoic biodiversity. *Biology Letters* **9**(1), 20120932. doi:10.1098/rsbl.2012.0932

Nix, H. (1991). Biogeography, pattern and process. In 'Rainforest Animals – Atlas of Vertebrates Endemic to 'Australia's Wet Tropics'. (Eds H. Nix and M. Switzer.) pp. 11–41. (Australian National Parks and Wildlife Service: Canberra.)

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., Kamoun, S., Sumlin, W. D., and Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* **55**, 595–609. doi:10.1080/10635150600852011

Popkin-Hall, Z. R., and Boyer, S. L. (2014). New species of mite harvestmen from southeast Queensland, Australia greatly extend the known distribution of the genus *Austropurcellia* (Arachnida, Opiliones, Cyphophthalmi). *Zootaxa* **3827**, 517–541. doi:10.11646/zootaxa.3827.4.5

Posada, D. (2008). jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* **25**, 1253–1256. doi:10.1093/molbev/msn083

Rix, M. G., and Harvey, M. S. (2012*a*). Australian assassins. Part III: A review of the assassin spiders (Araneae, Archaeidae) of tropical north-eastern Queensland. *ZooKeys* **218**, 1–55. doi:10.3897/zookeys.218.3662

Rix, M. G., and Harvey, M. S. (2012*b*). Phylogeny and historical biogeography of ancient assassin spiders (Araneae: Archaeidae) in

the Australian mesic zone: evidence for Miocene speciation within Tertiary refugia. *Molecular Phylogenetics and Evolution* **62**, 375–396. doi:10.1016/j.ympev.2011.10.009

Satler, J. D., Carstens, B. C., and Hedin, M. (2013). Multilocus species delimitation in a complex of morphologically conserved trapdoor spiders (Mygalomorphae, Antrodiaetidae, *Aliatypus*). *Systematic Biology* **62**, 805–823. doi:10.1093/sysbio/syt041

Schwendinger, P., and Giribet, G. (2005). The systematics of the south-east Asian genus *Fangensis* Rambla (Opiliones: Cyphophthalmi: Stylocellidae). *Invertebrate Systematics* **19**, 297–323. doi:10.1071/IS05023

Sharma, P., and Giribet, G. (2009). A relict in New Caledonia: phylogenetic relationships of the family Troglosironidae (Opiliones: Cyphophthalmi). *Cladistics* **25**, 279–294. doi:10.1111/j.1096-0031.2009.00252.x

Sharma, P., and Giribet, G. (2014). A revised dated phylogeny of the arachnid order Opiliones. *Frontiers in Genetics* **5**(255), 1–13.

Shear, W. A. (1980). A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the suborder (Arachnida, Opiliones). *American Museum Novitates* **2705**, 1–34.

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688–2690. doi:10.1093/bioinformatics/btl446

Stelbrink, B., Albrecht, C., Hall, R., and von Rintelen, T. (2012). The biogeography of Sulawesi revisited: is there evidence for a vicariant origin of taxa on Wallace's "anomalous island"? *Evolution* **66**, 2252–2271. doi:10.1111/j.1558-5646.2012.01588.x

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., and Kumar, S. (2011). MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**, 2731–2739. doi:10.1093/molbev/msr121

Truswell, E. (1993). Vegetation in the Australian Tertiary in response to climatic and phytogeographic forcing factors. *Australian Systematic Biology* **6**, 533–557. doi:10.1071/SB9930533

VanDerWal, J., Shoo, L. P., and Williams, S. E. (2009). New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *Journal of Biogeography* **36**, 291–301. doi:10.1111/j.1365-2699.2008.01993.x

Winter, J. (1984). Conservation studies of tropical rainforest possums. In 'Possums and Gliders'. (Eds A. Smith and I. Hume.) pp. 469–481. (Australian Mammal Society: Sydney.)