Contributions to the systematics and biogeography of the mygalomorph spider families Migidae and Idiopidae in Australia

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DECLARATION

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ABSTRACT

The genus *Blakistonia* Hogg, 1902 is a member of the spiny trapdoor spider family Idiopidae, and has a mostly semi-arid, southern Australian distribution. Prior to the publications in this thesis, *Blakistonia* contained only two species: *B. rainbowi* (Pulleine, 1919) and the type species *B. aurea* Hogg, 1902, with a third species, *B. exsiccatus* (Strand, 1907), being recently designated a *nomen dubium*.

Here, I undertook a systematic revision of *Blakistonia*, using a combined molecular and morphological approach. This firstly required a review of the taxonomic history of the genus and a reappraisal of the enigmatic species '*Blakistonia*' *rainbowi*, which was originally described in the idiopid genus *Aganippe* O. P.-Cambridge, 1877, and then mistakenly transferred to *Blakistonia*. Following the timely rediscovery of this species on Kangaroo Island, we demonstrated that '*B.*' *rainbowi* is in fact a valid species and member of the otherwise African genus *Moggridgea* O. P.-Cambridge, 1875 (family Migidae) and, accordingly, the species is transferred to that genus and family. The trapdoor spider genus *Moggridgea* is widespread across the Afrotropical region, and the rediscovery and redescription of *M. rainbowi* from Kangaroo Island was a highlight of this project.

I also investigated the biogeographic history and phylogenetic relationships of *M. rainbowi* within the family Migidae. Specimens of *Moggridgea* were sampled from Africa, and *Bertmainus,* a related Australian genus, were sampled from south-western Australia. Sanger sequencing methods were used to generate a robust six marker molecular dataset consisting of the nuclear genes 18S rRNA, 28S rRNA, ITS rRNA, *XPNPEP3* and *H3*, and the mitochondrial gene *COI*. Bayesian and maximum likelihood phylogenetic methods were used to analyse the dataset, and the key nodes were dated using BEAST. The resulting trees showed that *M. rainbowi* from Kangaroo Island is deeply nested within African *Moggridgea* and is unrelated to Australian members of the family. Significantly, the inter-specific divergence of *M. rainbowi* from African congeners significantly post-dates the separation of Africa from Gondwana and therefore does not support a vicariant origin for Australian *Moggridgea*. It also substantially pre-dates human colonisation of Kangaroo Island, a result which is further supported by phylogeographic structuring between separate populations on Kangaroo Island. These results provide strong support for the hypothesis that *Moggridgea* colonised Australia via long-distance trans-Indian Ocean dispersal.

To revise the taxonomy of *Blakistonia,* i.e. to redescribe the widespread type species, and to describe all new taxa**,** species limits were determined using both freshly collected and museum specimens for morphological characterisation. Sequence data from the *COI* barcoding gene were analysed using Bayesian, RAxML and neighbour-joining approaches.

The type species, *B*. *aurea*, is redescribed and 19 species are described as new. These species are *B. bassi* sp. n., *B. bella* sp. n., *B. birksi* sp. n., *B. carnarvon* sp. n., *B. emmottiorum* sp. n., *B. gemmelli* sp. n., *B. hortoni* sp. n., *B. mainae* sp. n., *B. maryae* sp. n., *B. newtoni* sp. n., *B. nullarborensis* sp. n., *B. olea* sp. n., *B.parva* sp. n., *B. pidax* sp. n., *B. plata* sp. n., *B.raveni* sp. n., *B. tariae* sp. n., *B. tunstill* sp. n., and *B. wingellina* sp. n. An illustrated key is provided for both male and females, and molecular diagnoses are supplied for all species for which molecular data are available. Wherever possible, live habitus and burrow photos are provided for each species, and a discussion of their conservation status is presented.

Finally, my general discussion provides a synopsis of recent research and its impact on providing a better understanding of the diversity, biogeography and conservation of mygalomorph spiders in Australia, and opportunities for future research.

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CHAPTER I: General Introduction

1.1. Mygalomorphae and Idiopidae

The infraorder Mygalomorphae comprises one of the three main groups within Araneae (Hedin & Bond, 2006), and includes trapdoor spiders, tarantulas and many other lesser known groups (Raven, 1985; Bond *et al*., 2012). Mygalomorph spiders differ from their sister lineage (the infraorder Araneomorphae) by a unique combination of life-history traits (Hamilton *et al.,* 2014) and the retention of primitive (symplesiomorphic) features, such as two pairs of book lungs, a longitudinal fang orientation, and lack of specialisation of spinning structures (Raven, 1985). They are an ancient group of spiders with a long evolutionary history (Penney *et al*., 2003), with the earliest mygalomorph fossil dating back to the Middle Triassic (242 Mya) (Selden & Gall, 1992; Penney & Selden, 2011). Mygalomorphs tend to be morphologically conservative relative to araneomorphs, particularly in genitalic and spinneret morphology (Bond & Hedin, 2006), and are a difficult group for accurate species delimitation (Main, 1969; Hedin & Bond, 2006; Hamilton *et al*., 2014; Godwin *et al.,* 2018). These spiders are renowned for their longevity, with life-cycles that are generally between 15–30 years (Bond *et al.,* 2012), and can take 4–8 years to reach sexual maturity (Main, 1978; Hamilton *et al.,* 2014; Rix *et al.,* 2017c). They are also mostly ground-dwelling, hunting prey from burrows where they spend the majority of their life (Godwin *et al*., 2018). The surrounding substrate can be used to camouflage burrows (Bond & Coyle, 1995), often making them difficult to see (Godwin *et al.,* 2018). Mygalomorphs tend to lead sedentary lives and have relatively poor powers of dispersal (Bond *et al.,* 2001; Bond & Stockman, 2008; Bond *et al*., 2012; Hamilton *et al*., 2014). This combination of traits makes mygalomorphs particularly suitable for evolutionary, biogeographical and conservation studies (Rix *et al*., 2017a (Appendix 6.1); Rix *et al*., 2017c (Appendix 6.3)). Mygalomorphs are distributed almost worldwide, with the majority of their diversity centred in South America, southern Africa, and Australasia (Hedin & Bond, 2006; Berlin, 2018).

Australia has a rich mygalomorph fauna (Main, 1969) which live in a range of habitats, from moist forests to desert environments (Main, 1957a; Main, 1962). Recent research on the group in Australia has focused on the families Nemesiidae (open-holed trapdoor spiders; see (Harvey *et al*., 2012; Castalanelli *et al*., 2017), Migidae (tree or pygmy trapdoor spiders; Harrison *et al.,* 2015; Harrison *et al.,* 2017), and Actinopodidae (mouse spiders; Miglio *et al.,* 2014). The spiny trapdoor spiders of the family Idiopidae have been of particular interest both historically (e.g. Main, 1957b, 1969; Main, 1985a) and in recent studies (e.g. Rix *et al.,* 2017a; Rix *et al.,* 2017c; Rix *et al*., 2017b (Appendix 6.2); Rix *et al.,* 2018a). The Idiopidae are considered to be one of the two most diverse mygalomorph families of the Australian

temperate mesic zone, along with Nemesiidae (Rix *et al.,* 2017a). They are particularly long-lived, with some female individuals having lifespans that exceed 40 years in the wild (Main, 1987; Mason, 2018), and all rely on burrows for shelter and prey capture. The Idiopidae are thought to have a Gondwanan origin, occurring on all former Gondwanan landmasses except Antarctica (Rix *et al.,* 2017a). In Australia, the vast majority of the idiopid fauna occupies temperate and sub-tropical regions (Main, 1985a) south of the Tropic of Capricorn, although they can also be found in the wet tropics of north-east Queensland and are sparsely distributed on Cape York Peninsula (Rix *et al*., 2017a; Rix *et al.,* 2017b). Several idiopid lineages have also successfully radiated into Australia's arid zone (Rix *et al.,* 2017a), although they are less common in severely arid regions (Main, 1985a). It is currently thought that the evolutionary origins of the Idiopidae in Australia pre-date both the separation of Australia from Antarctica during the breakup of Gondwana, and the aridification of the continent during the Eocene (Rix *et al.,* 2017a).

Until recently, the Idiopidae were thought to be "largely undescribed at the species level, with a confusing taxonomic history at the generic level" (Rix *et al*., 2017a). However, a major molecular phylogenetic analysis by Rix *et al*. (2017a), leading to a complete generic revision of the Australian fauna by Rix *et al.* (2017b), undertaken during the timespan of the current project, has provided much needed taxonomic stability for the family. This work led to a revised family- and genus-group classification for the monophyletic Australasian fauna, and recognised 10 genera in four tribes, of which two genera were new and six previously recognised generic names were placed as junior synonyms. However, at the species level, idiopid taxonomy is still challenging due to the conservative morphology of females, which are by far the most frequently collected, and due to a lack of genetic studies.

With characteristics typical of mygalomorph spiders, including limited powers of dispersal and long life-cycles (Rix *et al.,* 2017c), idiopid trapdoor spiders make ideal candidates for biogeographic studies. The ancestors of Australia's present-day invertebrate fauna were residents of a vastly different continent to the one we are familiar with today, and therefore the major climatic shift in Australia from rainforest to a predominantly arid landscape is often a focal point for such biogeographic studies. Currently, the arid-zone biome is considered to be the largest biome in Australia (Byrne *et al.,* 2008). However, it arose only relatively recently, starting in the late Eocene, with the final and most extreme phases of aridification occurring during the Plio-Pleistocene. The drying of the continent and subsequent contraction of continuous habitats into smaller, isolated patches, drove both allopatric speciation as well as extinction of niche-conserved lineages which failed to radiate into the newly formed arid zone (Bryant & Krosch, 2016), with a concomitant diversification of arid-adapted species evidenced by dated phylogenies (Byrne *et al*., 2008; Rix *et al.,* 2015a; *Rix et*

al., 2017a). Allopatric speciation due to habitat contraction and fragmentation driven by Australia's changing climate has been well documented in the literature (Schneider *et al.,* 1998; Moritz *et al*., 2000; Ponniah & Hughes, 2004; Byrne *et al.,* 2011; Cooper *et al.,* 2011; Rix & Harvey, 2012; Bryant & Krosch, 2016; Rix *et al.,* 2017a). In some groups, for example skinks (Chapple & Keogh, 2004), diving beetles (Leys *et al*., 2003; Cooper *et al*., 2007) as well as the plant genera *Tetratheca* (Crayn *et al.,* 2006) and *Gossypium* (Seelanan *et al.,* 1999; Liu *et al.,* 2001), sister lineage relationships can still be seen between mesic and arid-zone species (Byrne *et al.,* 2008; Byrne *et al*., 2011).

The same suite of life-history traits that are characteristic of most mygalomorph spiders, such as their specific habitat requirements and poor dispersal abilities, also make them vulnerable to habitat disturbance (Hedin *et al.,* 2013; Rix *et al*., 2017c). The latter characteristic plays a particularly important role in defining contemporary patterns of distribution. Although some mygalomorphs are able to disperse via ballooning (e.g. Coyle, 1983, 1985), most trapdoor spiders are unable to disperse in this way, and juveniles, as well as females, have sedentary lifestyles. Juvenile spiders reside in the maternal burrow and are only able to wander a few metres before establishing a burrow of their own (Main, 1978; Bond *et al*., 2001; Cooper *et al.,* 2011; Bond *et al.,* 2012). The juvenile spiders apparently time their exit to coincide with rainfall, which softens the ground and makes burrow establishment easier, as well as avoiding desiccation. The small distance they are able to disperse, combined with a long generation time, limits their ability to distribute themselves across the landscape (in both space and time). Once their burrow is established, trapdoor spiders are able to widen and lengthen the burrow, conduct repairs to the entrance, and are even able to create a new trapdoor if it is removed, damaged or destroyed (Rix *et al*., 2018c). However, it is unusual for adult mygalomorphs to relocate, as such moves require significant energy expenditure and also expose the spider to predation and desiccation (Mason *et al.,* 2013) and it is also unknown whether adult mygalomorphs can rebuild their burrows from scratch. Burrows are an investment in terms of time and effort (Mason *et al*., 2018a) and trapdoor spiders rely entirely on their burrow for shelter from predators, for reducing desiccation, for protection from extreme temperatures, and also as their sole base for prey capture (Coyle, 1986; Main, 1986). Burrows are also essential for successful recruitment, as they provide a brood chamber for eggs and spiderlings (Main, 1993). This complete dependence on their burrow, and almost certain death if their burrow is destroyed, increases their vulnerability to habitat disturbance.

The extreme habitat specificity, longevity and poor vagility of mygalomorphs (Hedin *et al*., 2013) are factors which place this group of spiders at greater risk to the challenges posed by human-driven changes to the landscape (Rix *et al*., 2017c). Much of southern Australia

underwent extensive land clearing following European settlement and has since been extensively grazed, stocked, planted and farmed. This modification of the ecosystem has, predictably, caused a severe decline in the region's biota, which is generally documented with a focus on Australia's more charismatic fauna, in particular mammals (e.g. Fusco *et al*., 2016; Fusco *et al*., 2017). However, invertebrates are potentially being 'hit the hardest' by landscape-level habitat modification. Within the invertebrate fauna, a number of trapdoor spiders are experiencing serious contemporary population declines (Rix *et al*., 2017c; Rix *et al*., 2018a). Despite this, only a single species, *Idiosoma nigrum* Main, 1952 is listed as threatened under the Commonwealth's Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act) (Rix *et al*., 2018a).

1.2. The genus *Blakistonia*

The idiopid genus *Blakistonia* was first described in 1902, from an adult male collected from Lower North Road, Adelaide, and from four females from Blakiston and the Mount Lofty Ranges, South Australia (Hogg, 1902). In addition to *Idiosoma* Ausserer, 1871, *Blakistonia* is considered to be one of the two dominant idiopid genera in South Australia (Main, 1957b) and the two are often found coexisting (Hogg, 1902; pers. obs). The prevalence of *Blakistonia* in parks, gardens, paddocks and along highways was noted in the early 20th century (Rainbow & Pulleine, 1918). Spider density was also noted as "several to the square yard" in some locations and was thought to play an important role in keeping invertebrate pest numbers under control (Rainbow & Pulleine, 1918). Despite being "somewhat doubtfully" constituted as a new genus when it was first described, it was morphologically circumscribed by Main (1985a), and the molecular and morphological studies of Rix *et al*. (2017a, 2017b) showed *Blakistonia* to be a valid, monophyletic genus within the Idiopidae.

Aside from the type species *B. aurea* Hogg, 1902, only two other species have historically been recognised within *Blakistonia*: '*B.*' *rainbowi* (Pulleine, 1918) from American River, Kangaroo Island (originally described in *Aganippe* O. P.-Cambridge, 1877, and previously of uncertain affinity), and *B. exsiccatus* (Strand, 1907), which was originally described in the genus *Cantuarides (*Strand, 1907). *Cantuarides* was later synonymised with *Blakistonia* by Main (1985a), due to records of *Blakistonia* being collected around Central Australia (in Uluru-Kata Tjuta National Park), and morphological characters including the presence of labial cuspules and a strongly procurved anterior eye row. However, *B. exsiccatus* was recently designated as a *nomen dubium* (Rix *et al*., 2017b) as the type locality is listed only as "Central Australia", which is too vague to allow for recollection, and the female syntypes are now lost.

1.3. The genus *Moggridgea*

Like the Idiopidae, the trapdoor spider family Migidae has a Gondwanan distribution and occurs in Africa, Madagascar, South America, Australia, New Zealand and New Caledonia. The genus *Moggridgea* O. P.-Cambridge, 1875 is one of three migid genera found in Australia but is most commonly found in the southern half of Africa (Griswold, 1987). Just two species had been previously described from Australia: *M. australis* Main, 1991 from Western River (Kangaroo Island), and *M. tingle* Main, 1991 from the Walpole-Nornalup region of southern Western Australia (Main, 1991). The latter species has now been removed from *Moggridgea* and transferred into a new genus, *Bertmainius* Harvey, Main, Rix & Cooper, 2015, which was delimited by both morphological and molecular criteria (Harvey *et al*., 2015), with seven new Western Australian species also being accommodated in the genus.

'*Blakistonia*' *rainbowi* has had a long and confusing taxonomic history. It was described by Pulleine (1919) and originally placed in the idiopid genus *Aganippe* (now *Idiosoma*). The original type specimens from American River, Kangaroo Island, have since been lost. *Aganippe rainbowi* was subsequently transferred to *Blakistonia* by Main (1985a, 1985b). No explanation for the transfer was provided, however, Main (1991) later clarified that, while appearing very "migid-like" in Pulleine's description and figures, *A. rainbowi* (then *B. rainbowi*) was not classified as a member of the Migidae due to the burrow having a stout, circular door and the presence of a rastellum and leg scopulae on the female (Harrison *et al.*, 2015). Subsequently, a new species of *Moggridgea* (*M. australis*) was described from the same type locality as *B. rainbowi* (Main, 1991). An exploration of the taxonomic status of this species from Kangaroo Island is included in the current study.

It was originally suggested by Main (1991) that these spiders are unlikely to disperse via rafting, and thus the presence of *Moggridgea* in Australia is likely to have predated the separation of Gondwana. However, past studies suggested that the Kangaroo Island species was more closely related to African *Moggridgea* than to *Bertmainius* from Western Australia (Cooper *et al*., 2011; Harvey *et al*., 2015). In the current study, the relationship between the Kangaroo Island species and its African congeners was examined in more detail, using a dated multigene phylogeny to examine alternative biogeographic hypotheses.

1.4. Aims of this project

Given the background information above, the aims of this study are as follows:

1 *Examine the taxonomic status of the Kangaroo Island* Blakistonia *species*. Preliminary evidence demonstrated that this species was misplaced in *Blakistonia*, and is more

closely related to the genus *Moggridgea*. A morphological assessment of newly collected specimens was then used to redescribe this species.

2 *Examine the phylogenetic placement of the Kangaroo Island species using a more detailed sampling of taxa and a multi-locus, dated phylogeny to assess its biogeographic history.* Three alternative biogeographic hypotheses were considered to account for the presence of *Moggridgea* on Kangaroo Island. The first hypothesis is Gondwanan vicariance, which would be supported by a divergence date consistent with the age of separation of Africa from the rest of Gondwana. The second hypothesis is a human-mediated introduction from Africa during European colonisation of the island, which would be supported by a very recent divergence date. The third hypothesis is trans-oceanic dispersal, which would be evidenced by a divergence that is more recent than vicariance, but much older than human colonisation of Kangaroo Island, and by phylogeographic structuring between the two known populations.

3 *Develop a complete taxonomic revision of the idiopid genus* Blakistonia. With the removal of *B. exsiccata* and *B. rainbowi* from *Blakistonia*, only the type species *B. aurea* remains within the genus. Preliminary examination of available museum specimens showed that many new species were in fact present, and a taxonomic revision was planned to describe all new species and to document their distributions and aspects of their biology (in particular, burrow morphology). Both male and female morphological data was used, along with sequence data for as many specimens as possible to provide molecular support for the delimitation of morpho-species. A dichotomous key was also produced for both males and females to aid in the identification of all *Blakistonia* species.

1.5. Structure of this thesis

The three results chapters in this thesis (Chapters 2, 3 and 4) are published. The reference list for each of these chapters is included within the publication. A separate list of references for the remaining chapters is provided at the end of this thesis. A General Discussion is presented after the results sections that aims to place the outcomes of this research into a broader framework regarding the systematics, biogeography and conservation of mygalomorph spiders in Australia, and to outline potential fruitful lines of research in future that build on the work presented here.

CHAPTER II: An African mygalomorph lineage in temperate Australia: the trapdoor spider genus *Moggridgea* (Araneae: Migidae) on Kangaroo Island, South Australia
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ii. permission is granted for the candidate in include the publication in the thesis; and

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An African mygalomorph lineage in temperate Australia: the trapdoor spider genus *Moggridgea* (Araneae: Migidae) on Kangaroo Island, South Australia

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Abstract The trapdoor spider genus *Moggridgea* O. Pickard-Cambridge, 1875 is widespread across the Afrotropical region, with a further two species recorded from southern Australia. One of these Australian species, *M. tingle* Main, 1991 from south-western Australia, has recently been transferred to a separate genus, along with six additional new species. However, consistent with previous research, we find that *M. australis* Main, 1991 from Kangaroo Island, South Australia, is not congeneric with the south-western Australian taxa, and appears to be a valid member of the otherwise African genus *Moggridgea*. This suggests a potential case of trans-oceanic dispersal, which would be remarkable for a mygalomorph spider. We redescribe this species based on newly collected specimens, and find that *Aganippe rainbowi* Pulleine, 1919, also from Kangaroo Island, is conspecific with *M. australis* and is the senior synonym, forming the new combination, *M. rainbowi* (Pulleine, 1919). We further discuss the ecology and biogeography of the species, and highlight avenues for future research.

Key words biogeography, dispersal, Mygalomorphae, taxonomy.

INTRODUCTION

The trapdoor spider family Migidae has a characteristic Gondwanan distribution, occurring on mainland Africa, Madagascar, southern South America, Australia (including Tasmania and Norfolk Island), New Zealand and New Caledonia, that is, almost all parts of the former super-continent with the exception of the Indian subcontinent and Antarctica. Currently, three genera are recorded from Australia: *Migas* L. Koch, 1873 and *Heteromigas* Hogg, 1902, both found in eastern Australia (Raven 1984), and *Moggridgea* O. Pickard-Cambridge, 1875 recorded from south-western Western Australia (Main 1991; Cooper *et al*. 2011) and Kangaroo Island, South Australia (Fig. 6) (Main 1991). Species of the genus *Moggridgea* are widespread and diverse (31 species) throughout the southern half of Africa (Griswold 1987; World Spider Catalog 2015), with only two species previously described from temperate Australia.

The first records of *Moggridgea* from Australia were from Western River (Kangaroo Island) (Fig. 6) and from the Walpole/Nornalup region of southern Western Australia (Main 1991). Main (1991) suggested that these spiders are unlikely to disperse via rafting, and thus the presence of the genus in Australia is likely to have predated the separation of Gondwana, indicating a long evolutionary history on the continent (Main 1991; Cooper *et al*. 2011). It has been shown previously that the relationships between *M. australis* Main, 1991 from Kangaroo Island, *M. tingle* Main, 1991 from Western Australia and the African *Moggridgea* species are particularly unusual and interesting, with molecular data suggesting that *M. australis* is much more closely related to African species than to *M. tingle* and its Western Australian relatives (see Hedin & Bond 2006; Cooper *et al*. 2011; Bond *et al*. 2012; Harvey *et al*. 2015). Indeed, the generic placement of the Western Australian taxa within *Moggridgea* has been considered dubious for at least a decade, based on both strong molecular (Hedin & Bond 2006; Cooper *et al*. 2011; Harvey *et al*. 2015) and morphological (Harvey *et al*. 2015) grounds. As a result, the Western Australian species have recently been transferred to a new genus by Harvey *et al*. (2015), to the exclusion of the South Australian *M. australis*.

The enigmatic South Australian *Moggridgea* are thus the focus of the current study, given their tantalising potential relationship to Afrotropical congeners. We here document the history of their discovery and their confusing taxonomic history, provide a detailed morphological description and assessment of their current systematic placement, and discuss the biogeography of the single Australian species.

MATERIALS AND METHODS

The specimens examined for this study are lodged in the South Australian Museum, Adelaide (SAMA). Those used for

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Figs 1–5. *Moggridgea rainbowi* (Pulleine): (**1**) living male, dorsal view (SAMA NN28257); (**2**) living female, dorsal view (SAMA NN28258); (**3**) living male (SAMA NN28257) and female (SAMA NN28258) at burrow entrance, male closest to trapdoor; (**4**) the coastal site south of American River, Kangaroo Island where *M. rainbowi* occurs; (**5**) detail of bank where burrows were located. Images courtesy of Nick Birks.

morphological examination were fixed in either 100% or 70% ethanol (EtOH), and preserved in 70% EtOH.

Auto-montaged images were taken at different focal planes (ca. 20–30 images) with a Leica DFC500 digital camera attached to a Leica MZ16A stereo microscope, using Leica Application Suite (LAS) version 2.5.OR1 software.

Female genitalia were prepared for imaging by submersion in lactic acid at room temperature overnight. Specimens were examined using an Olympus microscope (Type/Model # SZ6 head/SZ2-ilst base) with an LED light/flat base. Images were taken for purposes of measurements only using an Olympus digital microscope camera (Model # LC20, 2.0MP CMOS colour camera), and measurements were taken digitally using LC micro software, available for download from the Olympus website.

Total length is measured dorsally and includes the chelicerae, but excludes the spinnerets. Abbreviations used include anterior median eyes (AME), anterior lateral eyes (ALE), posterior median eyes (PME), posterior lateral eyes (PLE), prolateral (p), retrolateral (r), ventral (v), proventral (pv) and retroventral (rv).

TAXONOMY

Family Migidae Simon, 1889

Subfamily Miginae Simon, 1889

Genus *Moggridgea* O. Pickard-Cambridge, 1875

Moggridgea O. Pickard-Cambridge, 1875: 319.

Type species *Moggridgea dyeri* O. Pickard-Cambridge, 1875, by monotypy.

Diagnosis

Species of *Moggridgea* can be distinguished from all other Migidae by the combined presence of groups of erect, lamellate setae beneath patellae I, II, IV and rarely III (Griswold 1987, figs 4,5); by the absence of spines on tarsi I–IV (Griswold 1987); and by the shape of the ectal lobe of the pedipalpal tarsus, which is pointed apically and much longer than the mesal lobe (Griswold & Ledford 2001; Harvey *et al.*

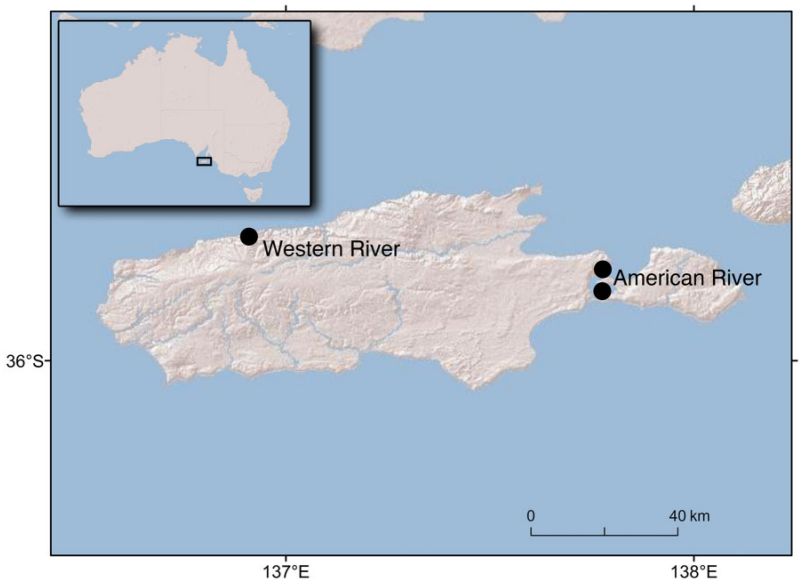


Fig. 6. Map of Kangaroo Island, South Australia, showing localities for the known populations of *Moggridgea rainbowi* at Western River and American River.

2015; Figs 16,17). A group of stout, elongate setae beneath femur II and an apical preening comb on metatarsus IV are also usually present (Griswold 1987). See Harvey *et al*. (2015) for a detailed discussion of the comparative morphology of *Moggridgea* relative to similar south-western Australian taxa.

Moggridgea rainbowi (Pulleine, 1919) comb. nov.

Aganippe rainbowi Pulleine, 1919: 74, plate XII, figures 1–3.
Blakistonia rainbowi (Pulleine): Main, 1985a: 51; Main, 1985b: 20.
Moggridgea australis Main, 1991: 390, figures 4a–b,d,5,6. **Syn. nov.**

Syntypes

Aganippe rainbowi: **AUSTRALIA: South Australia:** 1 ♂ and 2 ♀♀, American River, Kangaroo Island, May 1919 (originally stated to be lodged in Australian Museum, now lost); two syntype females, same data (SAMA, now lost).

Holotype

Moggridgea australis: **AUSTRALIA: South Australia:** ♀, coastal 'scenic walk', American River, Kangaroo Island, 11 November 1987, D. Hirst (SAMA 1990266).

Paratypes

Moggridgea australis: **AUSTRALIA: South Australia:** 1 ♀, same data as holotype (SAMA 1990267); 1 ♀, same data as holotype (SAMA 1990270); 1 ♀, 'short burrows in damp creek bank, above waterfall, Waterfall Creek', Western River Conservation Park, Kangaroo Island, 3 November 1987, D. Hirst (SAMA 1990268 with eggs); 1 juvenile, same data (SAMA 1990269).

Other material examined

AUSTRALIA: South Australia: 1 ♂, 6 km S. of American River, Kangaroo Island, hand collected from burrows on clay bank close to water's edge, 35°49′35′S, 137°46′36″E, 14 May 2013, N. Birks (SAMA NN28257); 1 ♀, same data (SAMA NN28258); 1 ♀, same data except 35°46′37′S, 137°46′33′E, 1 April 2014 (SAMA NN28428); 1 ♀, same data (SAMA NN25429); 1 ♂, same data except 35°46′36.5′S, 137°46′33′E, 12 April 2014 (SAMA NN28345); 1 ♀, same data (SAMA NN28346); 1 female, same data (SAMA NN28346.1); 1 juvenile, same data (SAMA NN28346.2); 1 juvenile, same data (SAMA NN28346.3); 3 juveniles, Waterfall Creek, Western River National Park, Kangaroo Island, 35°41′46″S, 136°54′34″E, 28 October 2005, M. Harvey, S. Cooper (SAMA NN28900); 1 juvenile, same data (SAMA NN28901); 1 juvenile, same data (SAMA NN28902).

Diagnosis

Males of *Moggridgea rainbowi* can be distinguished from all other described African congeners except *M. quercina* Simon, 1903 and *M. teresae* Griswold, 1987 by the combined presence of blunt-tipped setae on the abdomen (Figs 14,15) and the absence of a scopula on tarsus IV (Fig. 24); and from *M. quercina* and *M. teresae* by the presence of a swollen tarsus I (Figs 19–22) and the absence of a scopula on the distal metatarsus I (Figs 19–21). Females of *M. rainbowi* are most similar to at least 10 other species of African *Moggridgea* (*M. anactenidia* Griswold, 1987; *M. loistata* Griswold, 1987; *M. microps* Hewitt, 1915; *M. occidua* Simon, 1907; *M. pallida*

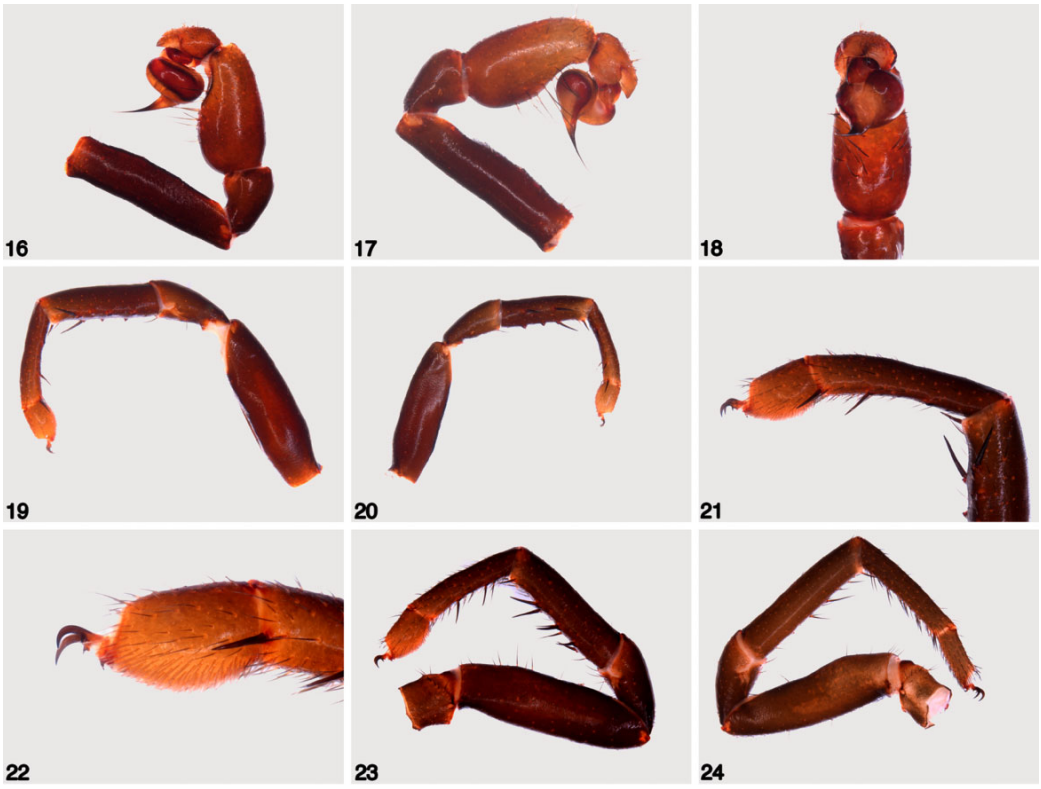
Figs 7–15. *Moggridgea rainbowi* (Pulleine), male (SAMA NN28257): (**7**) habitus, dorsal view; (**8**) carapace, dorsal view; (**9**) eye group, dorsal view; (**10**) cephalothorax, ventral view; (**11**) sternum, ventral view; (**12**) maxillae and labium, ventral view; (**13**) habitus, lateral view; (**14**) abdomen, ventral view; (**15**) abdomen, dorsal view.

Hewitt, 1914; *M. paucispina* Hewitt, 1916; *M. purpurea* Lawrence, 1928; *M. intermedia* Hewitt, 1913; *M. peringueyi* Simon, 1903; and *M. quercina*), all of which share the absence of pre-foveal setae and the absence of thorns or cuspules on the leg coxae; of these species, *M. rainbowi* is most similar to *M. intermedia*, with which it shares the presence of stout, inward-facing spermathecae (Figs 34,35) and the absence of thorn-like setae on femur I (Figs 31,32). *Moggridgea rainbowi* can be further distinguished from similar south-western Australian migid species by the strongly rugose male carapace (Fig. 8), by the presence of lateral pits on the pars cephalica (Figs 8,28), and by the shape of the ectal lobe of the pedipalpal tarsus (Figs 16,17), which is pointed apically and much longer than the mesal lobe.

Description

Adult male (based on SAMA NN28257)

Medium-sized migid spider (total length 9.1 mm). *Colouration* (in ethanol; Figs 7–15): Carapace uniformly dark reddish-brown, slightly darker around eyes (Fig. 9); sternum a lighter golden brown, darker towards anterior margins (Figs 10,11); labium and maxillae same golden brown as sternum (Figs 10,12), darker towards posterior margins; abdomen dark greyish-brown with lighter grey mottling, with pair of pale, irregular dorsal sigilla (Fig. 15); legs and pedipalp reddish-brown (Figs 16–24). *Cephalothorax*: Carapace 4.1 mm long, 4.0 mm wide, 1.5 mm high (at highest point), 1.03 × longer than wide; rounded in dorsal view (Fig. 8), caput straight in lateral view with slightly raised ocular area (Fig. 13), with shallow pits on lateral pars cephalica (Fig. 8); cuticle uniformly rugose; fovea strongly recurved, with slight median indentation; without pair of pre-foveal setae and largely devoid of setae except for few short setae anterior to ocular area. Length of clypeus twice diameter of AME; anterior margin slightly convex (Fig. 9). Eye group 1.2 mm wide, 0.3 mm long, 0.3 × carapace width; anterior eye row straight, posterior eye row slightly recurved; AME slightly smaller than ALE and separated by less than diameter of AME; ALE and PLE separated by about diameter of PLE; PME widely separated, oval (Fig. 9). Labium as wide as long; apex rounded, without cuspules but with 5 stout setae (Fig. 12). Sternum 2.6 mm long, 1.8 mm wide at widest part, sparsely setose, setae denser around margins, with two oval obliquely directed sigilla 1.8–2.2 × as long as wide, each separated anteriorly by their width (Fig. 11). Maxillae rectangular, without cuspules (Fig. 12). Chelicerae without rastellum or intercheliceral tumescence; fang furrow without basal swelling, promargin with 4 teeth (1 small, 3 large), retromargin with 4 teeth (3 small, 1 large); fang with keel; basal tooth absent. *Legs*: Coxae, trochanters and legs sparsely setose (Figs 11,19–24). Coxae without thorns or cuspules (Fig. 11); femur I with ventral carina (Figs 19,20);



Figs 16–24. *Moggridgea rainbowi* (Pulleine), male (SAMA NN28257): (**16**) left pedipalp, retrolateral view; (**17**) left pedipalp, prolateral view; (**18**) left pedipalpal tibia, cymbium and bulb, ventral view; (**19**) left leg I, retrolateral view; (**20**) left leg I, prolateral view; (**21**) left leg I metatarsus and tarsus, retrolateral view; (**22**) left leg I tarsus and tarsal claws, retrolateral view, showing swollen tarsus; (**23**) left leg 2, retrolateral view; (**24**) right leg IV, retrolateral view.

femur II prolaterally convex (Fig. 23); patellae I, II and IV with ventral patch of erect lamellate setae (Figs 19,20,23,24); tibia I not noticeably thickened (Figs 19,20); tibia III without depression; metatarsus I, II slightly bowed dorso-ventrally (Figs 19,20,23); metatarsus IV straight, cylindrical, with apical preening comb of 3 setae (Fig. 24); tarsi I, II swollen ventrally, tarsus I 1.24 × width of distal metatarsus I in lateral view (Figs 21,22). Scopulae entire beneath tarsus I, II (Figs 22,23); weak, entire beneath tarsus III; absent beneath tarsus IV. Paired tarsal claws of legs with 1 row of ventral teeth (Fig. 22) arranged: leg I p1 (large), r2 (1 large, 1 small); leg II p2 (1 large, 1 small), r1 (large); leg III p3 (1 large, 2 small), r2 (1 large, 1 small); right leg IV p2 (1 large, 1 small), r2 (1 large, 1 small); median tarsal claws without teeth. Spination: tibia I p2, pv4, rv5; metatarsus I pv3, rv3; tibia II p2, pv3, rv4; metatarsus II pv3, rv4; legs III, IV setose and diffusely spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae. *Leg and pedipalp measurements (in mm)*: Length of legs IV > II > I > III. Leg I: femur 3.7, patella 1.8, tibia 2.4, metatarsus 2.3, tarsus 0.7, total = 8.5. Leg II: femur 3.3, patella 1.6, tibia 2.3, metatarsus 2.0, tarsus 0.8, total = 10. Leg III: femur 2.6, patella 1.4, tibia 2.0, metatarsus 1.7, tarsus 0.9, total = 8.6. Leg IV (right): femur 3.4, patella 1.6, tibia 3.0, metatarsus 1.9, tarsus 1.0, total = 10.9. Pedipalp: femur 2.1, patella 0.8, tibia 1.5, tarsus 1.1, total = 5.5. *Abdomen*: Abdomen oval in dorsal view, 4.1 mm long, 3.1 mm wide, setose with rows of attenuate and blunt-tipped setae dorsally and laterally, with one pair of dorsal sigilla (Fig. 15). Two pairs of spinnerets; posterior median spinnerets one-segmented, contiguous; posterior lateral spinnerets largest, three-segmented, with short and domed apical segment (Fig. 14). *Pedipalp*: All segments without spines; patella without ventral patch of erect lamellate setae; tibia swollen basally; bulb uniform, globular, attached to cymbium by small lobe, with pointed apical ectal lobe; embolus simple, slender and tapering, slightly longer than length of bulb (Figs 16–18). *Variation (n = 4)*: Carapace 3.7–4.4 mm long, 3.8–4.2 mm wide. Labium with 5–8 stout setae. *Spination*: invariable.

Adult female (based on SAMA NN28258)

Medium-sized migid spider (total length 10.91 mm). *Colouration* (in ethanol; Figs 25–30): Carapace brown (Fig. 25), with darker brown thoracic furrows and black ocular area (Fig. 28); sternum a lighter yellowish-brown (Fig. 30); labium and maxillae same brown as sternum, darker towards posterior margins (Fig. 29); abdomen dark greyish-brown with lighter grey mottling, with pair of pale, irregular dorsal sigilla (Fig. 27); legs

Figs 25–35. *Moggridgea rainbowi* (Pulleine), female (SAMA NN28258): (**25**) habitus, dorsal view; (**26**) habitus, ventral view; (**27**) abdomen, dorsal view; (**28**) eye group and anterior region of carapace, dorsal view; (**29**) maxillae and labium, ventral view; (**30**) sternum, ventral view; (**31**) left leg I, prolateral view; (**32**) left leg I, retrolateral view; (**33**) left leg III, retrolateral view, showing tibial depression; (**34**) spermathecae, dorsal view; (**35**) detail of left spermatheca, dorsal view.

and pedipalp brown (Figs 31–33). *Cephalothorax*: Carapace 4.7 mm long, 4.3 mm wide, 3.6 mm high, 1.1 × longer than wide (Fig. 25); subquadrate in dorsal view, caput straight in lateral view, with pits on lateral pars cephalica (Fig. 28); cuticle smooth; fovea strongly recurved, with slight median indentation; without pair of pre-foveal setae, with 3 longitudinal rows of 5 setae posterior to ocular area, a few short setae between PME and anterior to ocular area, and carapace margin with a few small delicate setae. Length of clypeus slightly longer than diameter of AME; anterior margin slightly convex (Fig. 28). Eye group 1.7 mm wide, 0.8 mm long, 0.4 × carapace width; anterior eye row straight, posterior eye row recurved; AME two-thirds width of ALE and separated by less than diameter of AME; ALE and PLE separated by about

diameter of PLE; PME widely separated, oval (Fig. 28). Labium as wide as long; apex rounded, with 12 pointed cuspules (Fig. 29). Sternum 3.1 mm long, 2.4 mm wide, sparsely setose, setae denser around margins, with two broadly oval obliquely directed sigilla 1.3–1.6 × as long as wide, each separated anteriorly by their width (Fig. 30). Maxillae rectangular, with 20 (right) and 19 (left) pointed cuspules in median band (Fig. 29). Chelicerae without rastellum; fang furrow without basal swelling, promargin with 4 large teeth, retromargin with 5 teeth (4 small, 1 large); fang with keel; basal tooth absent. *Legs*: Coxae, trochanters and legs sparsely setose; all leg segments cylindrical except for patellae, tibiae, metatarsi and tarsi I–II of female which are flattened and rotated, forming 'basket' over anterior portion of body (Figs 31,32). Coxae without thorns or cuspules (Fig. 30); patellae I, II and IV with ventral patch of erect lamellate setae (Figs 31,32); tibia I not noticeably thickened (Figs 31,32); tibia III with shallow proximal depression (Fig. 33); metatarsus IV with apical preening comb of three setae. Paired tarsal claws of legs with 1 row of ventral teeth arranged: leg I p2 (1 large, 1 small), r2 (1 large, 1 small); leg II p2 (1 large, 1 small), r1 (large); leg III p2 (1 large, 1 small), r1 (1 large); right leg IV p1 (1 large), r3 (1 large, 2 small); median tarsal claws without teeth. Spination: tibia I pv4, rv7; metatarsus I pv6, rv8; tibia II pv4, rv7; metatarsus II pv7, rv7; legs III, IV setose and diffusely spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae; palpal tibia p1, pv1, r1; palpal tarsus pv2, rv3; pedipalp with prominent claw bearing one large ventral tooth. *Leg and pedipalp measurements (in mm)*: Length of legs IV > I > II > III. Leg I: femur 2.8, patella 1.7, tibia 1.8, metatarsus 1.5, tarsus 0.4, total = 8.2. Leg II: femur 2.7, patella 1.5, tibia 1.7, metatarsus 1.4, tarsus 0.6, total = 7.9. Leg III: femur 2.4, patella 1.5, tibia 1.6, metatarsus 1.2, tarsus 0.9, total = 7.3. Leg IV (right): femur 3.1, patella 2.0, tibia 2.4, metatarsus 2.0, tarsus 1.0, total = 7.6. Pedipalp: femur 2.0, patella 0.9, tibia 1.0, tarsus 0.6, total = 10.5. *Abdomen*: Abdomen setose, oval in dorsal view, 5.8 long, 4.3 wide, with one pair of dorsal sigilla (Figs 25,27). Two pairs of spinnerets; posterior median spinnerets one-segmented, contiguous; posterior lateral spinnerets largest, three-segmented, with short and domed apical segment (Fig. 26). *Genitalia*: Spermathecae paired, simple, unbranched, stout and inward facing, hemispherical and transparent distally, with sclerotised median band (Figs 34,35). *Variation* (American River, $n = 3$): Carapace 4.2–4.7 mm long, 3.7–4.3 mm wide. Labium with 12–14 pointed cuspules. Maxillae with 19–22 pointed cuspules. *Spination*: tibia I rv6–7; metatarsus I pv6–8; tibia II pv4–5, rv5–7; metatarsus II pv6–7, rv6–7. (Western River, $n = 4$): Carapace 4.3–5.3 mm long, 3.9–4.9 mm wide. Labium with 15–19 pointed cuspules. Maxillae with 20–38 pointed cuspules. Spination: tibia I pv6–7, rv 5–9; metatarsus I pv6–9, rv7–9; tibia II pb5–6, rv5–9; metatarsus II pv6–8; palp tibia p0–1, palp tarsus rv2–3.

Distribution

Moggridgea rainbowi is known only from Kangaroo Island, South Australia, at American River, and at Billy Goat Falls in the Western River Wilderness Protection Area (Fig. 6), but is likely to be more widely distributed on the island.

Biology

Pulleine (1919) found *M. rainbowi* to be highly abundant on 'rubbly clay banks', just above the high-water mark at American River, and suggested that at high tide the burrows must be very close to, if not in actual contact with, the salt water. The burrow was described as being a maximum of 6 cm long, straight and densely lined with silk. The lid was recorded to be stout, circular and 8 mm in diameter, with an attachment that occupied a quarter the circumference of the lid (Pulleine 1919, figs 4,5). Nick Birks, the collector of the new American River specimens that were photographed and used in the description (above), described the burrow of *M. rainbowi* as being short (up to 6 cm), with a wafer thin lid (Fig. 3), located in a yellow clay bank that would be soaked with salt spray at high tide (Figs 4,5). In contrast, some of the specimens recorded by Main (1991) were described as occupying short burrows, which were located in a damp creek bank in the Western River Wilderness Protection Area, a mesic site previously noted for its southern-temperate spider fauna (see Rix & Harvey 2012). Subsequent collecting has revealed more juvenile specimens from the Western River site. However, additional male specimens and molecular evidence are required to test whether the two populations are conspecific.

Remarks

Moggridgea rainbowi appears to be a member of the *M. quercina* group (see Griswold 1987), given the absence of thorns on coxae II and III. Within this group, it appears to be most similar to *M. quercina*, *M. teresae* and *M. intermedia*, given the presence on the male abdomen of blunt-tipped setae (Figs 14,15). It also shares with *M. quercina* and *M. teresae* the absence of a scopula on the leg IV of males (Fig. 24). These three species are known from the Western Cape Province of South Africa, with *M. quercina* and *M. teresae* only known from a small area between Cape Town and the Cape of Good Hope (Griswold 1987).

DISCUSSION

Moggridgea rainbowi is an enigmatic taxon with a confusing taxonomic history. The original description of *Aganippe rainbowi* by Pulleine (1919) is remarkably good for its time, and included habitus photographs of the female, an excellent illustration of the male pedipalp, and photographs of the burrow entrance and burrow trapdoor *in situ*. It was based on five specimens collected from American River (Kangaroo Island), which were reportedly lodged in the Australian Museum (Sydney) and the South Australian Museum (Adelaide). These specimens could not be traced at either institution, either historically (Main 1985a,b, 1991) or currently (G Milledge & K Sparks pers. comm. 2015) and appear to be lost. The identification of this species was therefore subsequently confused following the generic transfer of *A. rainbowi* to the idiopid genus *Blakistonia* Hogg, 1902 by

Main (1985a,b). No justification was provided by Main for this new combination, which was simply listed in an appendix. However, Main later suggested (Main 1991: 392) that, although the original description, figures and habits of *A. rainbowi* (then *B. rainbowi*) were very migid-like, Pulleine's description of the burrow having a stout, circular door, and the female reportedly having a rastellum and leg scopulae was sufficient evidence to exclude it from the Migidae. Main (1991) then went on to describe a new species of *Moggridgea* – *M. australis* – from the same type locality as *A. rainbowi*.

Clearly, the generic transfer by Main (1985a,b), the subsequent reasoning by Main (1991) and the description of a second migid from the same type locality as *A. rainbowi* have all clouded the true identification of Pulleine's (1919) species. As noted by Main (1991), the description, illustrations and habits of *A. rainbowi* are unequivocally of a species of Migidae. Main falsely attributed nomenclatural precedence to the female description (which appeared before the male description in Pulleine 1919), thus incorrectly assuming that the described female syntype was name-bearing. Main also assumed that because this female description mentioned a rastellum and scopulae, it could not be of a migid, despite the female photographs clearly showing a species of Migidae. Here we take a different and more parsimonious view, and on the basis of new material, including adult males from near the type locality, we transfer *A. rainbowi* out of the genus *Blakistonia* and into *Moggridgea*, and synonymise *M. australis* with its senior synonym *M. rainbowi*. Newly collected specimens from near American River have an identical biology, overall appearance and pedipalpal morphology to *A. rainbowi*, and we are confident that they are conspecific; therefore, no neotype is designated. We recognise that the female description in Pulleine (1919) does not have nomenclatural precedence and that, potential descriptive errors by Pulleine notwithstanding, the original description is nonetheless likely to be of the female specimen photographed in Plate XII, and not of an unrelated spider in another family. Indeed, the rest of the description is entirely consistent with the morphology of *M. rainbowi*. Unlike the south-western Australian species of Migidae, which have been found to belong to a separate genus (Harvey *et al*. 2015), *M. rainbowi* can be clearly included in the genus *Moggridgea* based on morphology (Main 1991; this study) and on molecular sequence data (Cooper *et al*. 2011; Harvey *et al*. 2015).

The occurrence of a single species of *Moggridgea* in Australia is rather surprising, as the genus is otherwise found only in the Afrotropical region (Griswold 1987). Main (1991) postulated a vicariant origin for the Australian species, suggesting that *Moggridgea* were likely to be incapable of long-distance dispersal across oceans. While most species of *Moggridgea* do occur on continental, mainland Africa, three are known from islands: *M. occidua* Simon, 1907 from Príncipe, *M. nesiota* Griswold, 1987 from the Comores, and *M. socotra* Griswold, 1987 from Socotra. While Príncipe and Socotra are continental fragments that may have retained a portion of their original biota after last fragmenting from the mainland, the Comores are volcanic in origin, with the current islands ranging from 0.1 to 7.7 mya (Schlüter & Trauth 2008). The only known location of *M. nesiota*, the island of Moheli (Griswold 1987), is thought to have formed 5.5 mya, suggesting that the presence of this species there can only be explained by dispersal from mainland Africa approximately 340 km away. The presence of *M. rainbowi* on Kangaroo Island is therefore tantalising, and raises the prospect that these spiders have undergone long-distance dispersal from Africa to the beaches of Kangaroo Island (ca. 10 000 km) where they have presumably remained since their arrival. While trans-oceanic dispersal at this scale would be remarkable for a mygalomorph spider, and a modern introduction cannot yet be ruled out, it is a hypothesis that requires further study using a multi-gene molecular dating approach.

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CHAPTER III: Across the Indian Ocean: A remarkable example of trans-oceanic dispersal in an austral mygalomorph spider (2017, PLoS One 12(8): e0180139 1–16).

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Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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RESEARCH ARTICLE

Across the Indian Ocean: A remarkable example of trans-oceanic dispersal in an austral mygalomorph spider

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Abstract

The Migidae are a family of austral trapdoor spiders known to show a highly restricted and disjunct distribution pattern. Here, we aim to investigate the phylogeny and historical biogeography of the group, which was previously thought to be vicariant in origin, and examine the biogeographic origins of the genus *Moggridgea* using a dated multi-gene phylogeny. *Moggridgea* specimens were sampled from southern Australia and Africa, and *Bertmainus* was sampled from Western Australia. Sanger sequencing methods were used to generate a robust six marker molecular dataset consisting of the nuclear genes *18S* rRNA, *28S* rRNA, *ITS* rRNA, *XPNPEP3* and *H3* and the mitochondrial gene *COI*. Bayesian and Maximum Likelihood methods were used to analyse the dataset, and the key dispersal nodes were dated using BEAST. Based on our data, we demonstrate that *Moggridgea rainbowi* from Kangaroo Island, Australia is a valid member of the otherwise African genus *Moggridgea*. Molecular clock dating analyses show that the inter-specific divergence of *M. rainbowi* from African congeners is between 2.27–16.02 million years ago (Mya). This divergence date significantly post-dates the separation of Africa from Gondwana (95 Mya) and therefore does not support a vicariant origin for Australian *Moggridgea*. It also pre-dates human colonisation of Kangaroo Island, a result which is further supported by the intra-specific divergence date of 1.10–6.39 Mya between separate populations on Kangaroo Island. These analyses provide strong support for the hypothesis that *Moggridgea* colonised Australia via long-distance trans-Indian Ocean dispersal, representing the first such documented case in a mygalomorph spider.

Introduction

The historical view of the biogeographical history of the Southern Hemisphere postulated that the terrestrial biota had largely vicariant origins [1], and that dispersal played a relatively

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limited role in taxa with southern-temperate or 'Gondwanan' ranges [2]. The sequential separation of the southern continental blocks since the Mesozoic [3] has led to lineages on multiple post-Gondwanan land fragments forming independent clades. In contrast, oceanic dispersal [1] was often discarded *a priori* as a primary explanation of distribution patterns in the Southern Hemisphere [3]. The idea that seemingly remarkable feats of long-distance dispersal were needed to explain the evolutionary history of many groups of organisms was first postulated by Darwin [4], but the concept has often been considered speculative and difficult to test–"a science of the improbable, the rare, the mysterious and the miraculous" [5]. The apparent poor suitability of many austral groups for oceanic dispersal (e.g. marsupials and ratite birds) appeared to further support vicariance as the more likely biogeographical scenario [3]. Indeed, the idea that vicariance was the key theory to explain the Gondwanan distribution of many southern-temperate groups proved difficult to challenge for many decades [6].

Over the past 20 years, new discoveries and more advanced methods, particularly molecular phylogenetic and dating methods, have brought the dispersal-vicariance debate full-circle. Using the fossil record and/or gene-specific rates of nucleotide evolution, molecular phylogenies with dated nodes now provide new perspectives on the evolutionary history of the flora and fauna of the Southern Hemisphere [6, 7]. Most importantly, molecular divergence dating provides the temporal perspective necessary to test and, where appropriate, reject vicariant biogeographic hypotheses [7]. Calculating the probability of a successful dispersal requires taking into account the number of dispersers, their probability of survival, their likelihood of establishing upon landing, and also the presence of prevailing winds, oceanic currents, hosts, vectors or any other underlying mechanisms that may affect movement and survival (any or all of which may include rafting as a plausible hypothesis) [8]. Recent molecular studies have shown that successful long-distance dispersal events have occurred in many groups of taxa, such as monkeys [9], lemurs [10] and geckos [11], a previously counter-intuitive conclusion without accessible dated molecular phylogenies.

The now well-documented occurrence of long-distance dispersal via rafting in a large range of taxa [8], highlights that trans-oceanic dispersal is not only restricted to organisms capable of flight [12], aerial dispersal (e.g. ballooning spiders [13]) or oceanic buoyancy (e.g. floating seeds [14]). Rafting generally involves large chunks of land and/or vegetation being washed out to sea, with rafting events being implicated in the colonisation of numerous isolated land masses including Australia [3], Madagascar [10,15], South America [7, 9,11], New Zealand [16] and newly formed Darwinian Islands such as the Galapagos islands, Canary Islands and Hawaii [17]. A case in point, and not surprising, is the coastal araneomorph spider genus *Amaurobioides*, which is hypothesised to have undergone several long distance, transoceanic dispersal events, facilitated by rafting [18].Spiders of the infraorder Mygalomorphae are well featured in vicariance biogeography literature (e.g. [19–22]) and more recently in molecular studies of phylogeography and species delimitation [23]. Mygalomorphs are a monophyletic group with a worldwide distribution [24–26]. They have unusually long life cycles, with some species living up to 30 years and requiring 5–8 years to reach reproductive maturity [27]. They are univoltine [28] with females and juveniles leading sedentary lifestyles [29]. Although ballooning of spiderlings has been documented in several genera (e.g. [30–33]) most mygalomorphs do not disperse aerially and are known to be relatively non-vagile, with juveniles often moving only a few metres from the maternal site (e.g. [25,31,34,35]). These life-history traits predispose mygalomorph spiders to geographic isolation through mechanisms such as continental drift, glaciation, orogenic activity and habitat fragmentation, resulting in a large number of taxa that have small geographical distributions [36–38]. It is the poor vagility, sedentary habits and patterns of fine-scale genetic structuring characteristic of many mygalomorph spiders [28] that make this group especially amenable to testing the vicariance paradigm [25].

The Migidae are a family of Mygalomorphae previously assumed to have a vicariant austral distribution. Eleven named genera occur in Africa, Madagascar, New Zealand, New Caledonia, South America and Australia [22,38]. The Australian migid fauna includes four genera: *Migas* L. Koch, 1873 and *Heteromigas* Hogg, 1902 from eastern Australia [39]; *Moggridgea* O. P.-Cambridge, 1904 from Kangaroo Island (KI), South Australia [40]; and *Bertmainius* Harvey *et al*., 2015 from south-western Australia [38]. Although displaying a putatively Gondwanan distribution, a cladistic study based on morphology suggested that the evolutionary history of the family cannot be explained by vicariance alone, with Australia appearing three times in the cladogram [22]. Recent molecular [35,38] and morphological [40] data suggest the only Australian *Moggridgea* species, *Moggridgea rainbowi* (Pulleine, 1919), groups with African *Moggridgea*, where all other congeneric species occur. The existence of an 'African' *Moggridgea* lineage in Australia immediately poses a number of tantalising biogeographic questions, and these form the basis of this study.

Here we test three alternative biogeographic hypotheses for the presence of *Moggridgea* in southern Australia, using a dated phylogenetic approach based on a comprehensive multigene dataset. The first (null) hypothesis is Gondwanan vicariance, which would be evidenced by a deep and very old divergence date from African congeners, consistent with the age of separation of Africa from the rest of Gondwana. This hypothesis was first suggested by Main [41] to explain the presence of *Moggridgea* (now treated as *Bertmanius*) in Western Australia. An alternative hypothesis (H_1) is a human-mediated introduction from Africa during the European colonisation of KI. This would be evidenced by a recent, extremely shallow (among conspecific) or low divergence date (among sister species) and, equally importantly, by a lack of phylogeographic structure on KI itself. The second alternative hypothesis (H_2) is trans-oceanic dispersal, which would be evidenced by both recent divergence from African species (relative to ancient African vicariance) and by demonstrable phylogeographic structuring among populations on KI. The implications of our results are discussed in regard to their broader impact, as an inability to reject H_2 would provide the first dated molecular evidence of long-distance oceanic dispersal in a mygalomorph spider, and would be an invaluable insight into the history and origins of southern hemisphere mygalomorph spider diversity. Our rejection of H_0 and H_2 provide the first solid evidence for long-distance oceanic dispersal in a mygalomorph spider, and has broader implications for better understanding the history and origins of southern hemisphere mygalomorph spider diversity.

Methods

Specimen sampling

Our dataset comprised seven specimens of *M. rainbowi* from two populations on KI separated by approximately 80 km (Western River [three specimens] and American River [four specimens]); five exemplar species of *Moggridgea* from South Africa; and seven species of *Bertmainius* from south-western Australia (see Table 1). The American River specimens were excavated from burrows above the high tide mark in May 2013, and initially preserved in 100% ethanol. These specimens were collected under permit number E26155-3 issued by the South Australian Department of Environment, Water and Natural Resources. All *M. rainbow* specimens from Western River, *Bertmainius* species from Western Australian and *Moggridgea* specimens from Africa were obtained from archived DNS samples stored in the Australian Biological Tissue Collection, provided with permission from the South Australian Museum. These DNA samples had been previously collected under annual collection permits issued to scientists from the Western or South Australian museums or donated by overseas colleagues. Legs 3 and 4 from the left side of each specimen were then kept in 100% ethanol, while the rest

Table 1. Registration numbers, locality data, and Genbank accession numbers for specimens used in the study.

Species	Registration numbers	Locality	Coordinates	Genbank accession numbers *COI*	Genbank accession numbers *ITS1-ITS2*	Genbank accession numbers *XPNPEP3*	Genbank accession numbers *18S*	Genbank accession numbers 28S	Genbank accession numbers *H3*
SCORPIONES									
Urodacus planimanus	T129654	WA: Bedfordale	32˚10'05"S, 116˚04'06"E	KY295225	-	KY295718	KY294838	KY294961	KY295099
ARANEAE									
Latrodectus hasseltii	T129059	WA: Welshpool	31˚59'08"S, 115˚55'57"E	KY295226	-	KY295719	KY294839	KY294962	KY295100
Aganippe sp.	T129362	WA: Serpentine NP	32˚22'05"S, 116˚00'26"E	KY295228	KY294976	KY295723	KY294841	KY294965	KY295103
Euoplos sp.	T129363	WA: Serpentine NP	32˚22'05"S, 116˚00'26"E	KY598258	KY294983	KY295725	KY294843	KY294970	KY295108
Cethegus fugax	T129260	WA: John Forrest NP	31˚53'54"S, 116˚05'49"E	KY295227	-	KY295722	KY294840	KY294963	KY295101
Moggridgea rainbowi	ABTC110307	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749981	MF169599	MF169538	MF169569	MF169628
Moggridgea rainbowi	ABTC110308	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749982	MF169600	MF169539	MF169570	MF169629
Moggridgea rainbowi	ABTC110309	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749983	MF169601	MF169540	MF169571	
Moggridgea rainbowi	SAM NN28257	SA: American River, Kangaroo Island	35˚46'35"S, 35˚46'35"S	MF169531	MF169535	MF169607	MF169547	MF169577	MF169632
Moggridgea rainbowi	SAM NN28345	SA: American River, Kangaroo Island	35˚46'36.5"S, 137˚46'33"E	MF169532	MF169536	MF169608	MF169548	MF169578	MF169633
Moggridgea rainbowi	SAM NN25429	SA: American River, Kangaroo Island	35˚46'37"S, 137˚46'3"E	MF169530	MF169534	-	MF169546	MF169576	MF169631
Moggridgea rainbowi	SAM NN28346.1	SA: American River	35˚46'36.5"S, 137˚46'33"E	MF169533	MF169537	-	MF169549	MF169579	MF169634
Moggridgea terrestris	MY357	South Africa: Eastern Cape Province	33˚07'31"S, 26˚36'40"E	JF749926	JF749986	MF169602	MF169541	MF169572	-
Moggridgea rupicoloides	MY360	South Africa: Eastern Cape Province	33˚23'26"S, 26˚26'11"E	JF749925	-	MF169603	MF169642	MF169573	-
Moggridgea intermedia	MY361	South Africa: Western Cape Province	33˚58'13"S, 23˚32'20"E	JF749928	JF749984	MF169604	MF169543	-	MF169630
Moggridgea mordax	MY371	South Africa: Northern Cape Province Hwy N14	28˚01'30"S, 22˚39'48"E	JF749929	-	MF169605	MF169544	MF169574	-

(*Continued*)

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Aganippe sp.	T129362	WA: Serpentine NP	32˚22'05"S, 116˚00'26"E	KY295228	KY294976	KY295723	KY294841	KY294965	KY295103
Euoplos sp.	T129363	WA: Serpentine NP	32˚22'05"S, 116˚00'26"E	KY598258	KY294983	KY295725	KY294843	KY294970	KY295108
Cethegus fugax	T129260	WA: John Forrest NP	31˚53'54"S, 116˚05'49"E	KY295227	-	KY295722	KY294840	KY294963	KY295101
Moggridgea rainbowi	ABTC110307	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749981	MF169599	MF169538	MF169569	MF169628
Moggridgea rainbowi	ABTC110308	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749982	MF169600	MF169539	MF169570	MF169629
Moggridgea rainbowi	ABTC110309	SA: Western River, Kangaroo Island	35˚41'46"S, 136˚54'34"E	JF749924	JF749983	MF169601	MF169540	MF169571	
Moggridgea rainbowi	SAM NN28257	SA: American River, Kangaroo Island	35˚46'35"S, 35˚46'35"S	MF169531	MF169535	MF169607	MF169547	MF169577	MF169632
Moggridgea rainbowi	SAM NN28345	SA: American River, Kangaroo Island	35˚46'36.5"S, 137˚46'33"E	MF169532	MF169536	MF169608	MF169548	MF169578	MF169633
Moggridgea rainbowi	SAM NN25429	SA: American River, Kangaroo Island	35˚46'37"S, 137˚46'3"E	MF169530	MF169534	-	MF169546	MF169576	MF169631
Moggridgea rainbowi	SAM NN28346.1	SA: American River	35˚46'36.5"S, 137˚46'33"E	MF169533	MF169537	-	MF169549	MF169579	MF169634
Moggridgea terrestris	MY357	South Africa: Eastern Cape Province	33˚07'31"S, 26˚36'40"E	JF749926	JF749986	MF169602	MF169541	MF169572	-
Moggridgea rupicoloides	MY360	South Africa: Eastern Cape Province	33˚23'26"S, 26˚26'11"E	JF749925	-	MF169603	MF169642	MF169573	-
Moggridgea intermedia	MY361	South Africa: Western Cape Province	33˚58'13"S, 23˚32'20"E	JF749928	JF749984	MF169604	MF169543	-	MF169630
Moggridgea mordax	MY371	South Africa: Northern Cape Province Hwy N14	28˚01'30"S, 22˚39'48"E	JF749929	-	MF169605	MF169544	MF169574	-

(*Continued*)

Table 1. (*Continued*)

Species	Registration numbers	Locality	Coordinates	Genbank accession numbers *COI*	Genbank accession numbers *ITS1-ITS2*	Genbank accession numbers *XPNPEP3*	Genbank accession numbers *18S*	Genbank accession numbers 28S	Genbank accession numbers *H3*
Bertmainius opimus	WAM T63108	WA: S. of Gracetown	33˚54'32"S, 115˚00'24"E	JF749900	JF749966	MF169622	MF169563	MF169593	MF169643
Bertmainius opimus	WAM T63179	WA: Shannon NP	34˚42'47"S, 116˚21'47"E	JF749920	JF749971	MF169627	MF169568	MF169598	-
Bertmainius opimus	WAM T63111	WA: Wellington Mill	33˚27'04"S, 115˚55'42"E	JF749917	JF749941	MF169623	MF169564	MF169594	MF169644

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of the body was transferred to 75% to allow for easier manipulation for morphological study. Cytochrome oxidase subunit I (*COI*) and internal transcribed spacer (*ITS*) sequences for *M. rainbowi* from Western River (KI), along with the *Moggridgea* species from South Africa and the *Bertmainius* species from Western Australia were taken from [35] and [38]. DNA from these specimens was sequenced for four additional genes: *XPNPEP3*, *28S*, *18S* and *H3* (see below).

Molecular methods

Approximately 3 mm^3 of muscle tissue was removed from the leg femora for DNA extraction. DNA was extracted using the Gentra DNA extraction PURE-GENE DNA Purification Kit (Gentra Systems, Minnepolis, MN, USA).

A 715 bp fragment of nuclear *18S* rRNA was amplified using the primers 18S_ai (5′-CCTGAGAAACGGCTACCACATC) and 18S_b0.5 (5′-GTTTCAGCTTTGCAACCAT-3′) [42]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing temperature of 50˚C for 35 s, then 72˚C for 2 mins, with a final elongation step of 72˚C for 10 mins.

An 852 bp fragment of nuclear *28S* rDNA was amplified using the primers 28Sa (5′-GACCCGTCTTGAAACACGGA-3′) and LSUR (5′-GCTACTACCACCAAGATCTGCA-3′) [42]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing temperature of 50˚C for 35 s, then 72˚C for 2 mins, with a final elongation step of 72˚C for 10 mins.

A 658 bp fragment of mitochondrial *COI* was amplified using the universal *COI* primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTG-3′) and HC02198 (3′-TAAACTTCAGGGTGACCAAAAAATCA-5′) [43]. PCR was performed under the following conditions: an initial denaturation step of 94˚C for 5 mins, followed by 34 cycles of 94˚C for 45 s, annealing temperature of 48˚C for 45 s, then 72˚C for 1 min, with a final elongation step of 72˚C for 10 mins.

A 738 bp fragment of nuclear Xaa-Pro aminopeptidase 3 (*XPNPEP3*) was amplified using the primers XPNPEP3_f2 (5′-GAAAGAAGATTAAAACTAATGGAAC-3′) and (5′-XPNPEP3_Ar_r1 CCAGCATCCATYAANACCA-3′) [44]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing temperature dropping from 55˚C to 45˚C for 35 s, then 72˚C for 1 min, with a final elongation step of 72˚C for 10 mins.

An 838 bp fragment of nuclear *ITS* rRNA (including *ITS1*, *5.8S* rRNA, *ITS2*) was amplified using the primers G923 (5′-CGTAACAAGGTTTCCGTAGGTGA-3′) and G925 (5′AGAGAACTCGCGAATTCCACGG-3′) (see [35]). PCR was performed under the following conditions:

an initial denaturation step of 94˚C for 9 mins, followed by six cycles of 94˚C for 45 s, annealing 68˚C for 45 s (-1˚C each cycle); 72˚C 60 s, then 28 cycles of 94˚C for 45 s, annealing 62˚C for 45 s, 72˚C for 60 s, with a final elongation step of 72˚C for 6 min. The enzyme used was AmpliTaq Gold DNA polymerase.

A 327 bp fragment of nuclear histone *H3* was amplified using the primers H3aF (5′-ATG GCTCGTACCAAGCAGACVGC-3′) and H3aR (5′-ATATCCTTRGGCATRATRGTGAC-3′) [45]. PCR was performed under the following conditions: an initial denaturation step of 95˚C for 5 mins, followed by 35 cycles of 95˚C for 20 s, annealing 48˚C for 35 s, then 72˚C for 2 mins, with a final elongation step of 72˚C for 2 mins. The enzyme used was MyTaq DNA polymerase.

The genes *18S*, *28S*, *XPNPEP3* and *H3* were amplified following [44], using MyTaq DNA Polymerase (Bioline, Taunton, MA), in a Bio-Rad T100 Thermal Cycler. For each 25 μL PCR reaction, 2 μL of template DNA, 5 μL of MyTaq buffer, 5 pm of each primer and 0.2 μL of MyTaq DNA polymerase were used. PCR products were visualised on 1.5% agarose gels using standard procedures, and PCR clean-up plus bi-directional sequencing was performed by the Australian Genome Research Facility (AGRF, Nedlands, WA). *COI* and *ITS* were amplified using Eppendorf Amplitaq Gold (Eppendorf, Westbury, NY, USA). For each 25 μL reaction, 2 μL of template DNA, 2.5 μL of PCR Gold Buffer, 3.5 μL of MgCl, 2.0 μL of deoxyribonucleotide triphosphate (dNTP), 10 pm of each primer, and 0.1μL Amplitaq Gold DNA polymerase was used. PCR products were verified by agarose gel electrophoresis (1% agarose), and PCR clean-up plus bi-directional Sanger sequencing was performed by AGRF (Waite Campus, Adelaide, S.A.). Sequences were submitted to GenBank (see Table 1 for accession numbers).

Phylogenetic analyses

Five non-migid outgroups were sourced from [44]: the scorpion *Urodacus planimanus* Pocock, 1893, the red-back spider *Latrodectus hasseltii* Thorell, 1870, the curtain-web mygalomorph spider *Cethegus fugax* Simon, 1908, and the idiopid trapdoor spiders *Aganippe* sp. O. P.-Cambridge, 1877 and *Euoplos* sp. (Table 1). All newly obtained sequences were edited with reference to chromatograms using Geneious [46]. Forward and reverse sequences were assembled, and the resulting consensus sequences were then aligned using the 'Geneious Alignment' function of Geneious. PartitionFinder [47] was used to select the model that best fit each gene, with the protein coding genes being divided into three codon positions. For *COI*, the General Time Reversible (GTR) [48] + gamma (G) [49] model was selected for the first codon position, the Felstein 81 (F81) [50] + invariant (I) I+G for the second codon position, and the Hasegawa, Kishino and Yano (HKY) [51] +I+G for the third. For *ITS1*, *ITS2* and *18S*, the model Kimura 80 (K80) [52] +G was chosen. For *5.8S* and *28S*, the GTR+I+G model was chosen. For *H3*, the GTR+I+G model was chosen for codon position one and the K80+G model was chosen for positions two and three. For *XPNPEP3*, the HKY+G model was chosen for all positions.

Phylogenetic reconstruction was undertaken using MrBayes 3.2.6 [53] employing the CIPRES Science Gateway [54]. In the Bayesian analysis, each codon position was modelled separately using the models listed above. All parameters were unlinked and the rates were allowed to vary over the partitions. For all reconstructions, two runs with four chains each were run simultaneously for 100 million generations, with every 1,000th tree sampled. A burnin of 1,000, chosen using the program Tracer 1.6 [55], was set for building the maximum clade credibility tree. The resulting tree was viewed using FigTree v1.3.1 [56] (Fig 1). A maximum likelihood analysis was also undertaken using RAxML [57] on the BlackBox server [58] with *COI*, *H3* and *XPNPEP3* partitioned by codons and *ITS1*, *5.8S*, *ITS2* and *28S* partitioned individually, with the GTR + G model used for all genes.

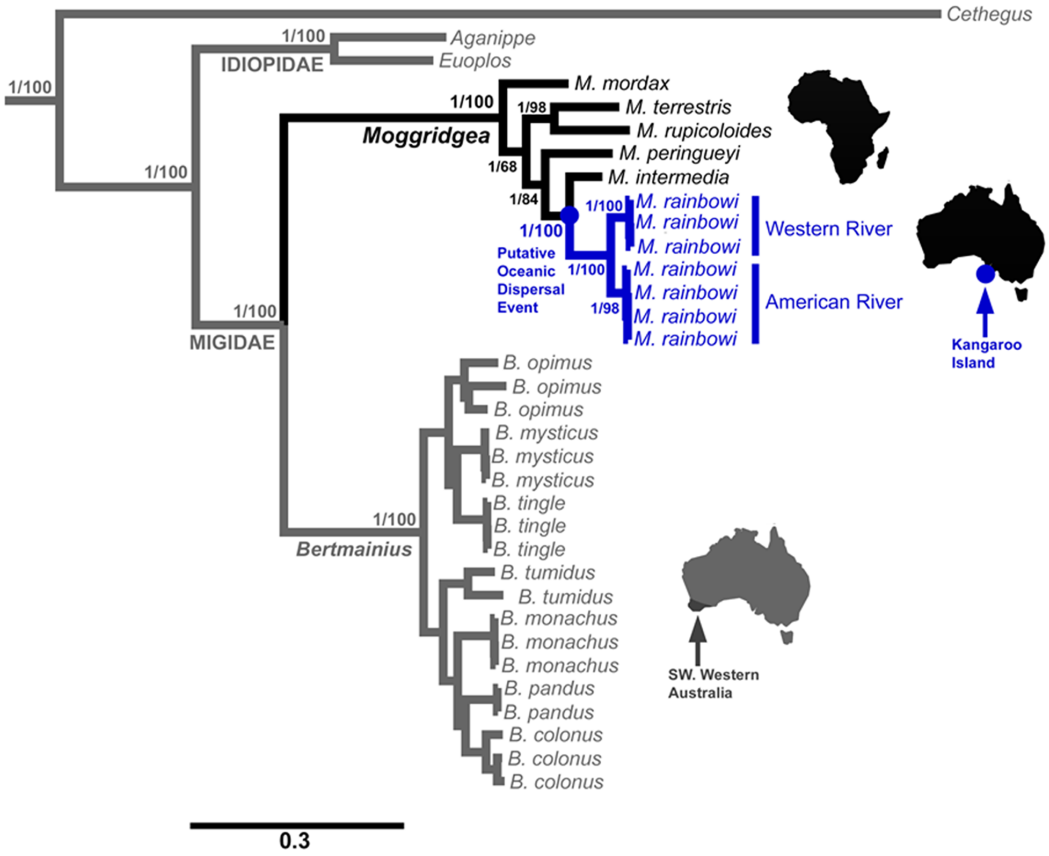

Fig 1. Combined *COI*, *ITS*, *H3*, *18S*, *28S* and *XPNPEP3* tree constructed using MrBayes and mixed models. Numbers on nodes represent posterior probabilities followed by maximum likelihood bootstrap values.

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Molecular clock analyses

Divergence dating analysis was performed using BEAST 1.8.0 [59] to determine the time of divergence of *M. rainbowi* from its African relatives. The program BEAUti 1.8.0 (part of the BEAST software package) was used to create.xml files to input into BEAST. Given the robustness of phylogenetic analyses placing *M. rainbowi* within the African *Moggridgea* clade (see Fig 1), we focused on the *Moggridgea* taxa only for our molecular clock analyses. Exclusion of distantly related taxa, such as *Bertmainius*, avoided potential issues with saturation of the third codon positions of *COI*. This still enabled us to effectively date the nodes of most interest, i.e. the divergence time between the closest African sister to *M. rainbowi*, *M. intermedia* (see [40]), and the divergence between the two KI *M. rainbowi* populations. We included only the specimens for which we had a complete set of sequence data; this allowed us to link the trees and resulted in a single tree for analysis. The gene *H3* had a larger proportion of missing data than the other genes, so was not included in the dating analysis. *28S* was also not included as it could not be sequenced for *M. intermedia*, which was found to be the closest relative to *M. rainbowi*.

Six separate BEAST analyses were carried out using different clock models, including a strict clock, uncorrelated lognormal clock and exponential relaxed clock, and both the GTR + G + I and HKY nucleotide substitution modes. Each analysis was run for 20 million generations with a burnin of 1 million generations (i.e. 10%), and the program Tracer 1.6 [55] was used to analyse the parameter distributions estimated from BEAST and check for convergence of the chains. Stationarity was checked for, and no evidence of non-stationarity was found in all BEAST runs. As fossil calibrations were unavailable to date nodes of the *Moggridgea* phylogeny, the mean *COI* substitution rate was fixed at 0.02 substitutions per site per million years, based on the estimates of 4% divergence between lineages per million years [by 34] for the trapdoor spider *Aptostichus simus* Chamberlin 1917. Rates for all other genes were estimated. Site models and clock models were unlinked and trees were linked. The tree priors selected for separate analyses were Speciation: Yule Process and Birth-Death Process, as both are suitable for inter-species relationships. Priors on the ucld.mean for each gene were defined as uniform with an initial value of 0.00115, an upper value of 0.0115 and a minimum value of 0.0001. The universal substitution rate estimated for arthropod mtDNA [60] was used to define the upper value. Due to the average slower pace of nuclear genes compared with mitochondrial ones, the initial value was one order of magnitude slower (as per [61]). TreeAnnotator [59] was used to produce a single "target" tree which was then visualised using FigTree v1.3.1 [56].

Results

Phylogenetic analysis

A maximum clade credibility tree was generated for the MrBayes analysis of the combined six gene, 4118 character, 36 taxa dataset (Fig 1). This analysis resolved the genera *Moggridgea* and *Bertmainius* as reciprocally monophyletic, with *M. rainbowi* from KI clearly embedded within the African *Moggridgea* lineage and sister to *M. intermedia* (posterior probability = 1, bootstrap value 100) (Fig 1). Furthermore, *M. rainbowi* formed a monophyletic group, but showed phylogeographic structure, with haplotypes reflecting the two geographic locations (Western River and American River). The Maximum Likelihood analysis of the same dataset produced a completely concordant tree (see Dryad digital repository, doi:10.5061/dryad.9cp00).

Molecular clock analyses

The time to most recent common ancestor (TMRCA) estimate for the African *M. intermedia* and KI *M. rainbowi*, the TMRCA of the KI Western River and American River populations of *M. rainbowi*, and the Posterior Mean and Posterior ESS values for all three clocks with GTR, HKY and PartitionFinder models, using both Speciation: Yule Process and Speciation: Birth-Death Process tree priors are summarised in Table 2. All analyses performed using the GTR+I +G models failed to achieve adequate convergence for many of the parameter estimates (i.e. posterior statistics with effective sample sizes <10 after 20 million generations). Analyses performed using the HKY model had posterior ESS values of >1400 for every clock model used. Combinations of clocks and models gave TMRCA estimates ranging between 2.27 Mya (strict clock, HKY model, Speciation: Yule Process, 95% Highest Posterior Density [HPD] 1.89–2.65) to 16.02 Mya (strict clock, GTR model, Speciation: Yule Process, 95% HPD 8.97–25.60) between the African *M. intermedia* and *M. rainbowi* from KI. The TMRCA values for the divergence time between the two separate KI populations ranged between 1.10 Mya (Strict clock, HKY model, Speciation: Birth-Death Process, 95% HPD 0.86–1.34) to 6.39 Mya (strict clock, GTR models, Speciation: Yule Process, 3.48–10.23).

Table 2. Estimates of time (in millions of years) to most recent common ancestors (TMRCA) and 95% highest posterior density (HPD) intervals for key nodes and posterior mean and effective sample size [ESS] values, generated using BEAST.

Parameters	TMRCA Node 1 (Moggridgea Dispersal) + 95% Highest Posterior Density	TMRCA Node 2 (KI Population Divergence) + 95% Highest Posterior Density	Posterior Mean	Posterior ESS
Strict Clock, GTR Models, Speciation: Yule Process	16.02	6.39	-6059.22	20.04
	8.87–25.60	3.48–10.23		
Strict Clock, HKY Models, Speciation: Yule Process	2.27	1.10	-6478.87	1449.97
	1.89–2.65	0.87–1.34		
Strict Clock, GTR Models, Speciation: Birth-Death Process	15.98	6.35	-5813.92	8.93
	8.63–25.96	3.55–10.37		
Strict Clock, HKY Models, Speciation: Birth-Death Process	2.27	1.10	-6259.82	1672.67
	1.91–2.67	0.86–1.34		
Exponential Clock, GTR Models, Speciation: Yule Process	10.59	4.06	-6021.34	5.93
	4.01–19.94	1.59–7.66		
Exponential Clock, HKY Models, Speciation: Yule Process	3.54	1.75	-6155.69	2310.32
	2.35–4.96	1.17–2.45		
Exponential Clock, GTR Models, Speciation: Birth-Death Process	10.49	3.69	-5789.97	7.62
	3.97–19.71	1.60–7.45		
Exponential Clock, HKY Models, Speciation: Birth-Death Process	3.54	1.73	-5936.87	1607.35
	2.36–4.92	1.16–2.40		
Lognormal Clock, GTR Models, Speciation: Yule Process	15.44	5.96	-6035.79	9.76
	5.36–27.15	1.62–11.13		
Lognormal Clock, HKY Models, Speciation: Yule Process	8.48	3.56	-6172.48	1701.01
	3.33–13.97	1.25–6.53		
Lognormal Clock, GTR Models, Speciation: Birth-Death Process	15.40	5.77	-5821.38	10.17
	5.41–27.32	1.51–10.63		
Lognormal Clock, HKY Models, Speciation: Birth-Death Process	8.48	3.47	-5953.30	1825.83
	3.32–14.12	1.22–6.37		

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Discussion

Our analyses show that *M. rainbowi* from KI is unequivocally related to African *Moggridgea*, with KI populations rendering the latter paraphyletic–a result consistent with previous morphological findings [40]. Our six-gene Bayesian analysis is also concordant with previous molecular results [35], with a deep and reciprocally-monophyletic separation between true *Moggridgea* and Australian *Bertmainius*, although the latter study was limited in its taxon and gene sampling and appropriate outgroups to confirm the exact relationships, compared with the current study.

But how did an otherwise African spider lineage end up on KI in southern Australia? To address this question we used two lines of evidence: divergence dating between African and Australian exemplars; and divergence dating between both the KI populations of *Moggridgea*. The (null) hypothesis of Gondwanan vicariance requires a very old divergence date of 110 + Mya between African and Australian *Moggridgea* to be consistent with the vicariant breakup of Gondwana [3]. The inferred split between *M. rainbowi* and African *M. intermedia* ranged from 2.27–16.02 Mya (Table 2), and the inferred age for the divergence of the two KI populations of *M. rainbowi* ranged from 1.10–6.39 Mya. Although there may be considerable uncertainty in the use of a 'borrowed' rate for *COI* to estimate divergence times, even if the HPD error margins for our dating estimate were doubled or tripled, it is clear that the dates for these

nodes are relatively recent, and not concordant with Africa's long isolation from the rest of Gondwana. Therefore, vicariance must be rejected as a plausible hypothesis for the presence of *Moggridgea* on KI.

The first of two alternative hypotheses (H_1) is that *Moggridgea* was accidentally introduced from Africa to KI by humans, such as explorers, sealers or European settlers who arrived in 1802 [62]. The sealers came from North America, and settled at what is now American River [63]. If humans brought *Moggridgea* to KI at any time from 1802 onwards (assuming a single introduction), intra-specific phylogeographic structure and genetic divergence equating to 1.10–6.39 Mya of isolation in different regions of KI would be highly unlikely.

While we cannot disprove more than one introduction of the same species, each with divergent mtDNA, to different locations on KI, the probability of two successful dispersal events for the same African species must be very low. Similarly, this hypothesis cannot be rejected on the basis of the divergence of *M. rainbowi* from *M. intermedia* alone, given our incomplete sampling of African taxa and the possibility of another unknown species in Africa being a closer relative to *M. rainbowi*. There is also the possibility of putatively unsampled littoral zone lineages from Africa, which would be more likely to be carried by explorers or oceanic vessels. However, no littoral species are so far known, although concentrated fieldwork would be required to confirm this. More than one introduction also seems highly unlikely due to the significant level of genetic differentiation between *M. rainbowi* populations at American River and Western River, which is consistent with *Moggridgea* arriving well before humans colonised the island.

The final hypothesis (H_2) predicts that *Moggridgea* is present in Australia due to long-distance dispersal from southern Africa. This proposition, which best fits the estimated divergence date of 2.27–16.02 Mya, cannot be rejected given current morphological and molecular evidence, and is our preferred explanation for the data. Long-distance dispersal of 10,000 km may be improbable for a sedentary trapdoor spider such as *Moggridgea*, but oceanic dispersal is not unprecedented for this genus, at least over shorter distances. Most species occur on mainland Africa, but three species are known from offshore islands. These include *M. occidua* (Simon, 1907) from Príncipe, *M. nesiota* Griswold, 1987 from Comoros, and *M. socotra* Griswold, 1987 from Socotra [64,40]. Príncipe and Socotra are both continental fragments of mainland Africa, and therefore their fauna may have originated by vicariance and not dispersal. However, the Comoros are volcanic in origin and were formed between 0.1 and 7.7 Mya [65]. *Moggridgea nesiota* Griswold 1987b is found on the island of Moheli, which was formed 5.5 Mya, suggesting that the presence of this species there can only be explained by dispersal from mainland Africa (approximately 340 km away). Although only a small fraction of the distance between the south-western Cape and KI, this distribution does suggest that *Moggridgea* is capable of oceanic dispersal, most likely facilitated by rafting given their burrow-dwelling existence. Colonisation by individuals who have arrived via rafting will inevitably occur in the littoral zone [66] which is consistent with the habitat of *M. rainbowi* at American River, where their burrows have only been found in vertical banks just above the high tide mark [40]. This habitat also provides further evidence of an unusual, possibly high degree of salt tolerance.

While this study represents the first robust evidence of long-distance trans-oceanic dispersal in a mygalomorph spider, oceanic dispersal at a smaller scale (e.g. as for *M. nesiota*) can be inferred for several other mygalomorphs. This is especially so for those species that occur on newly formed islands of volcanic origin (e.g. Galapagos Islands and Hawaii), and those that were once connected to a continental landmass, such as the Seychelles, the latter of which are part of the granitic Mascarene Plateau which broke off from the Indian Plate about 66 Mya) [17]. While some mygalomorphs found on non-continental islands are capable of ballooning (e.g. *Ummidia* Thorell, 1878 which is present on the volcanic island Saint Vincent in the Caribbean [67]; and *Conothele* Thorell, 1878 which occurs on some Pacific Islands and the

Seychelles [68,69]), there are also other mygalomorphs that cannot disperse this way, and yet are present on young, isolated landforms. The barychelid *Nihoa hawaiiensis* (Raven, 1988) [70] occurs on the Leeward Islands [71] which form part of the Society islands and has a very recent age progression of 1–4.5 Mya [72]. Species of a second barychelid genus, *Idioctis* L. Koch, 1874 inhabit numerous islands (i.e. Fiji, Western Samoa, Madagascar, the Seychelles, Christmas Island, and Caroline and Marshall Islands), as well as the intertidal or littoral zones of northern Australia, New Caledonia and the Solomon Islands [71]. Their habitat and distribution suggests oceanic dispersal may be the most plausible hypothesis to explain their distribution patterns [70]. A third barychelid genus, *Sason* Simon, 1887, occurs in the Seychelles, the Andaman and Mariana Islands, southern India, Ceylon, northern Australia and New Guinea [73]. Their arboreal nests may render them more amenable to oceanic travel; if an entire log or tree was dislodged and became oceanic flotsam, survival of a trans-oceanic journey may have been possible [19,20]. However, while the evidence supporting these hypothesised oceanic dispersals is compelling, none are yet supported by dated molecular phylogenies.

The direction of dispersal events can help draw conclusions about the origin of taxa. For example, taxa in Hawaii which rely on wind dispersal, such as birds and spiders, come primarily from the east [66], as predicted by storm patterns. However, taxa that disperse via rafting come mostly from the west, as predicted by oceanic currents. For dispersal via rafting, these currents may assist in the movement of buoyant objects, such as seed pods, over long distances [14]. Similarly, these currents could also be a driving force in the movement of a large vegetation rafts and other debris from Africa to Australia.

The origin of much of Australia's mygalomorph fauna has been attributed to invasion from the north and south of the continent [74], however the potential mechanisms of dispersal are not known [see 73]. The main difficulties with trans-oceanic dispersal for mygalomorphs have been discussed for ground spiders [75], and include prolonged exposure to desiccating atmosphere, lack of non-saline water, and the extremely small probability of juveniles settling in a suitable habitat, maturing, and mating [20]. However, dispersal via rafting cannot be ruled out for migids [22]. There are a number of other factors worth considering which may lead trapdoor spiders to be suited to oceanic dispersal, such as their low metabolic rate [76]. The use of silk-lined burrows with a snugly fitting trapdoor provides a relatively stable microhabitat, enabling trapdoor spiders to regulate temperature and humidity [77]. If a rafting event was facilitated by the movement of a large mass of earth or whole trees, it is plausible that spider burrows may remain intact for long periods. Nest building, defined as thickened silk placed in a pre-existing niche or cavity (requiring minimal excavation) has been well documented in African *Moggridgea*, and is more prevalent than true burrow building [64]. This method allows spiders to colonise arboreal habitats, which may aid their dispersal. Dispersal by a gravid female capable of producing numerous juveniles, would enhance the chance of a successful dispersal event and subsequent mating [20]. In addition, the ability of mygalomorph spiders to resist drowning and use stored oxygen is a critical survival tactic in terrestrial environments when burrows are temporarily flooded [78], and the same is likely to be true on oceanic rafts. While there is no doubt that large expanses of seawater pose a significant challenge to oceanic dispersal, they are clearly not insurmountable barriers, given enough time. With their low food intake requirements, protective burrows, and ability to 'hold their breath', small trapdoor spiders may be even better equipped for dispersal than previously realised.

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CHAPTER IV: Systematics of the Australian spiny trapdoor spiders of the genus *Blakistonia* Hogg (Araneae: Idiopidae) (2018, Zootaxa 4518(1), 1-76).

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Systematics of the Australian spiny trapdoor spiders of the genus *Blakistonia* Hogg (Araneae: Idiopidae)

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Abstract

A combined molecular and morphological approach was used to revise the Australian spiny trapdoor spiders of the genus *Blakistonia* Hogg. Where possible, our molecular approach used sequence data from the *COI* barcoding gene, which were analysed using Bayesian, RAxML and neighbour-joining approaches. These molecular data were combined with morphology to describe and diagnose the genus, to redescribe the type (and only previously valid) species, *B. aurea* Hogg, 1902, and to diagnose, describe and map 19 new species: *B. bassi* **sp. n.**, *B. bella* **sp. n.**, *B. birksi* **sp. n.**, *B. carnarvon* **sp. n.**, *B. emmottiorum* **sp. n.**, *B. gemmelli* **sp. n.**, *B. hortoni* **sp. n.**, *B. mainae* **sp. n.**, *B. maryae* **sp. n.**, *B. newtoni* **sp. n.**, *B. nullarborensis* **sp. n.**, *B. olea* **sp. n.**, *B. parva* **sp. n.**, *B. pidax* **sp. n.**, *B. plata* **sp. n.**, *B. raveni* **sp. n.**, *B. tariae* **sp. n.**, *B. tunstilli* **sp. n.**, and *B. wingellina* **sp. n.** The genus *Blakistonia* is found to be distributed throughout the Australian arid and semi-arid zones, from the Wheatbelt region of Western Australia to central Queensland and western Victoria.

Key words: taxonomy, morphology, arid zone, Arbanitinae, Arbanitini

Introduction

The spiny trapdoor spiders of the family Idiopidae are a diverse group of mygalomorph spiders with life spans that can exceed 40 years in the wild (Main 1987; Mason *et al*. 2018; B.Y. Main pers. comm.). They use silk-lined burrows for shelter and prey capture, and most species seal their burrows with a hinged door (e.g., Main 1985; Rix *et al.* 2017c). As well as their abilty to contruct the widest array of burrow morphologies of any mygalomorph

family, idiopids have also evolved a diverse range of morphological and behavioural adaptations which allow them to inhabit a variety of climatic zones and substrates (Rix *et al.* 2017a, c). This enables members of the family to occupy a wide range of habitats, from seasonally snow-bound, montane regions to semi-arid and seashore locations (Main 1985). Idiopids are generally rare in severely arid regions although populations may persist in pockets or refuges of more favourable habitats (Main 1982), and species in at least seven Australian genera have adapted to arid and semi-arid habitats since the Miocene (Rix *et al.* 2017a). Idiopids also have limited powers of dispersal and have a tendancy to exhibit restricted patterns of distribution (Rix *et al.* 2017a; see also Harvey 2002; Harvey *et al.* 2011).

Outside of Western Australia, the idiopid fauna of Australia's arid zone is dominated by two genera: *Idiosoma* Ausserer, 1871 (now the senior synonym of *Agannipe* O. P.-Cambridge, 1877 and *Anidiops* Pocock, 1897; tribe Aganippini) and *Blakistonia* (tribe Arbanitini) (Rix *et al*. 2017c)). *Blakistonia aurea* Hogg, 1902 was first collected on the Adelaide Plains and in the nearby Mount Lofty Ranges. Since the early 20th Century, it was recognised as one of the common trapdoor spiders of the Adelaide region and was said to be found "nearly everywhere in parks and gardens, paddocks, and the unploughed ground along the highways leading from the city" (Rainbow & Pulleine 1918: 81). In addition to *B. aurea*, three other species have been previously attributed to *Blakistonia*: *B. rainbowi* (Pulleine, 1918) from Kangaroo Island (originally described in *Aganippe* O. P.-Cambridge, 1877), which has since been transferred to the migid genus *Moggridgea* O. P.-Cambridge, 1875 (see Harrison *et al.* 2016, 2017); *B. bancrofti* Rainbow, 1914 from Queensland (designated as a *nomen dubium* by Rix *et al*. 2017c); and *B. exsiccatus* (Strand, 1907), which was originally described in the genus *Cantuarides* Strand, 1907. *Cantuarides* was later synonymised with *Blakistonia* by Main (1985), due to records of *Blakistonia* being collected around Central Australia (in Uluru-Kata Tjuta National Park), and morphological characters such as the presence of labial cuspules and the strongly procurved anterior eye row. However, *B. exsiccatus* has been recently designated as a *nomen dubium* (Rix *et al.* 2017c), as the female syntypes are lost and the type locality, "Central Australia", is too imprecise to allow for accurate identification or the collection of new specimens.

The genus *Blakistonia* was formally relimited based on male and female morphology and molecular markers by Rix *et al.* (2017c). The description of new idiopid species ideally requires males, sequence data or both to ensure identifications are accurate (Rix *et al.* 2017c). The aims of this study are therefore to fully revise the taxonomy of the genus, describing all new species, as well as to document their distributions and aspects of their biology (in particular their burrow morphology; Fig. 2A–I). We used freshly collected material wherever possible, as well as museum specimens, plus we sequenced a fragment of the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene for as many specimens as possible to provide a molecular delimitation of morphospecies.

Material and methods

Morphology. The 329 specimens examined for this study are lodged in the Australian Museum, Sydney (AM), the Queensland Museum, Brisbane (QMB), the South Australian Museum, Adelaide (SAM), and the Western Australian Museum, Perth (WAM) (see Table 1). Specimens used for morphological examination were fixed in either 100% or 70% ethanol and preserved long-term in 70% ethanol. Auto-montaged images were taken at different focal planes (*ca*. 20–30 images) with a Canon 7D digital camera using either a 100mm lens or a K2 lens with a P2 attachment, using CamLift, Lightoom, Zerene Stacker and Adobe Photoshop. Female genitalia were prepared for imaging by submersion in lactic acid at room temperature overnight. Specimens were examined using an Olympus B061 stereomicroscope, and images taken for measurement purposes using an Olympus digital microscope camera (Model # LC20, 2.0MP CMOS colour camera). Measurements were taken digitally using LC micro software, downloaded from the Olympus website and are given in millimetres. Total length was measured dorsally from the front of the carapace to the end of the abdomen; carapace height was taken at its highest point; sternum width was taken at its widest point; paired claw dentition is given for both claws on each leg, the pro-claw and the retro-claw. Abbreviations used throughout the text include: retrolateral tibial apophysis (RTA), anterior median eyes (AME), anterior lateral eyes (ALE), posterior median eyes (PME), posterior lateral eyes (PLE), prolateral (p), retrolateral (r), ventral (v), proventral (pv) and retroventral (rv). In the taxonomic section, all species are listed alphabetically, and '**sp. n.**' epithets are removed from the main text after the key to species. For variation, when the value was constant in all specimens, only one value is given.

Specimen sampling for molecular analyses. The molecular dataset comprised 92 specimens of *Blakistonia*,

each with tissue samples lodged in the SAM or the WAM (see Table 1). Freshly collected specimens were hand-collected and initially preserved in 100% ethanol. Legs III and/or IV from the left side of the body were then stored in 100% ethanol, while the rest of the specimen was transferred to 70% ethanol for long-term storage.

TABLE 1. Specimens used in the molecular analyses.

Taxon	Museum and registration number	Locality	Latitude	Longitude	*COI* GenBank accession number
DIPLURIDAE					
Cethegus fugax	WAM T129260	WA: John Forrest NP	31°53'54"S	116°05'49"E	KY295227
IDIOPIDAE					
Prothemenops sp.	WAM T131517	Thailand, Chonburi Province	13°14'31"N	101°02'49"E	KY295232
Blakistonia aurea	SAM NN20078	SA: Pyap	34°27'S	140°29°40°E	MH491198
Blakistonia aurea	SAM NN29556	SA: Hallett	33°20'27"S	138°54'10"E	MH491201
Blakistonia aurea	SAM NN29557	SA: Burra	33°36'39"S	138°59'14"E	MH491202
Blakistonia aurea	SAM NN29558	SA: Burra	33°37'05"S	138°59'17"E	MH491203
Blakistonia aurea	SAM NN29559	SA: Burra	33°36'58"S	138°59'24"E	MH491204
Blakistonia aurea	SAM NN29560	SA: Burra	33°36'58"S	138°59'24"E	MH491205
Blakistonia aurea	SAM NN29561	SA: Adelaide CBD	34°55'42"S	138°37'02"E	MH491206
Blakistonia aurea	SAM NN29562	SA: Adelaide CBD	34°55'42"S	138°37'02"E	MH491207
Blakistonia aurea	SAM NN29563	SA: Adelaide CBD	34°55'42"S	138°37'02"E	MH491208
Blakistonia aurea	SAM NN29567	SA: Whyalla	33°11'16"S	137°15'13"E	MH491211
Blakistonia aurea	SAM NN29568	SA: Whyalla	33°11'16"S	137°15'13"E	MH491212
Blakistonia aurea	SAM NN29570	SA: Pichi Richi	32°25'46"S	137°58'16"E	MH491213
Blakistonia aurea	SAM NN29571	SA: Pichi Richi	32°25'46"S	137°58'16"E	MH491214
Blakistonia aurea	SAM NN29574	SA: Quorn	32°24'51"S	138°06'53"E	MH491215
Blakistonia aurea	SAM NN29575	SA: Wilmington	32°36'33"S	138°08'02"E	MH491216
Blakistonia aurea	SAM NN29576	SA: Wilmington	32°37'02"S	137°59'40"E	MH491217
Blakistonia aurea	SAM NN29577	SA: Hawker	31°43'06"S	138°31'52"E	MH491218
Blakistonia aurea	SAM NN29578	SA: Hawker	31°42'56"S	138°31'45"E	MH491219
Blakistonia aurea	SAM NN29579	SA: Melrose	32°50'48"S	138°10'53"E	MH491220
Blakistonia aurea	SAM NN29581	SA: Kadina	33°57'25"S	137°43'07"E	MH491221
Blakistonia aurea	SAM NN29583	SA: Kadina	33°57'25"S	137°43'07"E	MH491222
Blakistonia aurea	SAM NN29584	SA: Coobowie	35°01'42"S	137°45'42"E	MH491223
Blakistonia aurea	SAM NN29587	SA: Port Vincent	34°46'44"S	137°50'08"E	MH491224
Blakistonia aurea	SAM NN29588	SA: Arthurton	34°21'58"S	137°49'46"E	MH491225
Blakistonia aurea	SAM NN29590	SA: Ardrossan	34°23'21"S	137°43'28"E	MH491226
Blakistonia aurea	SAM NN29592	SA: Maitland	34°23'52"S	137°39'59"E	MH491227
Blakistonia aurea	SAM NN29593	SA: Edithbourgh	35°03'35"S	137°38'45"E	MH491228
Blakistonia aurea	SAM NN29594	SA: Yorketown	35°04'24"S	137°32'01"E	MH491229
Blakistonia aurea	SAM NN29596	SA: Upper Sturt	35°01'04"S	138°41'26"E	MH491230
Blakistonia aurea	SAM NN29597	SA: Upper Sturt	35°01'04"S	138°41'26"E	MH491231
Blakistonia aurea	SAM NN29598	SA: Upper Sturt	35°01'04"S	138°41'26"E	MH491232
Blakistonia aurea	SAM NN29599	SA: Willunga	35°20'24"S	138°31'37"E	MH491233
Blakistonia aurea	SAM NN29600	SA: Willunga	35°20'24"S	138°31'37"E	MH491234

.....continued on the next page

TABLE 1. (Continued)

Taxon	Museum and registration number	Locality	Latitude	Longitude	*COI* GenBank accession number
Blakistonia aurea	SAM NN29601	SA: Willunga	35°20'24"S	138°31'37"E	MH491235
Blakistonia aurea	SAM NN29605	SA: Orroroo	32°44'12"S	138°37'05"E	MH491237
Blakistonia aurea	SAM NN29606	VIC: Chinkapook	35°11'20"S	142°56'16"E	MH491238
Blakistonia aurea	SAM NN29607	VIC: Meringur Reserve	34°22'01"S	141°20'04"E	MH491239
Blakistonia aurea	SAM NN29608	SA: Beetaloo Reservoir	33°12'38"S	138°13'34"E	MH491240
Blakistonia aurea	SAM NN29609	SA: Beetaloo Reservoir	33°12'38"S	138°13'34"E	MH491241
Blakistonia aurea	SAM NN29610	SA: Beetaloo Reservoir	33°12'38"S	138°13'34"E	MH491242
Blakistonia aurea	SAM NN29611	SA: Cobbler Creek	34°46'9.22"S	138°40'21.19"E	MH491243
Blakistonia aurea	SAM NN29612	SA: Cobbler Creek	34°46'9.22"S	138°40'21.19"E	MH491244
Blakistonia aurea	SAM NN29613	SA: Cobbler Creek	34°46'9.22"S	138°40'21.19"E	MH491245
Blakistonia aurea	SAM NN29614	SA: Morphett Vale	35°08'00.8"S	138°31'4"E	MH491246
Blakistonia aurea	SAM NN29615	SA: Eaglehawk Station	32°21'S	141°43'E	MH491247
Blakistonia aurea	SAM NN29620	SA: Black Hill CP	34°51'45.767"S	138°43'25.848"E	MH491251
Blakistonia aurea	SAM NN29621	SA: Black Hill CP	34°51'45.767"S	138°43'25.848"E	MH491252
Blakistonia aurea	SAM NN29623	SA: Echunga	35°7'8.64"S	138°48'9.93"E	MH491253
Blakistonia aurea	SAM NN29624	SA: Antsey Hill CP	34°50'27.887"S	138°44'43.517"E	MH491254
Blakistonia aurea	SAM NN29625	SA: Houghton	34°49'48.240"S	138°45'34.001"E	MH491255
Blakistonia aurea	SAM NN29627	SA: Para Wirra CP	34°41'28.128"S	138°49'30.041"E	MH491256
Blakistonia aurea	SAM NN29628	SA: Para Wirra CP	34°41'28.128"S	138°49'30.041"E	MH491257
Blakistonia aurea	SAM NN29629	SA: Para Wirra CP	34°41'28.128"S	138°49'30.041"E	MH491258
Blakistonia aurea	SAM NN29630	SA: Norton Summit	34°55'03.959"S	138°44'36.539"E	MH491259
Blakistonia aurea	SAM NN29631	SA: Norton Summit	34°54'45.63"S	138°42'35.36"E	MH491260
Blakistonia aurea	SAM NN29633	SA: Golden Grove	34°46'56.47"S	138°43'8.60"E	MH491261
Blakistonia aurea	SAM NN29634	SA: Morgan	34°2'7.12"S	139°40'20.17"E	MH491262
Blakistonia aurea	SAM NN29637	SA: Belair NP	35°00'18.40"S	138°38'07.08"E	MH491263
Blakistonia aurea	SAM NN29640	SA: Brown Hill Creek RP	34°59'13.59"S	138°39'11.41"E	MH491265
Blakistonia aurea	SAM NN29641	SA: Mount Crawford Forest Reserve	34°42'41.53"S	138°55'57.48"E	MH491266
Blakistonia aurea	SAM NN29796	SA: Kapunda	34°20'27.67"S	138°58'35.76"E	MH491267
Blakistonia aurea	SAM NN29797	SA: Terowie	33°15'27.83"S	138°54'25.67"E	MH491268
Blakistonia aurea	SAM NN29798	SA: Burra	33°40'43.87"S	138°57'42.87"E	MH491269
Blakistonia aurea	SAM NN29799	SA: Burra	33°36'50.69"S	138°59'8.09"E	MH491270
Blakistonia aurea	SAM NN29801	SA: Burra	33°40'43.86"S	138°57'42.87"E	MH491271
Blakistonia aurea	SAM NN29802	SA: Burra	33°36'50.69"S	138°59'8.09"E	MH491272
Blakistonia aurea	SAM NN29803	SA: Burra	33°40'43.86"S	138°57'42.87"E	MH491273
Blakistonia aurea	SAM NN29804	SA: Kapunda	34°20'27.74"S	138°58'35.76"E	MH491274
Blakistonia aurea	SAM NN29806	SA: Jamestown	33°16'5.99"S	138°37'20.60"E	MH491275
Blakistonia aurea	SAM NN29807	SA: Hallett	33°20'8.92"S	138°53'18.31"E	MH491276
Blakistonia aurea	SAM NN29808	SA: Burra	33°39'54.25"S	139° 2'2.04"E	MH491277
Blakistonia bassi	SAM NN29619	SA: Ashton	34°55'55.61"S	138°44'49.67"E	MH491250
Blakistonia birksi	SAM NN29003	SA: Ngarkat CP	35°37'00"S	140°46'00"E	MH491200

.....continued on the next page

TABLE 1. (Continued)

Taxon	Museum and registration number	Locality	Latitude	Longitude	*COI* GenBank accession number
Blakistonia birksi	SAM NN29617	SA: Cleland CP	34°58'32.178"S	138°42'40.799"E	MH491248
Blakistonia birksi	SAM NN29618	SA: Cleland CP	34°58'32.178"S	138°42'40.799"E	MH491249
Blakistonia birksi	SAM NN29638	SA: Mark Oliphant CP	35°01'50.88"S	138°42'26.58"	MH491264
Blakistonia birksi	WAM T131984	VIC: Grampians NP	37°08'49"S	142°26'48"E	MH491279
Blakistonia mainae	WAM T141136	WA: Mount Ragged	33°26'47"S	123°28'15"E	MH491281
Blakistonia mainae	WAM T141137	WA: Mount Ragged	33°26'43"S	123°28'07"E	MH491282
Blakistonia mainae	WAM T141138	WA: Mount Ragged	33°26'44"S	123°28'08"E	MH491283
Blakistonia maryae	SAM NN26663	SA: Scrubby Peak	33°3'23"S	136°19'40°0"E	MH491199
Blakistonia maryae	SAM NN29565	SA: Tumby Bay	34°22'27"S	136°05'18"E	MH491209
Blakistonia maryae	SAM NN29566	SA: Tumby Bay	34°22'27"S	136°05'18"E	MH491210
Blakistonia maryae	SAM NN29604	SA: Gawler Ranges	32°33'24"S	135°35'20"E	MH491236
Blakistonia nullarborensis	WAM T141139	WA: Balladonia	32°24'57"S	124°20'34"E	MH491284
Blakistonia nullarborensis	WAM T141140	WA: Cocklebiddy	32°02'12"S	126°05'28"E	MH491285
Blakistonia nullarborensis	WAM T141141	WA: Moonera	31°59'17"S	126°33'11"E	MH491286
Blakistonia nullarborensis	WAM T141142	WA: Madura	31°53'54"S	126°54'30"E	MH491287
Blakistonia pidax	SAM NN20064	SA: Strangways Springs	29°08'14"S	136°34'00"E	MH491197
Blakistonia wingellina	WAM T132916	WA: Wingellina	26°02’22.2”S	128°58’32.9”E	MH491280
Blakistonia ‘sp. 1’	WAM T121587	WA: Yamarna	28°5'53.31"S	123°33'0.77"E	MH491278

DNA sequencing. For all sequenced material, ‘DNA’ superscript codes have been added to the material examined sections for each species. Approximately 3 mm^3 of muscle tissue was removed from the leg femora for DNA extraction. DNA was extracted using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Venlo, Netherlands). A 657 bp fragment of the *COI* gene was amplified using the universal *COI* primers LCOI490 (5’-GGTCAACAAATCATAAAGATATTG-3’) and HC02198 (5’-TAAACTTCAGGGTGACCAAAAAATCA-3’) (Folmer *et al.* 1994). PCR was performed under the following conditions: an initial denaturation step of 94°C for 5 min, followed by 34 cycles of: 94°C for 45 s; annealing temperature of 48°C for 45 s; then 72°C for 1 min; with a final elongation step of 72°C for 10 min. The *COI* fragment was amplified using Eppendorf Amplitaq Gold (Eppendorf, Westbury, NY, USA). For each 25 µL reaction, 2 µL of template DNA, 2.5 µL of PCR Gold Buffer, 3.5 mM $MgCl_2$, 2.0 mM of deoxyribonucleotide triphosphate (dNTP), 1.0 µL of each primer (10 mM concentration), and 0.1 µL of Amplitaq Gold DNA polymerase was used. PCR products were verified by agarose gel electrophoresis (with 1% agarose), and PCR clean-up plus bi-directional sequencing was performed by the Australian Genome Research Facility (AGRF; Waite Campus, University of Adelaide, South Australia). Autapomorphic nucleotide substitutions are reported for each species, relative to the 657 bp reference *COI* fragment of *B. aurea* (GenBank MH491253). See Table 1 for GenBank accession numbers of sequences analysed in this study.

Phylogenetic analyses. All newly obtained sequences were manually edited with reference to chromatograms using Geneious Version 9.0 (https://www.geneious.com; Kearse *et al.* 2012). Forward and reverse sequences were assembled, and the resulting consensus sequences were then aligned using the ‘Geneious Alignment’ function with default parameters. PartitionFinder Version 1.1.1 (Lanfear *et al.* 2012) was used to select the nucleotide substitution model for each codon position (CP) of the *COI* alignment. For CP 1, the Kimura 80 (K80) (Kimura 1980) + gamma (G) (Yang 1996) model was chosen. For CP 2, a General Time Reversible (GTR) (Rodriguez 1990) + invariant sites + G model was selected. For CP 3, a GTR + G model was chosen.

A neighbour-joining (NJ) tree was created using Tamura-Nei pairwise distances in Geneious (Fig. 3). *Cethegus fugax* (Simon, 1908) (Dipluridae) and a species of the idiopid genus *Prothemenops* Schewendinger, 1991 were chosen as outgroups for the study, with sequences taken from Rix *et al.* (2017a). Phylogenetic reconstruction was also undertaken using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist and Huelsenbeck 2003) via the CIPRES Science Gateway (Miller *et al.* 2010). Each codon position was modelled separately using the models listed above. All parameters were unlinked and the rates were allowed to vary over the partitions, which allowed each codon position to evolve at a different rate. For all reconstructions, four chains were run simultaneously for 100 million generations, with every 1,000th tree sampled. A burnin of 1,000 was chosen using the program Tracer Version 1.6 (Rambaut *et al.* 2014). The resulting consensus tree was viewed using FigTree v1.3.1 (Rambaut & Drummond 2010), with the posterior probabilities displayed adjacent to each node (Fig. 4). A maximum likelihood (ML) analysis was also undertaken using RAxML (Stamatakis 2014) on the BlackBox server of CIPRES, with the GTR + G model used for all codon partitions. Bootstrap values are shown on Figure 4 after posterior probability values for key concordant nodes. Inter- and intraspecific pairwise distances were calculated using MEGA7 (Kumar *et al*. 2016).

FIGURE 1. Images of live *Blakistonia*. A, female *B. aurea* Hogg, 1902 from Chinkapook, Victoria; B, female and male *B. aurea* from Adelaide, South Australia; C, male *B. aurea* from Morgan, South Australia; D, female *B. bassi* **sp. n.** from Ashton, Mount Lofty Ranges, South Australia; E, F, female *B. birksi* **sp. n.** from Mark Oliphant Conservation Park, Mount Lofty Ranges, South Australia; G, female *B. mainae* **sp. n.** from Mount Ragged, Cape Arid, Western Australia; H, female *B. maryae* **sp. n.** from Gawler Ranges National Park, South Australia; I, female *B. nullarborensis* **sp. n.** from east of Madura, Western Australia. Images A, H by M. Rix; B, E, F by N. Birks; C by M. Newton; D by S. Harrison; G, I by M. Harvey. All images used with permission.

FIGURE 2. Images of *Blakistonia* burrows. A, *B. aurea* Hogg, 1902 burrow with scalloped edge from Humbug Scrub, South Australia; B, *B. aurea* burrow from Parra Wirra Recreation Park, South Australia; C, *B. aurea* burrow, Mount Lofty Ranges, South Australia; D–E, *B. bassi* **sp. n.** burrow from Ashton, Mount Lofty Ranges, South Australia; F, *B. birksi* **sp. n.** burrow from Mark Oliphant Conservation Park, Mount Lofty Ranges, South Australia; G, *B. mainae* **sp. n.** burrow from Mount Ragged, Cape Arid National Park, Western Australia; H–I, *B. maryae* **sp. n.** burrow showing twig-lining from Scrubby Peak, Gawler Ranges, South Australia; J, *B. maryae* **sp. n.** burrow showing twig-lining from Tumby Bay, Eyre Peninsula, South Australia; K, *B. maryae* **sp. n.** burrow from Gawler Ranges, South Australia; L, *B. nullarborensis* **sp. n.** burrow from Cocklebiddy, Western Australia. All images by S. Harrison except: C by N. Birks; H, by N. Birks; I, by N. Birks; all used with permission.

Results and discussion

DNA barcode analysis. For this study, we applied a species concept that integrated molecular monophyly with morphology. Neighbour-joining analysis revealed six major lineages comprised of eight of the 20 recognised species (Fig. 4). The first lineage consisted of *B. bassi* **sp. n.** from the Mount Lofty Ranges; the second lineage

consisted of *B. pidax* **sp. n.** from northern South Australia, *Blakistonia* 'sp. 1' from the Goldfields of Western Australia and *B. maryae* **sp. n.** from the Eyre Peninsula and Gawler Ranges, South Australia; the third lineage consisted of two Western Australian species, *B. mainae* **sp. n.** and *B. nullarborensis* **sp. n.** from Mount Ragged and the Nullarbor Plain, respectively; the fourth lineage consisted of individuals from the South Australian and Victorian species *B. birksi* **sp. n.**; and the fifth and sixth lineages consisted of two clades of *B. aurea*. Seven species-group lineages were consistently recovered in the NJ, Bayesian and ML analyses, with high support for each of four species represented by multiple individuals (i.e., posterior probability > 0.95 for *B. mainae* **sp. n.**, *B. birksi* **sp. n.**, *B. nullarborensis* **sp. n.**, and *B. maryae* **sp. n.**). Molecular data also allowed us to confidently link males and females of *B. birksi* **sp. n.**, despite their disparate localities. All methods struggled to resolve the large, genetically diverse and broadly distributed *B. aurea*. Although the species was recovered as monophyletic in the NJ analysis, it formed an unresolved polytomy in the Bayesian and ML analyses. The greatest mean inter-specific *COI* pairwise distance was 31%, between *B. bassi* **sp. n.** and *Blakistonia* 'sp. 1', and the smallest was 14%, between *B. birksi* **sp. n.** and *B. aurea*. Among those species sampled for multiple individuals, *B. birksi* **sp. n.** and *B. maryae* **sp. n.** were the most genetically diverse species at 10% mean intra-specific *COI* pairwise distance, followed by *B. aurea* at 8%, *B. nullarborensis* **sp. n.** at 2%, and *B. mainae* **sp. n.** at 0.02%. As the full barcoding fragment for *B. wingellina* **sp. n.** was not recovered due to sub-optimal preservation conditions, this species is delineated genetically using pairwise distances calculated from an incomplete fragment only. *Blakistonia wingellina* was found to be most similar to *B. aurea* at 11%.

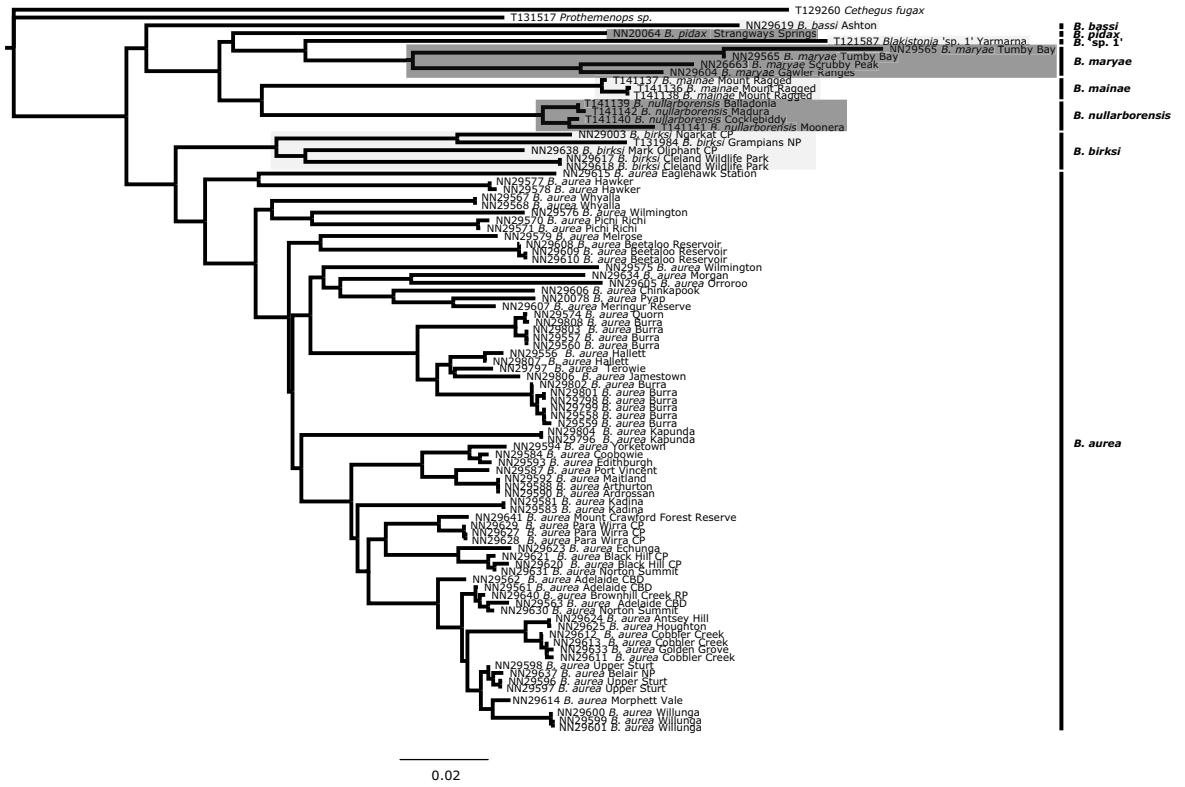


FIGURE 3. Tamura-Nei neighbour-joining tree of the mitochondrial *COI* dataset, showing relationships within *Blakistonia*.

FIGURE 4. Bayesian majority-rule consensus tree of the mitochondrial *COI* dataset. Maximum likelihood analysis of the same produced a congruent or concordant tree. Bootstrap values are shown after posterior probability values < 1.0 for key nodes. All other nodes have a posterior probability of 1.0.

Morphological analysis. We recognise 16 species using morphological criteria based on adult male specimens, but 12 species were previously stored in 70% ethanol in museum collections and sequence data were generally unobtainable. These include *B. bella* **sp. n.**, *B. carnarvon* **sp. n.**, *B. emmottorum* **sp. n.**, *B. gemmelli* **sp. n.**, *B. hortoni* **sp. n.**, *B. newtoni* **sp. n.**, *B. olea* **sp. n.**, *B. parva* **sp. n.**, *B. plata* **sp. n.**, *B. raveni* **sp. n.**, *B. tariae* **sp. n.** and *B. tunstilli* **sp. n.** However, *B. pidax* **sp. n.**, and the male of *B. birksi* **sp. n.**, despite not being freshly collected specimens, were able to be sequenced. Three species are described from females only: *B. bassi* **sp. n.**, *B. wingellina* **sp. n.**, and *B. nullarborensis* **sp. n.** Males and females of *B. maryae* **sp. n.** have been tentatively linked based on distribution and general morphology (colour and size). All described species are able to be recognised by morphology alone, except for *B. nullarborensis* **sp. n.** and *B. wingellina* **sp. n.**, which while distinguishable from all other *Blakistonia* by the trapezoidal eye group, can only be morphologically separated with males. As the only known specimen of *Blakistonia* 'sp. 1' is a juvenile, this specimen is not formally described as a new species, although the molecular data clearly demonstrate it is new. We have therefore provided only a brief summary and molecular diagnosis for this specimen at the end of the Taxonomy section.

Species delineation. The morphological and molecular datasets analysed here were largely concordant. Morphological species concepts, driven largely by male autapomorphies, were found to be consistent with *COI* delineation. The recognition of 19 new species requires an expanded description and diagnosis for *Blakistonia* compared to that of Hogg (1902) and Main (1985), an issue discussed and addressed by Rix *et al.* (2017c). The most useful character found for recognising species was the mating spur on the tibia I of males, which has two forms, the first being a pair of prolateral clasping spurs each with a raised cuticular base, bearing multiple terminal peg-like macrosetae (e.g., Figs 5G–I, 8G–I) (N.B.: the terminal peg-like macrosetae were highly variable, sometimes even differing on both sides of the same spider, and therefore not diagnostic). The second form has either two thickened prolateral macrosetae in a similar position to the prolateral clasping spurs (Figs 11G–I, 21G–I), or a single macroseta (Figs 9G–I, 14G–I), the latter of which was found to be invariable within species with the exception of *B. maryae* **sp. n.** The shape of the eye group was also found to be a useful diagnostic feature, using both overall shape (e.g., square [Fig. 5D], wider than long [Fig. 7D], or longer than wide [Fig. 22D]) and the relative size of the AME (e.g., large AMEs [Fig. 21D], or regular AMEs [Fig. 25D]). Burrow morphology was also a useful auxillary diagnostic tool, with several species deviating from the D-shaped burrow of *B. aurea* (Fig. 2A–C) (e.g., *B. mainae* **sp. n.** [Fig. 2G], *B. birksi* **sp. n.** [Fig. 2F], *B. bassi* **sp. n.** [Fig. 2D, E] and *B. maryae* **sp. n.** [Fig. 2H, I, K]). However, *B. nullarborensis* **sp. n.** also builds a D-shaped burrow (Fig. 2L) identical to that of *B. aurea.*

Species delineation was made from all available data, including morphology, mitochondrial sequence data and distributional data. Results from morphological and molecular analyses, although broadly concordant, also showed slight differences. Previously suggested species divergence *COI* limits for arachnids include 5% and 8% (Parmakelis *et al.* 2006), and 9.5% for some Australian mygalomorph taxa (Castalanelli *et al.* 2014), suggesting that genetically diverse groups such as *B. aurea*, *B. birksi* **sp. n.** and *B. maryae* **sp. n.**—which have mean intra-specific pairwise distances of 8%, 10% and 10%, respectively—may comprise species complexes. However, as these genetic differences could not be substantiated by clear, consistent morphological characters and as more rigorous quantitative methods were not used to test multi-gene coalescence or the barcode gap in *Blakistonia*, we did not take this approach for these species. Indeed, for *B. aurea*, all genetically divergent specimens (such as those from Hawker and Eaglehawk) are females that are morphologically indistinguishable from the main *B. aurea* clade and which also build identical doors. Furthermore, *B. aurea* has a very broad distribution, ranging from the north-eastern Eyre Peninsula, through the Yorke Peninsula, Flinders Ranges, Fleurieu Peninsula, Mount Lofty Ranges, and western Victoria, so a higher degree of genetic diversity would be expected. In the case of *B. birksi* **sp. n.**, the specimen from the Grampians is a juvenile and therefore cannot be described on morphology alone. Individuals from Mark Oliphant Conservation Park and Cleland Conservation Park have a pairwise difference of 9%; however, they are morphologically identical and build identical round, indented burrows. The male of *B. birksi* **sp. n.** from Ngarkat Conservation Park differs from the other specimens by 1% (Grampians) and 12% (Cleland); however, its general morphology supports its inclusion in *B. birksi* **sp. n.** Intra-specific distances between individuals of *B. maryae* **sp. n.** range from 15% (between Tumby Bay and Gawler Ranges) to 0.04% (between Scrubby Peak and Gawler Ranges), however, due to the lack of consistent morphological differences, we were unable to justify dividing the species.

Conservation implications. Measuring the decline of a group of invertebrates that are taxonomically poorly known is inherently problematic; however, this important issue was recently broached by Rix *et al.* (2017b). In the case of *Blakistonia*, the highly restricted distributions of some of the new species described here points to their vulnerability to threatening processes. Indeed, although *B. aurea* and *B. birksi* **sp. n.** have fairly widespread distributions, they are the exception to all other species of *Blakistonia*, and the paucity of specimens of *B. birksi* **sp. n.** in museum collections suggest that although widespread, its area of occupancy may be limited. Most other species (*B. pidax* **sp. n.**, *B. bassi* **sp. n.**, *B. carnarvon* **sp. n.**, *B. raveni* **sp. n.**, *B. emmottorum* **sp. n.**, *B. gemmelli* **sp. n.**, *B. newtoni* **sp. n.**, *B. olea* **sp. n.**, *B. plata* **sp. n.**, *B. tariae* **sp. n.**, *B. wingellina* **sp. n.**, *B. tunstilli* **sp. n.** and *Blakistonia* 'sp. 1') are known only from single locations. For species in remote locations that were not revisited during this study and are known only from museum specimens, lack of collecting may be a contributing factor to their restricted distributions. However, *B. bassi* **sp. n.** is located in the Mount Lofty Ranges, an area that has been extremely well collected, both historically and recently. Despite this, *B. bassi* **sp. n.** has been found only on a single mossy embankment at Ashton, and was absent from museum collections prior to this study. This single population, in a well collected area, most likely warrants *B. bassi* **sp. n.** to be listed as

Endangered under the Environmental Protection and Biodiversity Conservation (EPBC) Act. *Blakistonia maryae* **sp. n.** appears to be endemic to the Eyre Peninsula, and was also absent from museum collections, while *B. mainae* **sp. n.** is only known from Cape Arid National Park, *B. bella* **sp. n.** is found in only two locations in northern South Australia, and *B. nullarborensis* **sp. n.** is found only on the Nullarbor Plain. This tendency for short-range endemism suggests that populations of *Blakistonia* are inherently vulnerable to threats such as habitat destruction.

Taxonomy

Family Idiopidae Simon, 1889

Subfamily Arbanitinae Simon, 1903

Tribe Arbanitini Simon, 1903

Genus *Blakistonia* Hogg, 1902

Blakistonia Hogg, 1902: 131. Type species *Blakistonia aurea* Hogg, 1902, by original designation. Rix *et al*, 2017c: 582.
Cantuarides Strand, 1907: 8. Type species *Cantuarides exsiccatus* Strand, 1907, by original designation (synonymised by Main, 1985: 39).

Diagnosis. Most species of *Blakistonia* can be distinguished from those of other Arbanitinae by the following combination of characters (*sensu* Rix *et al.* 2017c): a relatively narrow carapace in dorsal view (e.g., Figs 5A, 6A) (relative to species of *Euoplos* Rainbow, 1914); a square or subquadrate eye group (e.g., Figs 5D, 7D); the presence of scopulae on tarsi I and II of females (e.g., Fig. 18G, H); and the absence of a distal retrolateral tibial apophysis on the male pedipalp (e.g., Fig. 5J, L). Species of *Blakistonia* can be further distinguished from those of most Euoplini, Arbanitini and Aganippini by the square or subquadrate eye group. Some species of *Eucyrtops* (tribe Aganippini) have a similar subquadrate eye group to species of *Blakistonia* (e.g., *Eucyrtops eremaeus* Main, 1957), and some *Blakistonia* can have a marginally trapezoidal eye group (e.g., *B. nullarborensis* **sp. n.** [Fig. 20D] and *B. wingellina* **sp. n.** [Fig. 28D]). However, similar species of Aganippini can be distinguished from *Blakistonia* by a more strongly attenuate base to the RTA (Rix *et al.* 2017c). See Rix *et al.* (2017c) for diagnostic molecular characters.

Description. Small to large idiopid spiders, usually dark brown to golden or orange-brown in colour (Fig. 1A–I). Carapace oval-shaped (e.g., Figs 6A, 9A, 10A), commonly with line of setae between fovea and eye group (Fig. 8D), and males with fringe of setae around lateral carapace (Fig. 14A); fovea procurved in females and commonly straight in males (Fig. 5A) or slightly procurved (Fig. 6A). Eye group square (Fig. 5A) or subquadrate (Figs 7D, 22D), rarely trapezoidal (Figs 20D, 28D); anterior eye row always strongly procurved (Figs 5D, 6D, 7D). Chelicerae with rastellum of several strong conical spines in both males and females and with a row of teeth on each edge of furrow, the teeth decreasing in size from distal to proximal end. Maxillae rectanguloid, wider behind than in front, with setae becoming longer towards interior margins; maxillary cuspules present in some males (Fig. 17F) and all females (Fig. 6F), becoming denser towards interior margins; labium wider than long, with slightly recurved or straight posterior edge, with two longer clumps of curved setae on anterior lateral edges; labial cuspules present in some males (Fig. 14F) and some females (Fig. 15F). Sternum without distinct sigilla or with three distinct pairs in which anterior pair are smallest, the median pair bigger and the posterior pair largest, as in most mygalomorphs. Abdomen oval, typically with chevron pattern dorsally (Figs 9A, 10A) and 1–5 pairs of unsclerotised sigilla (Figs 15A, 28A) in females and also males of *B. olea* **sp. n.**, but not distinct in *B. nullaborensis*. Legs with scopulae ventrally on tarsi I, II (Fig. 7G, H) and metatarsi I, II of all females and some males (Fig. 11A), and palpal tarsus of females. Male tibia I with either prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 8G–I), two prolateral macrosetae (Fig. 11G–I), or a single prolateral macroseta (Fig. 9G–I). Leg tarsi with three claws, one row of teeth on paired claws; female pedipalp claw without teeth. Male pedipalp with short, pointed RTA with broad base; RTA covered in spinules (Fig. 14 J–L); cymbium with field of spinules disto-dorsally in most

species, sometimes spine-like; embolus simple, slightly twisted, most species with broad base (Fig. 5J–L). Spermathecae paired, simple, unbranched, stout and outward facing, oval-shaped in most species, covered in opaque mottled brown glandular nodules (Fig. 18I). Four spinnerets, posterior lateral pair three-segmented, apical article short with domed or conical tip, posterior median pair small, digitiform.

Distribution. *Blakistonia* has a distribution that is centred on southern South Australia (Rix *et al.* 2017c), especially Adelaide and the Mount Lofty Ranges, and extending north into the central arid zone and into the southern Northern Territory around Uluru-Kata Tjuta National Park. They are also sparsely distributed in Queensland, western inland New South Wales, western Victoria, south-western Western Australia and eastern inland Western Australia, near the Western Australian/South Australian/Northern Territory border. *Blakistonia* are absent from mesic south-eastern Australia (east of the Grampians Range), the northern half of the Northern Territory and most of arid New South Wales and western inland/northern Western Australia (see Rix *et al*. 2017c, fig. 68 and Figures 29–34 for summary distribution maps.)

Composition. *Blakistonia* includes one previously described species, *B. aurea* Hogg, 1902, and 19 new species: *B. bassi* **sp. n.**, *B. bella* **sp. n.**, *B. birksi* **sp. n.**, *B. carnarvon* **sp. n.**, **sp. n.**, *B. emmottorum* **sp. n.**, *B. gemmelli* **sp. n.**, *B. hortoni* **sp. n.**, *B. mainae* **sp. n.**, *B. maryae* **sp. n.**, *B. newtoni* **sp. n.**, *B. nullarborensis* **sp. n.**, *B. olea* **sp. n.**, B. *parva* **sp. n.**, *B. pidax* **sp. n.**, *B. plata* **sp. n.**, *B. raveni* **sp. n.**, *B. tariae* **sp. n.**, *B. tunstilli* **sp. nov.** and *B. wingellina* **sp. n.**

Biology and remarks. *Blakistonia* is a diverse group, both in distribution and number of species. Spiders are found in a variety of habitats, from mossy banks in the mesic, high rainfall zone of the Mount Lofty Ranges, to arid desert areas such as those in northern and inland South Australia and Western Australia. The burrows of the most common species, *B. aurea*, are characteristically D-shaped, slightly indented and plug-like (Fig. 2B, 2L); however, other species build a variety of different burrows, including round, indented, plug-like lids (Fig. 2F–G, K), wafer-like lids (Fig. 2D, E), and also burrows that are twig-lined (Fig. 2H–J). Wandering *Blakistonia* males are usually collected after rainfall events, most frequently in March to May, but have also been collected later in the year from June to September.

Key to the species of *Blakistonia* known from Australia

NB. Males are unknown for *B. bassi* **sp. n.**, *B. nullarborensis* **sp. n.**, and *B. wingellina* **sp. n.** Females are unknown for *B. bella* **sp. n.**, *B. carnarvon* **sp. n.**, *B. emmottorum* **sp. n.**, *B. gemmelli* **sp. n.**, *B. hortoni* **sp. n.**, *B. newtoni* **sp. n.**, *B. olea* **sp. n.**, *B. parva* **sp. n.**, *B. pidax* **sp. n.**, *B. plata* **sp. n.**, *B. raveni* **sp. n.**, *B. tariae* **sp. n.**, and *B. tunstilli* **sp. n.**

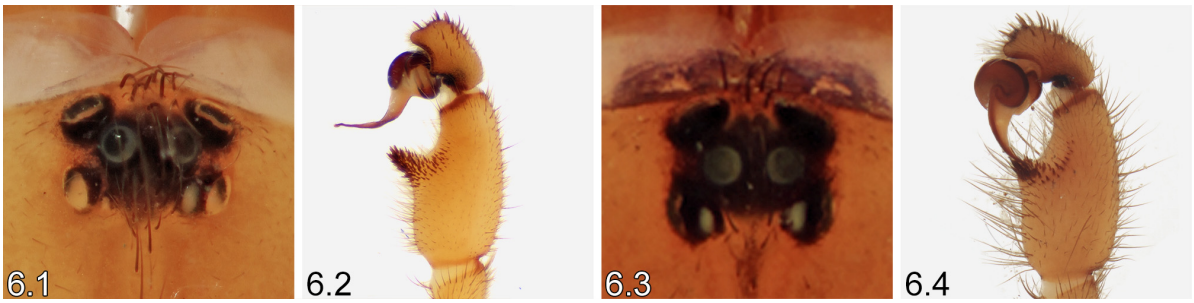
1. Males . . . 2
- Females . . . 18
2. Tibia I with prolateral clasping spurs (2.1) . . . 3
- Tibia I with one or two prolateral macrosetae but without clasping spurs (2.2, 2.3) . . . 8

3. Abdomen strongly patterned with dark cardiac stripe (Fig. 3.1) . . . . . *Blakistonia bella* **sp. n.**
- Abdomen with or without strong pattern but never with dark cardiac stripe (3.2, 3.3) 4

4. Cymbium with thick spinules (4.1, 4.2) 5
- Cymbium with setae but without spinules (4.3) . . . . . *Blakistonia pidax* **sp. n.**

5. Spinules on palpal tibia roughly similar or only slightly shorter than those on RTA (5.1, 5.2) 6
- Spinules on tibia much shorter than those on RTA (5.3). . . . . *Blakistonia tunstilli* **sp. n.**

6. Eye group subquadrate (6.1); spinules on cymbium sparse, thick, spine-like and form rows (6.2) . . . . . *Blakistonia emmottorum* **sp. n.**
- Eye group square (6.3); spinules on cymbium thick and spine-like (6.4). 7



7. RTA relatively short and stout, with field of spinules extending only marginally onto palpal tibia (7.1); abdominal pattern very strong (7.2) . . . . . *Blakistonia gemmelli* **sp. n.**

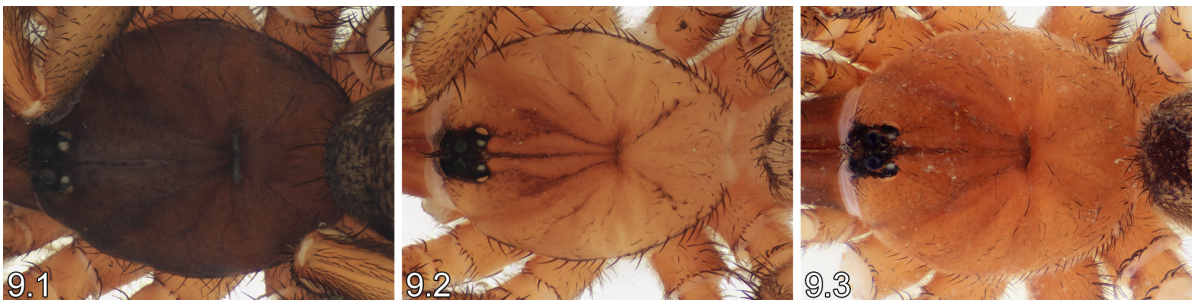
- RTA longer, with field of spinules extending further onto tibia (Fig. 7.3); abdominal pattern weak (7.4) . . . . . *Blakistonia aurea* Hogg, 1902

8. Tibia I with 1 prolateral macroseta (8.1, 8.2) 9

- Tibia I with 2 prolateral macrosetae (8.3) 13

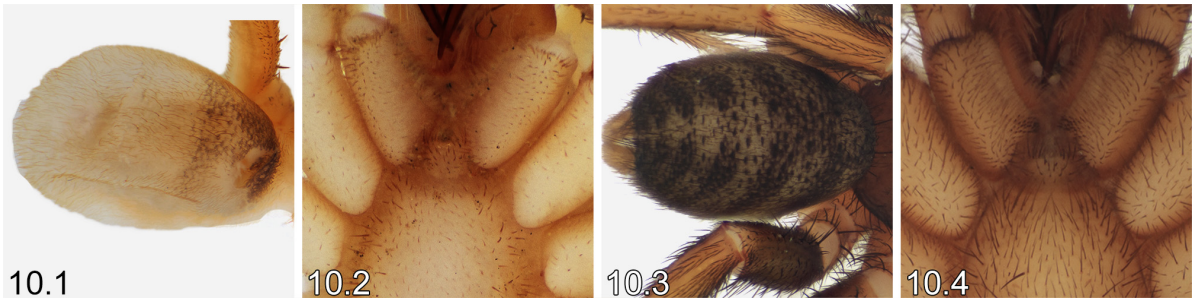
9. Carapace dark brown (9.1); eye group subquadrate (9.1) 10

- Carapace golden-brown (9.2, 9.3); eye group square (9.2, 9.3) 11



10. Maxillae without cuspules (10.2); abdominal pattern weak or non-existant (10.1) . . . . . *Blakistonia plata* **sp. n.**

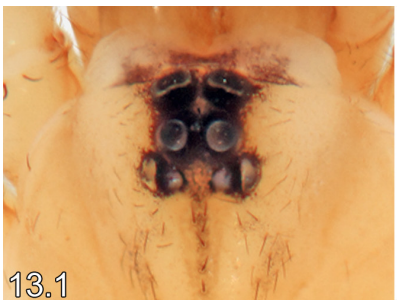
- Maxillae with cuspules (10.4); abdominal pattern very strong (10.3) . . . . . *Blakistonia birksi* **sp. n.**

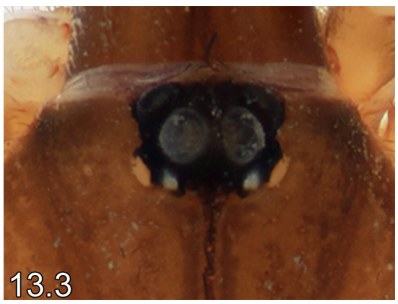


11. Field of spinules on palpal tibia in thin, rounded crescent-shape, and ventral margin of tibia distal to RTA strongly concave in prolateral view (11.1) . . . . . *Blakistonia newtoni* **sp. n.**
- Field of spinules on palpal tibia not in rounded crescent shape (11.2, 11.3) 12

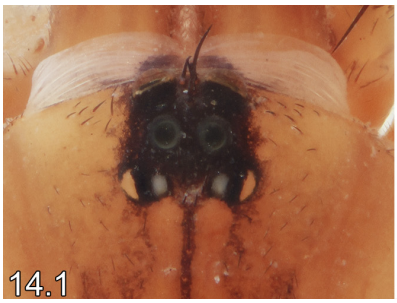
12. Field of spinules on palpal tibia relatively narrow (12.1) . . . . . *Blakistonia maryae* **sp. n.** (in part*)
- Field of spinules on palpal tibia relatively dense and broad (12.2). . . . . *Blakistonia hortoni* **sp. n.**

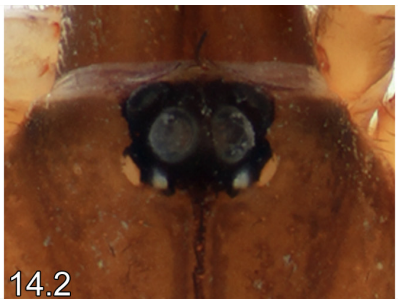
13. Eye group longer than wide (13.1) . . . . . .*Blakistonia parva* **sp. n.**
- Eye group wider than long or square (13.2, 13.3). 14



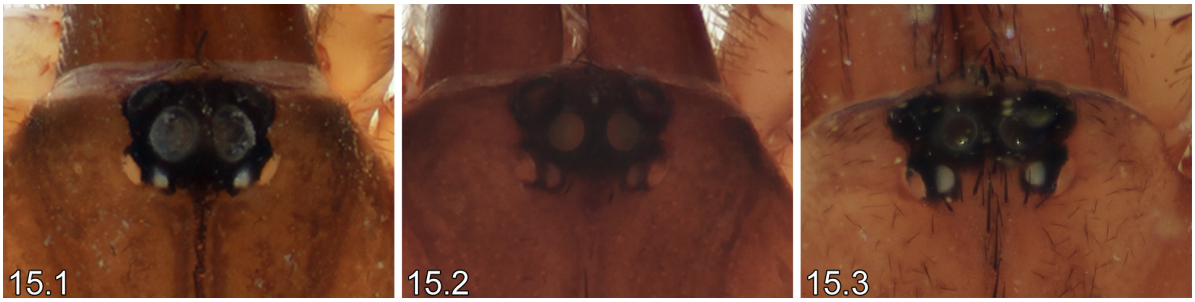


14. Eye group square (14.1) . . . . . *Blakistonia maryae* **sp. nov.** (in part*)
- Eye group wider than long (14.2, 14.3). 15





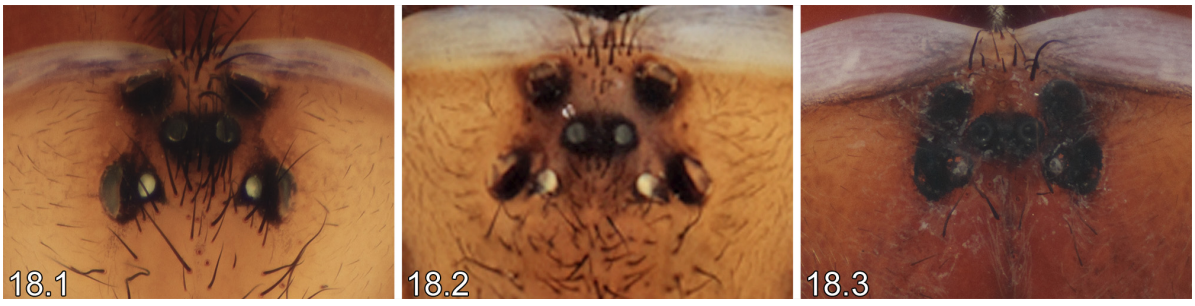
15. AME significantly larger than ALE (15.1) . . . . . *Blakistonia olea* **sp. n.**
- AME of similar or smaller diameter than ALE (15.2, 15.3) 16



16. Distinctive dark ring around edge of carapace (16.1, 16.2) 17
- Carapace fairly uniform in colour (16.3) . . . . . *Blakistonia tariae* **sp. n.**

17. Embolus narrows/tapers after midpoint (17.1) . . . . . *Blakistonia carnarvon* **sp. n.**
- Embolus narrows/tapers at midpoint (17.2) . . . . . *Blakistonia raveni* **sp. n.**

18. Eye group distinctly trapezoidal (18.1, 18.2) . . . . . *Blakistonia wingellina* **sp. n.** or *Blakistonia nullarborensis* **sp. n.****
- Eye group square or subquadrate (18.3) 19

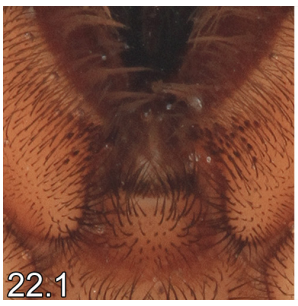


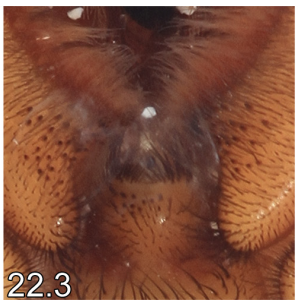
19. Carapace covered in fine golden hairs (19.1) . . . . . *Blakistonia bassi* **sp. n.**
- Carapace without fine golden hairs (19.2, 19.3) 20

20. Abdominal chevrons almost black (20.1) . . . . . *Blakistonia birksi* **sp. n.**
- Abdominal chevrons lighter brown (20.2, 20.3) 21

21. Book lungs brown or dark brown, in contrast to abdomen (21.1) . . . . . *Blakistonia mainae* **sp. n.**
- Book lungs similar colour to abdomen (21.2, 21.3) 22

22. Cuspules absent from labium (22.1); trapdoor usually twig-lined (22.2) . . . . . *Blakistonia maryae* **sp. n.**
- Cuspules present on labium (22.3); trapdoor distinctly D-shaped with no twig-lines (22.4) . . . . *Blakistonia aurea* Hogg, 1902





* Males of *B. maryae* **sp. n.** are unusual in having one or two prolateral macrosetae on tibia I in different individuals.

** Females of *B. wingellina* **sp. n.** and *B. nullarborensis* **sp. n.** are unusual in having a trapezoidal eye group, similar to species of Aganippini.

***Blakistonia aurea* Hogg, 1902**
(Figs 5A–L, 6A–I)

Blakistonia aurea Hogg, 1902: 132, fig. 25B–E, pl. 13, figs 1–2. Simon, 1903: 903, figs 1051, 1056–1057. Rainbow & Pulleine, 1918: 104, pl. 13, fig. 8, pl. 14, fig. 6, pl. 15, fig. 7. Main, 1964: 30, figs A–G. Main, 1985: 40, figs 146–157, 203–204, 211–212. Rix *et al*., 2017c: 586, figs 43, 45, 49–51.
Aganippe villosa Rainbow & Pulleine, 1918: 96, pl. 21, fig. 44 (synonymised by Main, 1985: 40).

Type material (of *B. aurea*). **AUSTRALIA: *South Australia*:** male syntype, Lower North Road, Adelaide; 4 female syntypes, Blakiston and Mount Lofty Ranges (purportedly BMNH, SAM; presumed lost).

Type material (of *A. villosa*). AUSTRALIA: *South Australia*: female holotype, Bridgewater (AMS KS6156; examined).

Material examined (exemplar specimens for descriptions and variation). **AUSTRALIA: *South Australia*:** 1 male, Valley View, 34°50’29”S, 138°39’41”E, 3 April 2013, hand collected, W. Chau (SAM NN29564); 1 female, Echunga, 35°7’9S, 138°48’10”, 20 March 2015 (SAM NN29623[DNA]); 1 female, Moralana Drive, 31°43’06”S, 138°31’52”E, 4 May 2013, dug from burrow in dry grass paddock, S.E. Harrison, M.L. Harrison (SAM NN29577[DNA]); 1 female, Maitland-Ardrossan Road, 34°23’21”S, 137°43’28”E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29590[DNA]); 1 female, Pages Flat, off Pages Flat Road, 35°20’24”S, 138°31’37”E, 3 September 2013, dug from burrow on dry roadside with sparse grass, S.E. Harrison, M.L. Harrison (SAM NN29601[DNA]); 1 female, Norton Summit, 34°55’04”S, 138°44’37”, 30 April 2015, dug from burrow in mossy clay bank, S.E. Harrison, N. Birks (SAM NN29630[DNA]); 1 male, Satsuma Crescent, Golden Grove, 34°46’56”S, 138°43’9”, 1 June 2015, hand drowned in water in tarpaulin, A.J. Lewis (SAM NN29633[DNA]); 1 male, Morgan, 34°2’7.12”S, 139°40’20”, 15 June 2015, hand wandering at night, M. Newton (SAM NN29634[DNA]); 1 male, Pyap, Murray Mallee, 34°27’S, 140°29’40”E, 17 June 1991, hand collected from house verandah after rain, L.N. Nicolson (SAM NN20078[DNA]); 1 male, Mitcham, Adelaide Plains, 34°58’S, 138°37’E, 25 March 1979, hand collected at night under porchlight, R.V. Southcott (SAM NN20047); 1 male, Weetootla Well, Balcanoona Creek, Flinders Ranges, 30°29’S, 139°13’E, 8 May 1989, pitfall, D. Hirst (SAM NN20096). ***Victoria*:** 1 male, Mildura, 34°32’S, 142°12’E, 23 July 1992, P. Hudson (SAM NN20082). ***New South Wales*:** 1 female, Eaglehawk Station, 32°21’S, 141°43’E, N. Birks (SAM NN29615[DNA]).

Other material examined. AUSTRALIA: *South Australia*: 1 male, Crystal Brook Golf Course, Mid-North, 33°21’S, 138°12’E, 12 April 1998, hand collected after rain, D. Hirst (SAM NN20006); 1 male, Crystal Brook Golf Course, Mid-North, 33°21’S, 138°12’E, 12 April 1998, hand collected after rain, D. Hirst (SAM NN20007); 1 male, Windsor Gardens, Adelaide Plains, 34°52’S, 138°39’E, May 1994, D. Hirst (SAM NN20009); 1 male, Crystal Brook Golf Course, Mid-North, 33°21’S, 138°12’E, 29 March 1991, dug from burrow, H. Kairl (SAM NN20013); 1 male, Angaston, Mt Lofty Ranges, 34°30’S, 139°03’E, 23 March 1950 (SAM NN20015); 1 male, Para Wirra National Park, North Oval, 34°42’40”S, 138°49’34”E, 25 April 1989, hand collected, dead, from *Latrodectus hasseltii* web, D. Hirst (SAM NN20016); 1 male, Para Hills, Adelaide Plains, 34°48’S, 138°39’E, 9 March 1982, hand collected from lounge room of house, T. Morley (SAM NN20017); 1 male, Parafield Gardens, Adelaide, Adelaide Plains, 34°46’S, 138°36’E, 13 April 1972, hand collected from floor of house, J. Hall (SAM NN20022); 1 male, Monarto, Murray Mallee, 35°04’S, 139°07’E, 23 May 1978, S. Gifford (SAM NN20023); 1 male, Magill, Adelaide Plains, 34°54’S, 138°40’E, 4 May 1994, G. Davies (SAM NN20024); 1 male, Adelaide, Adelaide Plains, 34°56’S, 138°36’E, March 1988, hand collected from swimming pool (SAM NN20025); 1 male, Two Wells, Adelaide Plains, 34°35’S, 138°31’E, 1 April 1994, hand collected after light rain, J.A. Mcmara (SAM NN20026); 1 male, Two Wells, Adelaide Plains, 34°35’S, 138°31’E, 1 April 1994, hand collected after light rain, J.A. Mcmara (SAM NN20027); 1 male, Hawthorn, Adelaide Plains, 34°58’S, 138°36’E, 15 March 1985, S. Barker (SAM NN20029); 3 males, Hawthorn, Adelaide Plains, 34°58’S, 138°36’E, 30 March 1988, S. Barker (SAM NN20031–3); 1 male, Windsor Gardens, Adelaide Plains, 34°52’S, 138°39’E, 22 March 1989, D. Hirst (SAM NN20034); 1 male, Magill, Adelaide Plains, 34°54’S, 138°40’E, May 1967, R. Briggs (SAM NN20035); 1 male, Adelaide, St Peters College, Mt Lofty Ranges, 34°55’S, 138°40’E, 23 March 1953, D. McEwen and N. Birks (SAM NN20038); 1 male, Blackwood, Mt Lofty Ra., 35°01’S, 138°36’E, April 1967, hand collected from bathroom,

Mrs Kenny (SAM NN20039); 1 male, Wayville, Adelaide, Adelaide Plains, 34°56'S, 138°35'E, 2 July 2011 (SAM NN20040); 1 male, Edwardstown, 12 Price Street, Adelaide Plains, 34°59'S, 138°34'E, 12 April 1989, D. Jones (SAM NN20043); 1 male, Edwardstown, 12 Price Street, Adelaide Plains, 34°59'S, 138°34'E, 12 April 1989, D. Jones (SAM NN20044); 1 male, Langhorne Creek, 35°25'S, 139°15'E, August 1997, R. Eckert (SAM NN20050); 1 male, Mitcham, Adelaide Plains, 34°58'S, 138°37'E, 28 March 1984, hand collected wandering below porch light, R.V. Southcott (SAM NN20051); 1 male, Mitcham, Adelaide Plains, 34°58'S, 138°37'E, 12 April 1978, R.V. Southcott (SAM NN20052); 1 male, Blackwood, Mt Lofty Ranges, 35°01'S, 138°36'E, April 1967, hand collected from bathroom, Mrs Kenny (SAM NN20060); 1 male, Blackwood, Mt Lofty Ranges, 35°01'S, 138°36'E, April 1967, hand collected from bathroom, Mrs Kenny (SAM NN20061); 1 male, Old Boolcoomata, Olary Plains, 32°10'36"S, 140°18'04"E, August 1996, pitfall, North Olary Plains Survey, (SAM NN20109); 1 male, Hawthorn, Adelaide Plains, 34°58'S, 138°36'E, 2 April 1981, found dead in swimming pool, S. Barker (SAM NN20661); 1 male, Hawthorn, Adelaide Plains, 34°58'S, 138°36'E, 2 April 1981, found dead in swimming pool, S. Barker (SAM NN20662); 5 males, Belair National Park, Mt Lofty Ranges, 35°01'S, 138°36'E, April 1967, hand collected from bathroom, Mrs Kenny (SAM NN20678–52); 1 male, Adelaide Plains, 34°54'S, 138°37'E, 3 April 2004, S. Bishop (SAM NN22302); 1 male, Tracy, Mid-North, 33°13'50"S, 139°02'34"E, 27 Oct–1 Nov 2003, pitfall, Mid North & Yorke Peninsula Survey (SAM NN22401); 1 male, Happy Valley, Mt Lofty Ranges, 35°04'S, 138°34'E, 11 May 2016, found wandering around while raining, M. Wilkinson (SAM NN28533); 1 female, Hallett, 33°20'27"S, 138°54'10"E, 15 March 2013, dug from burrow dug from burrow in dry grass paddock, S.E. Harrison, J. Schofield (SAM NN29556[DNA]); 1 female, Teliqua Field Site, off Eastern Road, north east of Burra, 33°36'39"S, 138°59'14"E, 16 March, dug from burrow in dry grass paddock, S.E. Harrison, J. Clayton (SAM NN29557[DNA]); 1 female, same data except 33°37'05"S, 138°59'17"E, 16 March (SAM NN29558[DNA]); 2 females, same data except 33°36'58"S, 138°59'24"E, 15 March 2013, (SAM NN29559[DNA], NN29560[DNA]); 3 females, reserve off East Terrace, Adelaide CBD, 34°55'42"S, 138°37'02"E, 20 March 2013, dug from burrow in dry creek bank, S.E. Harrison, N. Birks (SAM NN29561[DNA], NN29562[DNA], NN29563[DNA]); 1 male, 14 Nanette Drive, Valley View, 34°50'29"S, 138°39'41"E, 3 April 2013, found in shed, W. Chau (SAM NN29564); 2 females, on road to Mount Middleback, off Port Lincoln Highway, south west of Whyalla, 33°11'16"S, 137°15'13"E, 2 May 2013, dug from burrow near paddock fence in saltbush paddock, S.E. Harrison, M.L. Harrison (SAM NN29567[DNA], NN29568[DNA]); 2 females, Pichi Richi Park, Pichi Richi Pass, Flinders Ranges, 32°25'46"S, 137°58'16"E, 3 May 2013, dug from burrow in dry grass, S.E. Harrison, M.L. Harrison (SAM NN29570[DNA], NN29571[DNA]); 1 female, Burnt Down Creek, Hilder Road, off Horrocks Highway, 32°24'51"S, 138°06'53"E, 3 May 2013, dug from burrow near creek bed, in dry grass/scrub, S.E. Harrison, M.L. Harrison (SAM NN29574[DNA]); 1 female, Wilmington-Hammond Road, off Horrocks Highway, 32°36'33"S, 138°08'02"E, 3 May 2013, dug from burrow under gum trees on road verge, S.E. Harrison, M.L. Harrison (SAM NN29575[DNA]); 1 female, Nectar Brook Road, off Main North Road, 32°37'02"S, 137°59'40"E, 3 May 2013, dug from burrow on rocky road verge next to dry grass paddock, S.E. Harrison, M.L. Harrison (SAM NN29576); 1 female, Moralana Scenic Drive, before Black Gap, 31°42'56"S, 138°31'45"E, 4 May 2013, dug from burrow under large gum trees, S.E. Harrison, M.L. Harrison (SAM NN29578[DNA]); 1 female, Survey Road (dirt road between Melrose and Port Germein), 32°50'48"S, 138°10'53"E, 5 May 2013, dug from burrow on dry creek bank in paddock under gumtree, S.E. Harrison, M.L. Harrison (SAM NN29579[DNA]); 1 female, Lindsay Terrace, Kadina, 33°57'25"S, 137°43'07"E, 5 May 2013, dug from burrow on dry grassy verge, S.E. Harrison, M.L. Harrison (SAM NN29581[DNA]); 1 female, Lindsay Terrace, Kadina, 33°57'25"S, 137°43'07"E, 5 May 2013, dug from burrow on dry grassy verge, S.E. Harrison, M.L. Harrison (SAM NN29583[DNA]); 1 female, Hicky's Drive, Coobowie, 35°01'42"S, 137°45'42"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29584[DNA]); 3 juveniles, Saint Vincent Highway, Port Vincent, 34°46'44"S, 137°50'08"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29587[DNA]); 1 female, Arthurton Road, 34°21'58"S, 137°49'46"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29588[DNA]); 1 female, Honnor Road (off Minlaton-Maitland Road), 34°23'52"S, 137°39'59"E, 7 May 2013, dug from burrow in dry grass paddock near fence, S.E. Harrison, M.L. Harrison (SAM NN29592[DNA]); 1 female, Lake Fowler Road (at intersection of Edithbourgh Road and Yorketown Road), 35°03'35"S, 137°38'45"E, 8 May 2013, dug from burrow in dry grass paddock

near fence, S.E. Harrison, M.L. Harrison (SAM NN29593[DNA]); 1 female, on unnamed road from Port Moorowie toward Yorketown (extension of McEacherns Beach Road), 35°04'24"S, 137°32'01"E, 8 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29594[DNA]); 3 females, 8 Whitewood Drive, Upper Sturt, 35°01'04"S, 138°41'26"E, 28 July 2013, dug from burrow on steep clay bank, S.E. Harrison, N. Birks (SAM NN29596[DNA], NN29697[DNA], NN29798[DNA]); 2 females, Pages Flat, off Pages Flat Road, 35°20'24"S, 138°31'37"E, 3 September 2013, dug from burrow on dry roadside with sparse grass, S.E. Harrison, M.L. Harrison (SAM NN29599[DNA], NN29600[DNA]); 1 female, Orroroo, off Orroroo-Peterborough Road, 32°44'12"S, 138°37'05"E, 12 November 2013, dug from burrow in mallee trees next to road, M.G. Rix, S.E. Harrison (SAM NN29605[DNA]); 3 females, Beetaloo Reservoir, on road to entrance, near gate, 33°12'38"S, 138°13'34"E, 2 April 2014, dug from burrow in mossy, grassy bank, S.E. Harrison, M.S. Harvey (SAM NN29608[DNA], NN29609[DNA], NN229610[DNA]); 3 females, Cobbler Creek, in reserve, 34°46'9"S, 138°40'21"E, 16 October 2014, dug from burrow in clay bank of Nature Reserve, A. Lewis (SAM NN29611[DNA], NN29612[DNA], NN29613[DNA]); 1 female, Morphett Vale, 35°08'01"S, 138°31'4"E, 15 May 2013, hand collected in garden, N. Birks (SAM NN29614[DNA]); 2 females, Black Hill Conservation Park, 34°51'46"S, 138°43'26", 22 December 2014, dug from burrow in natural clay bank, S.E. Harrison, M.L. Harrison (SAM NN29620[DNA], NN29621[DNA]); 1 female, Antsey Hill Conservation Park, Lower North East Road, Horton, 34°50'28"S, 138°44'44", 1 April 2015, dug from burrow in high rocky bank on side of road, S.E. Harrison (SAM NN29624[DNA]); 1 female, 42–43 Lower North East Road, Houghton, 34°49'48"S, 138°45'34", 1 April 2015, dug from burrow in very hard rocky bank, S.E. Harrison (SAM NN29625[DNA]); 2 females, Para Wirra Conservation Park, Yattalunga, 34°41'28"S, 138°49'30", 1 April 2015, dug from burrow in clay bank, S.E. Harrison, B. Horton (SAM NN29627[DNA], NN29628[DNA]); 1 juvenile, same data (SAM NN29629[DNA]); 1 female, Teringie Drive, Norton Summit, 34°54'46"S, 138°42'35", 30 April 2015, dug from burrow in driveway cutting, S.E. Harrison, N. Birks (SAM NN29631[DNA]); 1 female, Beetaloo reservoir, on road to entrance, near gate, 33°12'38"S, 138°13'34"E, 5 May 2014, dug from burrow in mossy, grassy bank, S.E. Harrison (SAM NN29632); 1 female, Belair National Park, 35°00'18"S, 138°38'07", 20 August 2015, dug from burrow in mossy bank on side of walking trail, S.E. Harrison, D. Stringer and A. Lewis (SAM NN29637[DNA]); 1 female, Brown Hill Conservation Park, 34°59'14"S, 138°39'11"E, 16 February 2016, dug from burrow in mossy bank on side of walking trail, S.E. Harrison, D. Bass (SAM NN29640[DNA]); 1 female, Mount Crawford Forest Reserve, 34°42'41"S, 138°55'57"E, 16 February 2016, dug from burrow in clay bank next to roadside, S.E. Harrison, M. Harrison (SAM NN29641[DNA]); 1 female, Kapunda, 34°20'28"S, 138°58'36"E, 2 December 2014, pulled out of burrow with optiscope, J. Clayton (SAM NN29796[DNA]); 1 female, Terowie, 33°15'28"S, 138°54'26", 2 April 2013, dug from burrow, J. Clayton (SAM NN29797[DNA]); 1 female, Burra, 33°40'44"S, 138°57'43"E, 27 September 2014, pulled out of burrow with optiscope, J. Clayton (SAM NN29798[DNA]); 1 female, Tiliqua Reserve, 33°36'51"S, 138°59'8"E, 15 July 2013, dug from burrow, J. Clayton (SAM NN29799[DNA]); 1 female, Burra, 33°40'44"S, 138°57'43"E, 23 September 2013, dug from burrow, J. Clayton (SAM NN29801[DNA]); 1 female, Tiliqua Reserve, 33°36'51"S, 138°59'8"E, 15 July 2013, dug from burrow, J. Clayton (SAM NN29802[DNA]); 1 female, Burra, 33°40'44"S, 138°57'43"E, 27 September 2014, dug from burrow, J. Clayton (SAM NN29803[DNA]); 1 female, Kapunda, 33°20'28"S, 138°58'36"E, 2 December 2014, dug from burrow, J. Clayton (SAM NN29804[DNA]); 1 female, Jamestown, 33°16'6"S, 138°37'21"E, 23 February 2015, pulled out of burrow with optiscope, J. Clayton (SAM NN29806[DNA]); 1 female, Hallett, 33°20'9"S, 138°53'18"E, 18 July 2013, dug from burrow, J. Clayton (SAM NN29807[DNA]); 1 female, Baldina station, near Burra, 33°39'54"S, 139°2'2"E, 18 July 2013, dug from burrow, J. Clayton (SAM NN29808[DNA]); 1 male, Mallala, 34°27'S, 138°31'E, 1900 (KS.43729); 1 male, Hawthorn, 29 Angas Road, 34°58'S, 138°36'E, 17 May 1969, S. Barker (WAM T141078); 2 males, Torrens Gorge, Adelaide, 34°51'S, 138°44'E, 20 March 1974, S. Barker (WAM T141079); 1 male, Hawthorn, 34°58'S, 138°36'E, 1 April 1983, S. Barker (WAM T141080); 3 males, Hawthorn, 34°58'S, 138°36'E, 1 April 1983, S. Barker (WAM T141081–3); 1 male, Westbourne Park, 60 Monmouth Road, 34°58'S, 138°35'E, 4 August 1954, K. Main (WAM T141098); 1 male, Dublin, 34°27'S, 138°21'E, 16 May 1986, B.Y. Main (WAM T141105); 2 males, Hawthorn, 34°58'S, 138°36'E, 18 April 1986, S. Barker (WAM T141115). ***Victoria:*** 1 female, Chinkapook, off Pier-Millan-Chinkapook Road, 35°11'20"S, 142°56'16"E, 13 November 2013, dug from burrow in mallee woodland, M.G. Rix, S.E. Harrison (SAM NN29606[DNA]); 1 female, Meringur Flora and

Fauna Reserve, N. of Meringur, 34°22'01"S, 141°20'04"E, 14 November 2013, dug from burrow in *Casuarina* woodland, M.G. Rix, S.E. Harrison (SAM NN29607[DNA]).

Diagnosis. Males of *B. aurea* can be distinguished from those of *B. maryae*, *B. plata*, *B. birksi*, *B. newtoni*, *B. hortoni*, *B. parva*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 5G–I); from those of *B. bella*, by the absence of a dark dorsal cardiac stripe (Fig. 5A); from those of *B. pidax*, by the presence of thickened spine-like setae on the cymbium (Fig. 5J–L); from those of *B. emmottorum*, by the square eye group (Fig. 5D); from those of *B. tunstilli*, by the spinules of the palpal tibia being similar to or only slightly shorter in length to those on the RTA (Fig. 5J, L); and from those of *B. gemmelli*, by the relatively long RTA (with the field of RTA spinules extending further onto the tibia) (Fig. 5J), and by the moderate to weak abdominal pattern (Fig. 5A). Females of *B. aurea* can be distinguished from those of *B. bassi*, *B. mainae*, *B. maryae*, *B. wingellina* and *B. nullarborensis* by the combined absence of a trapezoidal eye group (Fig. 6D), the absence of golden hairs on the carapace and the absence of dark brown on the book lungs (in contrast to abdomen colour) (Fig. 6C); from those of *B. birksi* by abdominal chevrons being lighter brown (as opposed to chevrons being dark brown to black) (Fig. 6A); and from those of *B. maryae* by the presence of labial cuspules (Fig. 6E, F).

All life stages of *B. aurea* can also be distinguished from those of other species with sequence data except *B. bassi* by the following nucleotide substitutions (*n*=71 specimens): T(547), A or G(549); and from those of *B. bassi* by the following nucleotide substitutions: T(68), T(102), C(199), T(216), A(255), G(264), T(336), C(339), A(367), T(426), G(433), C(462), C(470), T(479), G(520), C(535), G(546).

Description. *Male* (SAM NN29564). Medium-sized idiopid spider (total length 16.3).

Colour (in ethanol; Fig. 5A–C): Carapace, legs and pedipalp golden-brown, with darker line between fovea and eye group (Fig. 5A); sternum also, darker towards anterior margins; labium golden-brown, maxillae slightly darker yellow brown, chelicerae dark red-brown (Fig. 5E, F); abdomen yellow-brown without noticeable chevron pattern (Fig. 5A, C).

Cephalothorax: Carapace 7.4 long, 5.9 wide, 4.7 high, 1.3 times longer than wide; oval (Fig. 5A), caput low, ocular area raised (Fig. 5C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of thickened setae between fovea and eye group; carapace sparsely setose, with indistinct lines of setae radiating from fovea, concentrated and forming fringe on lateral margins; median clump of thickened setae on clypeus and both sides of eye group (Fig. 5D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.1 wide, 1.1 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row very slightly recurved; AME only slightly smaller than ALE and separated by about AME diameter; PLE only slightly larger than ALE and separated by just over about PLE diameter; PME pale, about half size of PLE, and separated from PLE by less than its own diameter (Fig. 5D). Labium without cuspules (Fig. 5F).Sternum 3.4 long, 2.8 wide, evenly setose; three pairs of faint sigilla (Fig. 5E). Maxillae with 5 (left) and 7 (right) cuspules (Fig. 5E, F).

Legs: diffusely setose and spinose on all surfaces; tarsi I, II slightly ventrally flattened; tarsi and distal metatarsi I, II scopulate (Fig. 5G–I). Paired tarsal claws with 1 row of ventral teeth: leg I p6 (6 large), r6 (6 large); leg II p5 (5 large), r5 (5 large); leg III p5 (5 large), r4 (4 large); leg IV r5 (5 large), r5 (5 large).

Spination: Tibia I with prolateral clasping spurs, distal-most spur with 2 terminal peg-like macrosetae, proximal-most with 3 terminal peg-like macrosetae (Fig. 5G–I); r3. Leg II: tibia p1; metatarsus p3; metatarsus p1, r4. Leg III: patella p3; tibia p2, r1; metatarsus p6, r9; tarsus p3, r5. Leg IV: tibia p1, r1; metatarsus p9, r2; tarsus p8, r5.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 6.2, patella 3.2, tibia 4.4, metatarsus 4.6, tarsus 2.7, total = 21.9. Leg II: femur 5.2, patella 2.7, tibia 3.7, metatarsus 4.5, tarsus 2.3, total = 18.4. Leg III: femur 6.2, patella 3.2, tibia 4.4, metatarsus 4.6, tarsus 2.7, total = 21.9. Leg IV: femur 6.2, patella 3.5, tibia 6.1, metatarsus 6.5, tarsus 3.4, total = 25.7. Pedipalp: femur 4.9, patella 2.1, tibia 3.3, tarsus 1.5, total = 11.8.

FIGURE 5. *Blakistonia aurea* Hogg, male (SAM NN29564): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, clasping spur, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 5 mm (A, G), 2 mm (J).

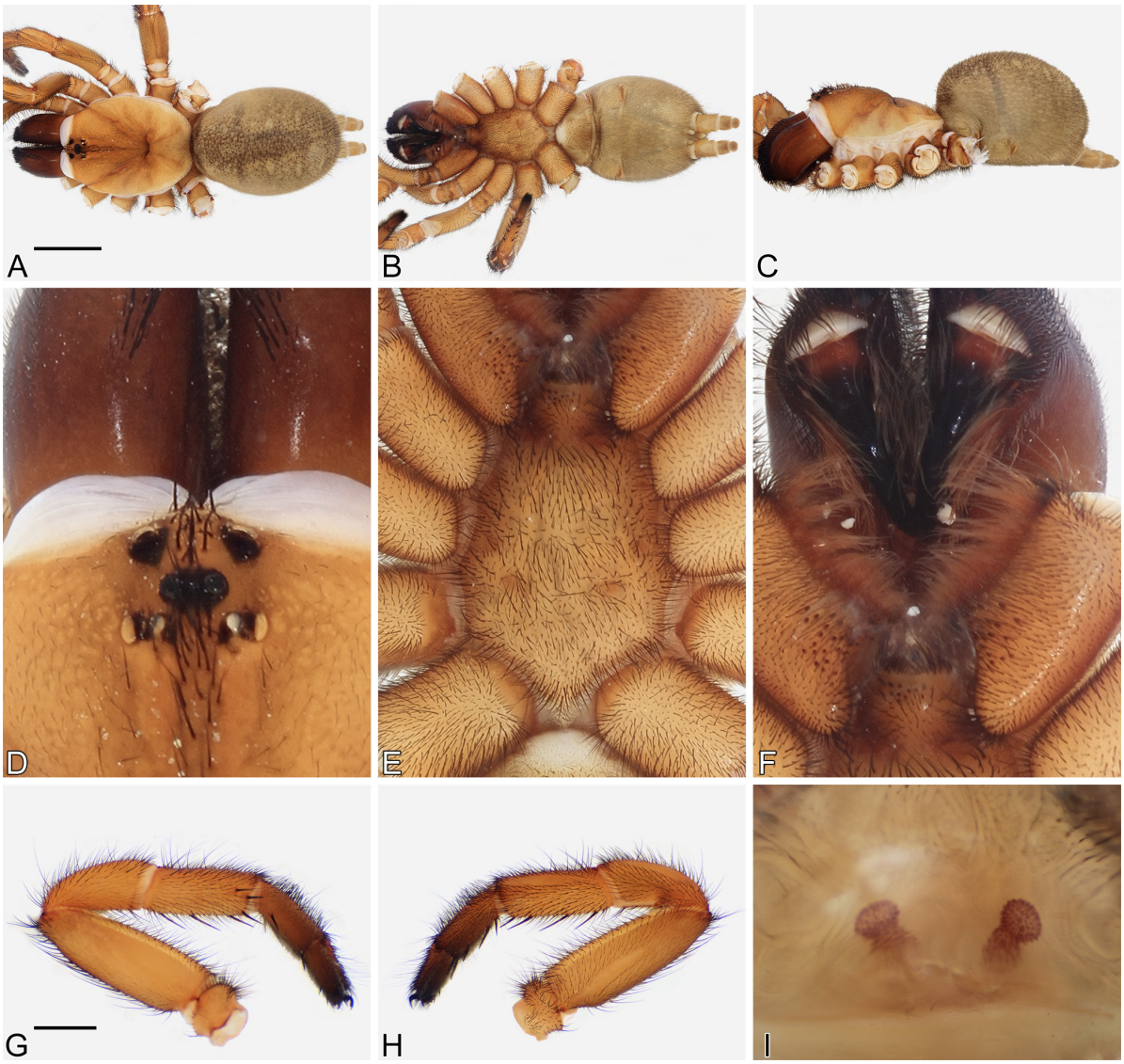


FIGURE 6. *Blakistonia aurea* Hogg, female (SAM NN29623): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 2 mm (G).

Pedipalp: Femur with dorsal spines, patella with thickened ventral setae; tibia short and swollen, RTA short and pointed, covered in short, dense spinules for just over half distance between base of apophysis and distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip noticeably twisted, just over length of bulb; cymbium covered with rows of short spinules, getting longer and denser on distal cymbium (Fig. 5J–L).

Abdomen: Setose, oval, 2 pairs of unsclerotised dorsal sigilla; 8.9 long, 5.7 wide (Fig. 5A).

Variation (n=7): Carapace 4.8–7.6 long, 5.0–6.2 wide, no labial cuspules. Spination: Leg I: tibia r1–3, metatarsus r0–3. Leg II: tibia p1–2, r3–7; metatarsus p0–3, r3–8, tarsus r0–5. Leg III: patella p0–4; tibia p1–4, r–3; metatarsus p6–11, r5–12. Leg IV: tibia p0–2, r0–3; metatarsus p7–11, r3–8; tarsus p0–0, r1–5.

Female (SAM NN29623^{DNA}). Large idiopid spider (total length 19.4).

Colour (in ethanol; Fig. 6A–C): Carapace, legs and pedipalp golden-brown, with darker line between fovea and eye group (Fig. 6A); sternum golden-brown, darker towards anterior margins; labium as sternum, maxillae slightly darker yellow brown, chelicerae dark reddish brown (Fig. 6E, F); abdomen yellowish brown with faint chevron pattern (Fig. 6A, C); dorsal femur the darkest (Fig. 6G, H).

Cephalothorax: Carapace 8.6 long, 7.2 wide, 7.2 high, 1.2 times longer than wide; oval (Fig. 6A); caput moderately raised, ocular area flat (Fig. 6C); cuticle uniformly smooth; fovea procurved; one row of thick setae between fovea and eye group; small, fine setae scattered very sparsely across carapace, concentrated and form very fine, indistinct fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 6D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.7 wide, 1.3 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.1; posterior eye row straight; AME slightly smaller than ALE and separated by about ALE diameter; ALE and PLE separated by about twice the ALE diameter; PME pale, only slightly smaller than PLE, and separated from PLE by just less than its own diameter (Fig. 6D). Labium with *ca.* 11 cuspules (Fig. 6F).Sternum 5.1 long, 4.2 wide, moderately setose with setae densely grouper and longer around margins; 2 pairs of faint sigilla of similar side near posterior half of lateral margins (Fig. 6E). Maxillae with *ca*. 44 (left) and 24 (right) cuspules (Fig. 6E, F).

Legs: moderately setose and diffusely spinose, with retrolateral side of all legs being least setose and dorsal sides of III and IV with thick, dense, spine-like setae; distinct upright setae on metatarsi I, II; femora I, II, and pedipalp laterally bowed; tarsi and metatarsi I, II, and palpal tarsi heavily scopulate (Fig. 6G–I). Paired tarsal claws: leg I p2 (1 large, 1 small) r0; leg II p2 (1 large, 1 small), r2 (1 large, 1 small); leg III p0, r0; right leg IV p2 (2 large), r0. Pedipalp claw with 2 large teeth.

Spination: Leg I: tibia p3, r4; metatarsus p2, r5; tarsus p2, r4 (Fig. 6G, H). Leg II: tibia p2, r4; metatarsus p3, r7; tarsus p2, r4. Leg III: patella p5; tibia p6, metatarsus p7, r6; tarsus with ventral patch of 9 short spines. Right leg IV: metatarsus p7, r1; tarsus with 16 spines ventrally. Pedipalp: patella p1; tibia p6, r6; tarsus p3, r3.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 5.0, patella 3.4, tibia 3.0, metatarsus 2.3, tarsus 1.8, total = 15.5. Leg II: femur 4.5, patella 3.2, tibia 2.7, metatarsus 2.4, tarsus 1.9, total = 14.7. Leg III: femur 4.0, patella 3.1, tibia 2.6, metatarsus 2.7, tarsus 2.00, total = 14.4. Leg IV (right): femur 5.7, patella 4.0, tibia 4.8, metatarsus 4.2, tarsus 2.3, total = 21.0. Pedipalp: femur 4.5, patella 2.6, tibia 2.5, tarsus 3.4, total = 13.0.

Abdomen: Setose, oval, three pairs of unsclerotised dorsal sigilla; 10.8 long, 7.8 wide (Fig. 6A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, oval-shaped, covered in opaque mottled brown nodules (Fig. 6I).

Variation (n=7): Carapace 6.3–9.9 long, 5.4–8.7 wide, 7–17 labial cuspules. Spination: Leg I: tibia p2–7, r4–7; metatarsus p2–4, r5–6; tarsus p1–2, r2–4. Leg II: tibia p0–2, r4–5; metatarsus p3–5, r5–7; tarsus p2–3, r4–7. Leg III: patella p3–5; tibia p1–6, r0–1; metatarsus p7–10, r1–4; tarsus with about 10–20 spines ventrally. Pedipalp: patella p0–1, r0–1; tibia p4–9, r5–7; tarsus p1–3, r1–4.

Distribution. *Blakistonia aurea* has the broadest distribution of all species in the genus. It is found throughout the north-eastern Eyre Peninsula, the Yorke Peninsula, Flinders Ranges, Fleurieu Peninsula, and Mount Lofty Ranges, as well as western Victoria and far south-western New South Wales (Fig. 30).

Remarks. *Blakistonia aurea* reaches a high population density in some areas around Adelaide and the Fleurieu Peninsula in optimal conditions. The preferred habitat is clay banks, and the spiders can often be found on roadside cuttings and creek banks. Males are often found after rain in swimming pools or wandering on verandas. The spiders build a characteristic thick D-shaped plug burrow (Fig. 2A–C). Rainbow and Pulleine (1918) and Main (1985) observed that spiders sometimes construct a burrow with an unusual crenulated edge, simulating a clam-shell (Fig. 2A). These populations were sampled and included in the molecular study, which confirmed that they did fall within *B. aurea*, suggesting that this is a behavioural adaption to certain conditions. We have examined the holotype of *Ag. villosa* and agree with its synonymy following Main (1985).

***Blakistonia bassi* sp. n.**
(Fig. 7A–I)

Type material. AUSTRALIA: ***South Australia:*** Holotype female, off Pound Road, Ashton, Mount Lofty Ranges, , 34°55'55.608"S, 138°44'49.667"E, 22 December 2014, hand collected from mossy roadside bank, S.E. Harrison, M. Harrison (SAM NN29619^{DNA}). Paratypes: 2 females, same data as holotype except 13 May 2016, S.E. Harrison, N. Birks (SAM NN28529, NN28530).

Diagnosis. Females of *B. bassi* can be distinguished from all other species of *Blakistonia* by the fine, golden hairs that cover the carapace (Fig. 7A, D). Males are unknown.

All life stages of *B. bassi* can also be distinguished from those of other species with sequence data by the following nucleotide substitutions (*n*=1 specimen): G(3), C(87), C(102), T(111), G(199), C(205), T(207), T(255), C(339), A(390), C(462), C(479), C(481), G(546), G(573), G(591); and by the following unique molecular motifs: TT(30–31), GAC(66–68), GCT(367–369), AAG(372–374), GG(432–433), TGC(456–458), TGGA (468–471).

Description. *Holotype female* (SAM NN29619)**:** Medium-sized idiopid spider (total length 18.5).

Colour (in ethanol; Fig. 7A–C): Carapace, legs and pedipalp dark red-brown, darker around fovea and lateral margins of caput, with darkened line from fovea to eye group (Fig. 7A); sternum, labium and maxillae uniformly golden-brown, chelicerae dark red-brown (Fig. 7E, F); abdomen dark brown with indistinct mottled chevron pattern (Fig. 7A, C).

Cephalothorax: Carapace 7.8 long, 7.2 wide, 6.3 high, 1.1 times longer than wide; oval (Fig. 7A), caput high, ocular area flat (Fig. 7C); cuticle smooth, with pits outward from fovea and both sides of caput, and also two diagonally inward-facing indentations posteriorly; fovea procurved; two indistinct parallel rows of setae from fovea to eye group, less noticeabe both sideson both sides of caput; smaller fine setae also scattered across carapace, concentrated and form fringe around lateral margins; one long seta in fovea; median clump of thickened setae on clypeus (Fig. 7D); carapace with fine cover of thin golden hairs (Fig. 7A, D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.6 wide, 1.1 long, 0.2 of carapace width; anterior eye row strongly procurved; PLE–PLE/ALE–ALE ratio 1.1; posterior eye row slightly recurved; AME about equal in size to ALE and separated by twice diameter of ALE/AME; ALE and PLE separated by just over ALE diameter; PME similar in size to ALE/AME and about half size of PLE, and separated from PLE by about its own diameter (Fig. 7D). Labium without cuspules (Fig. 7F). Sternum 5.0 long, 3.3 wide, evenly setose with setae becoming longer towards anterior margin. Maxillae with *ca*. 35 cuspules on both sides (Fig. 7E, F).

Legs: moderately setose and diffusely spinose; distinct upright setae on distal metatarsi I, II; femora I, II, and pedipalp laterally bowed; tarsi and metatarsi I, II and palpal tarsi scopulate (Fig. 7G–I). Paired tarsal claws with 1 row of ventral teeth: leg I p2 (1 large, 1 small) r1 (1 large, 1 small); leg II p2 (1 large, 1 small), r2 (1 large, 2 small); right leg III p2 (2 large), r1 (1 large); right leg IV p2 (1 large, 1 small), r1 (1 large); median tarsal claw without teeth. Pedipalp claw with 1 large and 1 small tooth.

Spination: Leg I: tibia p3, r4; metatarsus p2, r5; tarsus with patch of 5 short spines scattered over ventral surface (Fig. 7G, H). Leg II: tibia p4, r4; metatarsus p4, r5; tarsus with patch of 3 short spines ventrally. Right leg III: patella p3; tibia p3, r3; metatarsus p12, r8; tarsus with patch of 8 spines scattered ventrally. Right leg IV: metatarsus p10, r6; tarsus with *ca*. 20 short spines scattered ventrally. Palp: patella p1, tibia p8, r6; tarsus p1, r1.

Leg and pedipalp measurements: Length of legs IV > II > I > III. Leg I: femur 4.3, patella 3.1, tibia 2.7, metatarsus 2.1, tarsus 1.7, total = 13.9. Leg II: femur 4.2, patella 3.1, tibia 2.6, metatarsus 1.9, total = 14.9. Leg IV (right): femur 5.5, patella 3.9, tibia 4.0, metatarsus 3.7, tarsus 2.2, total = 19.3. Pedipalp: femur 4, patella 2.2, tibia 2.1, tarsus 2.5, total = 10.8.

Abdomen: Setose, oval, one pair of very small, faint, unsclerotised dorsal sigilla; 10.7 long, 7.3 wide (Fig. 7A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, oval-shaped with lobe on anterior end, covered in opaque, mottled brown nodules (Fig. 7I).

Variation (n=3): Carapace 7.8–9.0 long, 6.0–8.0 wide, no labial cuspules. Spination: Leg I: tibia p3–4, r4; metatarsus p2–3, r3–5; tarsus with 3–6 spines ventrally. Leg II: tibia p3–4, r4; metatarsus p4, r4–5; tarsus with 3–4 spines ventrally. Leg III: patella p2–3; tibia p0–3; r2–3; metatarsus p6–13, r6–8; tarsus with 8–13 spines ventrally. Leg IV: metatarsus p8–12, r3–6; tarsus with 10–20 spines ventrally. Pedipalp patella p1–2; tibia p7–8, r4–6; tarsus p1, r1–2.

Etymology. This species is named in honour of Daniel Bass, for his unwavering support of this research.

Distribution. *Blakistonia bassi* is known from only a single roadside cutting at Ashton in the Mount Lofty Ranges, (Fig. 31). A number of active burrows were found in 2017; however, the species has not been found elsewhere in the Mount Lofty Range despite extensive historical collection, and was not discovered anywhere else as part of this project.

Remarks. The burrow (Fig. 2D, E) is similar to that of *Idiosoma* in its thin, cryptic, flap-like nature, and certainly different to the D-shaped, plug-like burrow typical of *B. aurea*. All burrows found were adorned with moss and cryptic in appearance (Fig. 2D, E).

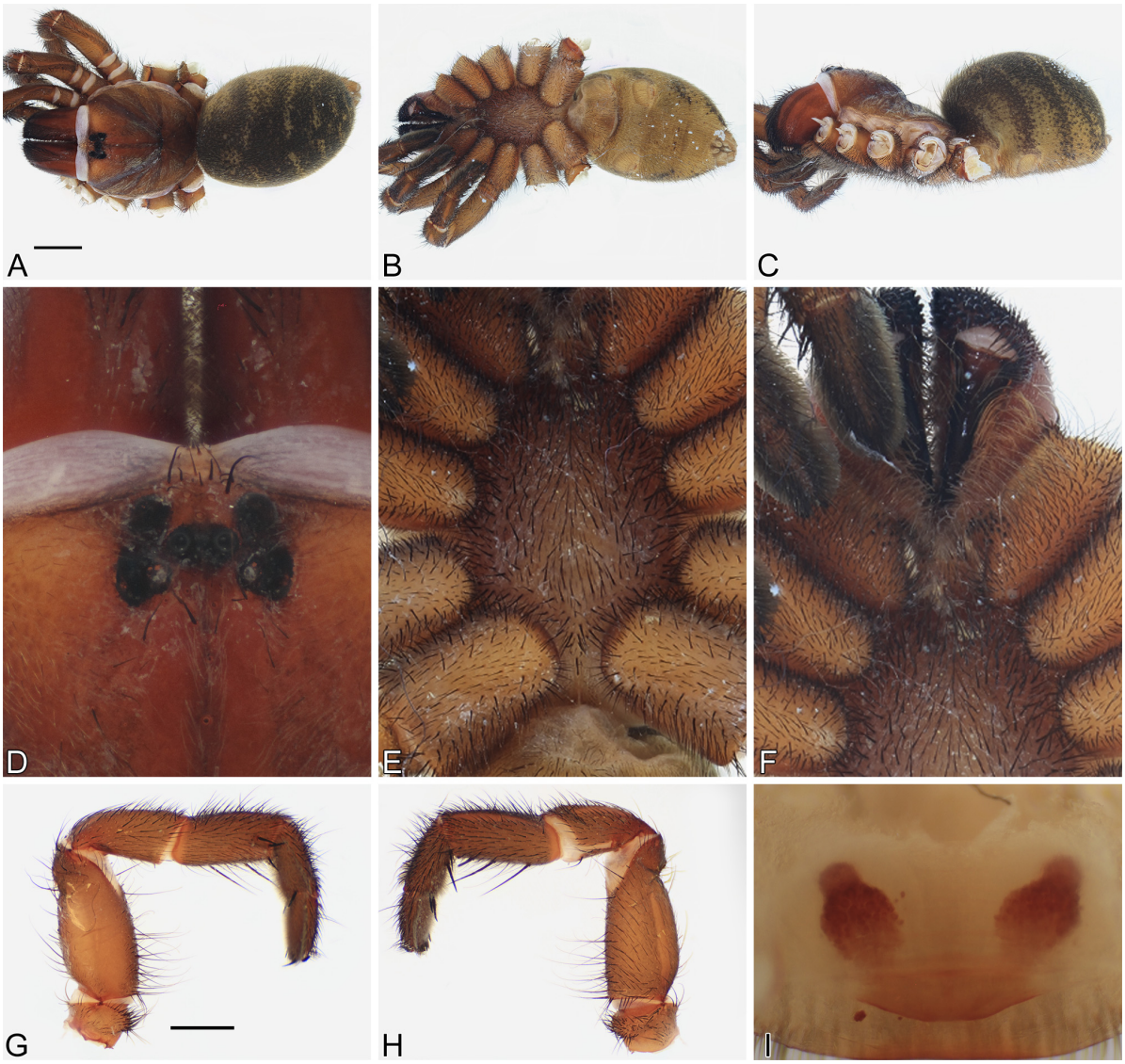


FIGURE 7. *Blakistonia bassi* **sp. n.**, holotype female (SAM NN29619): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 2 mm (G).

***Blakistonia bella*, sp. n.**
(Fig. 8A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Johnson's Bore, 29°10'59"S, 136°10'43"E, 6–7 October 1995, pitfall trap, D.E.L.M. Stony Deserts Survey (SAM NN20063).

Other material examined. AUSTRALIA: *South Australia:* 1 male, Strangways Springs, 29°28'58"S, 136°35'49"E, 25–30 September 1995, pitfall trap, D.E.L.M. Stony Deserts Survey (SAM NN20087).

Diagnosis. Males of *B. bella* can be distinguished from those of *B. plata*, *B. birksi*, *B. newtoni*, *B. maryae*, *B. hortoni*, *B. parva*, *B. olea*, *B tariae*, *B. carnarvon*, and *B. raveni* by the prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 8G–I). Males of *B. bella* can be distinguished from those of *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli* and *B. aurea* by the strongly patterned abdomen with a dark dorsal cardiac stripe (Fig. 8A). Females are unknown.

Description. *Holotype male* (SAM NN20063). Large idiopid spider (total length 15.4mm).

Colour (in ethanol; Fig. 8A–C): Carapace, legs and pedipalp uniform pale golden orange-brown (Fig. 8A); sternum very similar, darker towards anterior margins; labium and maxillae as sternum, chelicerae dark brown (Fig. 8E, F); abdomen golden orange-brown with distinctive pattern of seven dark chevrons not extending down sides of abdomen (Fig. 8A, C).

Cephalothorax: Carapace 7.4 long, 6.7 wide, 5.2 high, 1.1 times longer than wide; oval (Fig. 8A), caput low, ocular area flat (Fig. 8C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; thin, indistinct rows of fine setae radiating out from fovea, with thickest row between fovea and eye group, culminating in group of longer, thickened setae directly posterior to eye group; smaller fine setae also scattered across carapace, concentrated and forming fringe onlateral margins; median clump of thickened setae on clypeus (Fig. 8D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.2 wide, 1.2 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.1; posterior eye row straight; AME *ca.* half size of ALE and separated by about diameter of AME; ALE and PLE separated by *ca*. two diameters of ALE; PME similar in size to AME and about half size of PLE, and separated from PLE by less than its own diameter (Fig. 8D). Labium without cuspules (Fig. 8F). Sternum 4.0 long, 3.2 wide , evenly setose; three pairs of sigilla, doubling in size from anterior to posterior, anterior two pairs separated from edge by their own diameter, posterior pair separated from margin by just over their own diameter (Fig. 8E). Maxillae without cuspules (Fig. 8E, F).

Legs: moderately setose; tibiae I, II without spines, legs III and IV with few spines; setae on patellae of legs III and IV thickened and in rows, with no setae between rows; tarsi I, II slightly ventrally flattened; tarsi and distal metatarsi I, II weakly scopulate (Fig. 8G–I). Paired tarsal claws: leg I p7 (7 large) r5 (5 large); leg II p5 (5 large), r5 (5 large); leg III p5 (5 large), r5 (4 large, 1 small); leg IV p4 (4 large), r5 (5 large).

Spination: Tibia I with prolateral bifid apophyses, distal-most apophysis with 2 teeth, proximal-most with 4 teeth (Fig. 8G–I). Leg II without spines. Leg III: patella p5; metatarsus p3, r5. Leg IV: patella p5; metatarsus IV p4, r5.

Leg and pedipalp measurements: Length of legs I > II > IV > III. Leg I: femur 7.9, patella 3.7, tibia 4.8, metatarsus 5.6, tarsus 2.9, total = 24.9. Leg II: femur 7.0, patella 3.5, tibia 4.7, metatarsus 4.8, tarsus 3.0, total = 23.0. Leg III: femur 5.7, patella 3.0, tibia 4.1, metatarsus 5.1, tarsus 3.0, total = 20.9. Leg IV (right): femur 5.7, patella 3.0, tibia 4.1, metatarsus 5.2, tarsus 3.0, total = 21.0. Pedipalp: femur 4.3, patella 2.2, tibia 3.7, tarsus 1.8, total = 12.0.

Pedipalp: All segments without spines; patella with thickened ventral setae; tibia short, swollen, RTA short, pointed, covered in short, dense spinules continuing almost to distal tibia, becoming sparser; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, slightly twisted with flanged tip, slightly longer than bulb; cymbium covered in rows of short spinules, becoming longer towards distal edge (Fig. 8J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 8.0 long, 5.5 wide (Fig. 8A).

Variation (n=2): Carapace 7.4–6.1 long, 5.4–6.7 wide, no labial cuspules. Spination: invariable.

Etymology. The specific name is taken from the Latin *bellus* (meaning 'beautiful') and refers to the distinctively patterned abdomen.

Distribution. *Blakistonia bella* is known only from inland South Australia, at Johnson's Bore, south-west of Lake Eyre, and Strangways Springs, on Stuart Creek Station (Fig. 31).

Remarks. Both specimens of this species were collected in pitfall traps during the 'Stony Deserts Biological Survey', conducted between 1994 and 1997 (Brandle 1998). The male holotype was collected in a tree-lined drainage channel in October, unusually late in the year for male *Blakistonia* to be out searching for females.

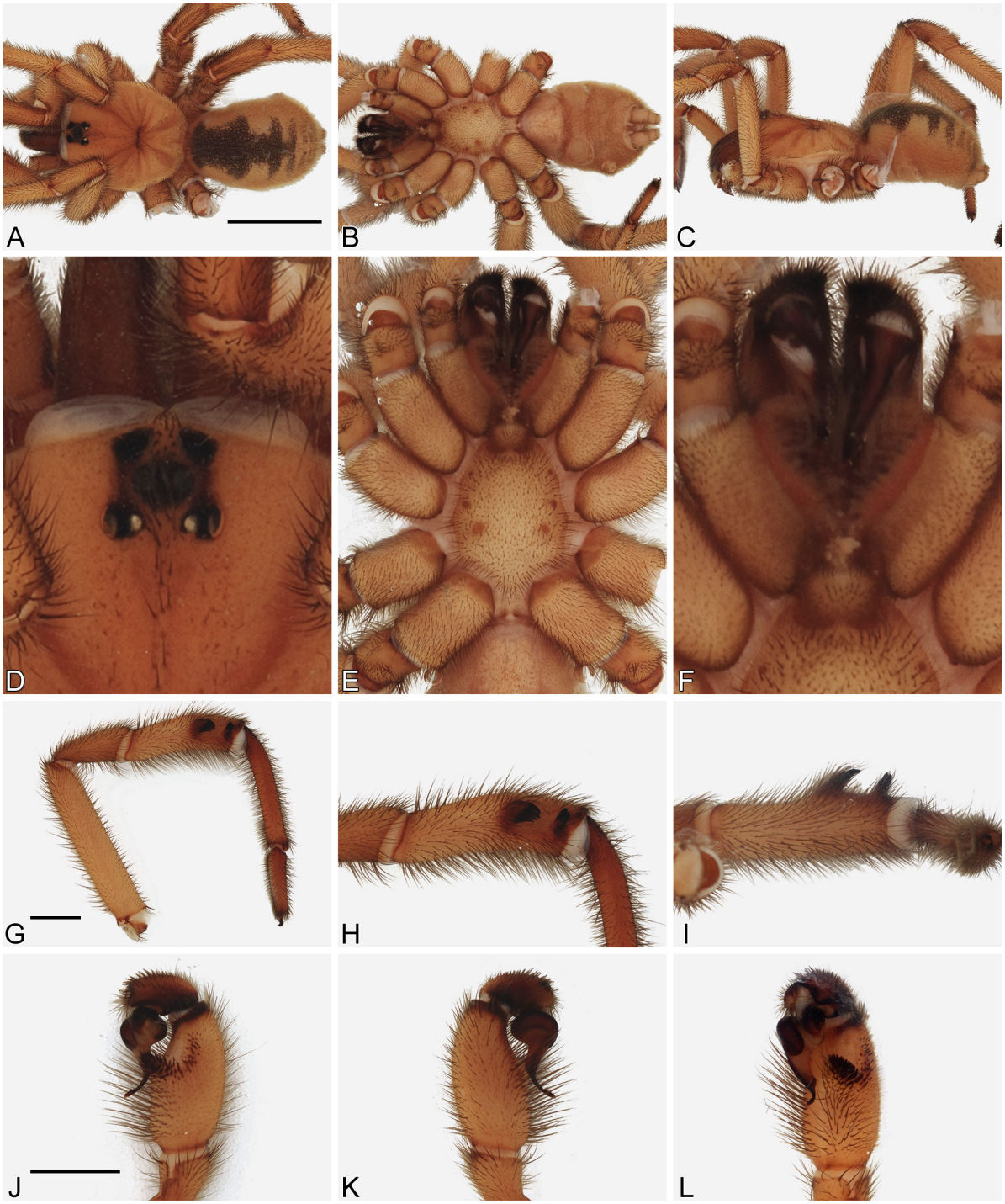


FIGURE 8. *Blakistonia bella* **sp. n.**, holotype male (SAM NN20063): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, clasping spur, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 5 mm (A), 2 mm (G, J).

***Blakistonia birksi*, sp. n.**
(Figs 9A–L, 10A–I)

Type material. AUSTRALIA: ***South Australia:*** holotype male, Ngarkat Conservation Park, 35°37'00"S, 140°46'00"E, July 2006, pitfall trap in heath on sand, L. Jansen (SAM NN29003^{DNA}). Paratypes: 12 males, Ngarkat Conservation Park, 35°37'00"S, 140°46'00"E, July 2006, pitfall trap in heath on sand, L. Jansen (SAM NN29642–53); 2 females, Cleland Conservation Park, 34°58'32.178"S, 138°42'40.799"E, 22 December 2014, hand collected from burrows in clay bank, S. and M. Harrison (SAM NN29618^{DNA}).

Other material examined. AUSTRALIA: ***South Australia:*** 1 juvenile, Cleland Conservation Park, 34°58'32.178"S, 138°42'40.799"E, 22 December 2014, hand collected from burrows in clay bank, S. Harrison, M. Harrison (SAM NN29617^{DNA}); 2 juveniles, Mark Oliphant Conservation Park, 35°01'50.879"S, 138°42'26.579"E, 20 August 2015, dug from mossy bank, S.E. Harrison, S. Stringer, A. Lewis (SAM NN29635 and NN29636); 2 females, same data except 25 August 2015, S.E. Harrison, N. Birks (SAM NN29638^{DNA} and NN29639). ***Victoria:*** 1 juvenile, Grampians National Park, Reid's Lookout Road, 37°08'49"S, 142°26'48"E, 16 November 2013, hand collected from burrow in clay bank in sclerophyll forest, M.G. Rix, S. Harrison (WAM T131984^{DNA}).

Diagnosis. Males of *B. birksi* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 9G–I); from those of *B. parva*, *B. maryae*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the presence of one, rather than two, prolateral macroseta on tibia I (Fig. 9G–I); from those of *B. hortoni*, *B. maryae* and *B. newtoni* by a subquadrate rather than square eye group (Fig. 9D); and from those of *B. plata* by the presence of cuspules on the maxillae (Fig. 9F) and a strong abdominal pattern (Fig. 9A). Females of *B. birksi* can be distinguished from those of all other *Blakistonia* except *B. bassi* by abdominal chevrons that are almost black, and very dark brown between the chevrons (Fig. 10A); and from those of *B. bassi* by the absence of light golden hairs on the carapace (Fig. 10A).

All life stages of *B. birksi* can also be distinguished from those of other species with sequence data except *B. aurea* by the following nucleotide substitution (n=5 specimens): C(387); and from by *B. aurea* by the following unique nucleotide substitution: A(520).

Description. *Holotype male* (SAM NN29003)**.** Small idiopid spider (total length 8.0).

Colour (in ethanol; Fig. 9A–C): Carapace uniform dark chocolate brown (Fig. 9A); labium, maxillae sternum orange-brown, darker towards anterior and lateral margins; chelicerae dark brown (Fig. 9E, F); abdomen dark chocolate brown, distinctive pattern of seven mottled chevrons, for full width of abdomen (Fig. 9A, C); legs and pedipalp concolorous with sternum but darker dorsally (Fig. 9G–L).

Cephalothorax: Carapace 3.8 long, 3.6 wide, 2.8 high, 1.1 times longer than wide; oval (Fig. 9A), caput low, ocular area raised (Fig. 9C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; two thick setae posterior to eye area smaller, fine setae scattered very sparsely across carapace, concentrated and form fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 9D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.9 wide, 0.5 long, 0.3 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row straight; AME similar in size to ALE and separated by about AME diameter; ALE and PLE separated by about twice ALE diameter; PME about one-third of AME and about half of PLE, and separated from PLE by less than its own diameter (Fig. 9D). Labium without cuspules (Fig. 9F). Sternum 2.7 long, 2.1 wide, evenly setose; three pairs of small sigilla (Fig. 9E). Maxillae with 29 (left) and 38 (right) (Fig. 9E, F).

Legs: setose and diffusely spinose; tarsi I, II ventrally swollen; tarsi and distal metatarsi I, II weakly scopulate (Fig. 9G–I). Paired tarsal claws: leg I p7 (6 large, 1 small), r9 (8 large, 1 small); leg II p7 (6 large 1 small), r7 (6 large, 1 small); leg III p6 (6 large), r6 (6 large); leg IV p8 (8 large), r9 (6 large, 3 small).

Spination: Leg I tibia with single prolateral macroseta (Fig. 9G–I), r2; metatarsus p1, r1. Leg II tibia p1 r1; metatarsus p1 r2; legs III and IV setose and diffusely spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I> II > III. Leg I: femur 4.3, patella 2.0, tibia 3.2, metatarsus 2.7, tarsus 1.8, total = 14.0. Leg II: femur 4.1, patella 2.0, tibia 2.9, metatarsus 2.7, tarsus 2.0, total = 13.7. Leg III: femur 3.4, patella 1.5, tibia 2.2, metatarsus 2.7, tarsus 1.8, total = 11.6 Leg IV: femur 4.6, patella 2.1, tibia 3.8, metatarsus 4.0, tarsus 2.3, total = 16.8. Pedipalp: femur 2.3, patella 1.3, tibia 2.4, tarsus 1.2, total = 7.2.

Pedipalp: All segments without spines; patella with thickened ventral setae distally; tibia short and swollen, RTA

short and pointed, covered in long setae and short, dense spinules, forming a line about as wide as apophysis and covering about two-thirds of the distance to distal tibia, becoming sparser towards distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, slightly twisted at end and without flanged tip, about twice length of bulb; cymbium covered in rows of short, sparse spinules, becoming longer closer to distal edge (Fig. 9J–L).

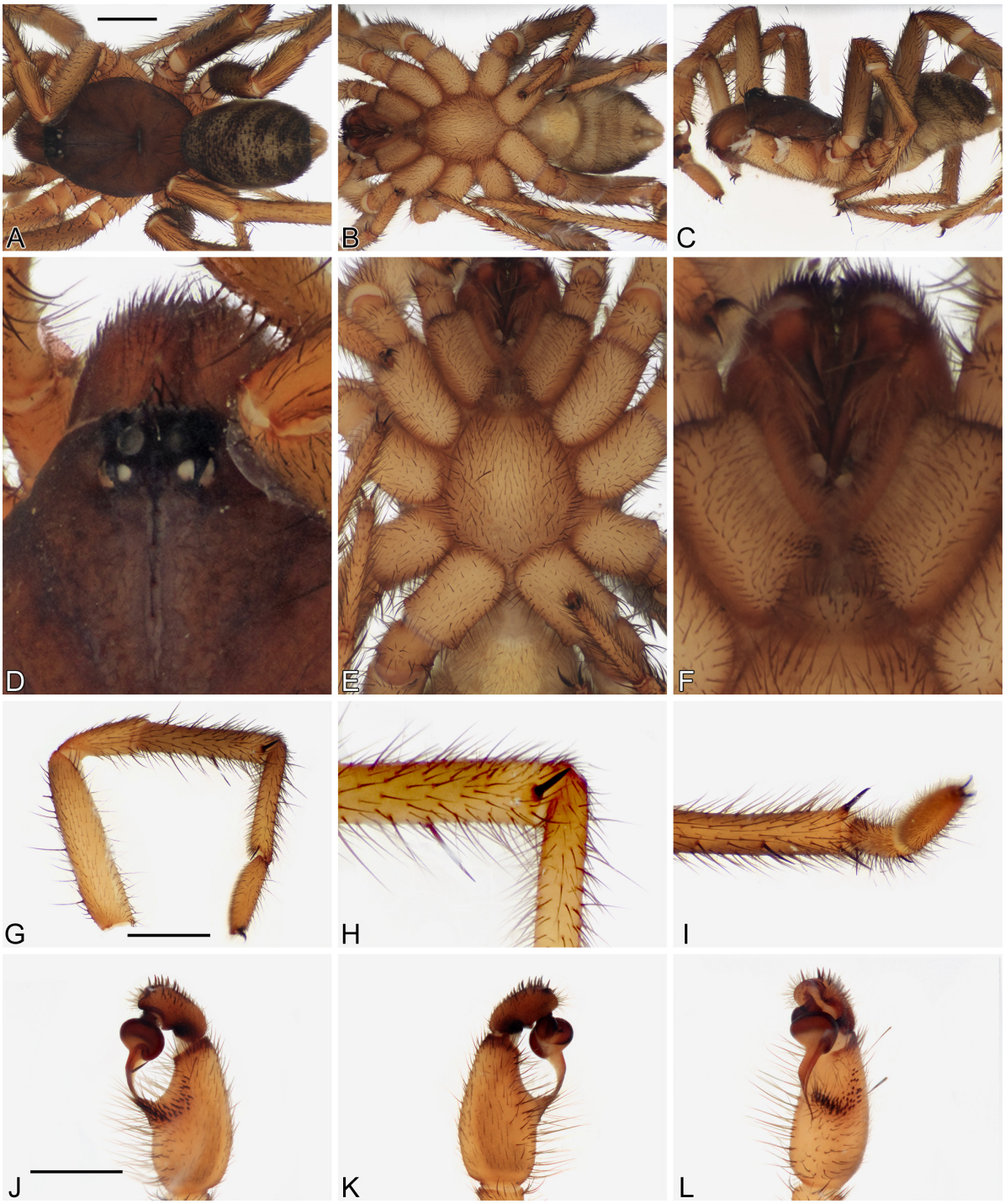


FIGURE 9. *Blakistonia birksi* **sp. n.**, holotype male (SAM NN29003): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macroseta, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G, J).

FIGURE 10. *Blakistonia birksi* **sp. n.**, paratype female (SAM NN29618): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 2 mm (G).

Abdomen: Setose, oval, dorsal sigilla not evident; 4.2 long, 2.7 wide (Fig. 9A).

Variation (n=13): Carapace 3.8–4.6 long, 3.1–3.6 wide, labial cuspules 0–5. Spination: Leg I: tibia p0–2, r1–2; metatarsus p0–1, r1–2. Leg II: tibia p0–1, r1–3; metatarsus p0–1, r1–4.

Paratype female (SAM NN29618). Medium-sized idiopid spider (total length 15.4).

Colour (in ethanol; Fig. 10A–I): Legs, pedipalp and carapace dark golden-brown, slightly darker on both sides of caput and around margins (Fig. 10A); sternum golden-brown, darker towards anterior and lateral margins; labium and maxillae golden-brown, chelicerae red-brown (Fig. 10E, F); abdomen brown with distinct pattern of seven mottled chevrons (Fig. 10A, C).

Cephalothorax: Carapace 7.0 long, 5.2 wide, 5.2 high, 1.3 times longer than wide; oval (Fig. 10A); caput high, with ocular area raised (Fig. 10C); cuticle uniformly smooth; fovea procurved; one row of thickened setae between fovea and eye group; small, fine setae also scattered very sparsely across carapace, slightly more concentrated on caput, and form fine, indistinct fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 10D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.2 wide, 0.8 long, 0.2 of

carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.1; posterior eye row slightly recurved; AME slightly smaller than ALE and separated by *ca*. 1.5 diameter of ALE; ALE and PLE separated by *ca*. twice diameter of ALE; PME pale, about 0.67 of PLE, and separated from PLE by just less than its own diameter (Fig. 10D). Labium with *ca*. 11 cuspules (Fig. 10F). Sternum 4.1 long, 2.8 wide, moderately setose with setae becoming denser and longer around margins; 2 pairs of faint sigilla evident (Fig. 10E). Maxillae with 11 (left) and 15 (right) cuspules, (Fig. 5E, F).

Legs: moderately setose and diffusely spinose; femora I, II, and pedipalp laterally bowed; tarsi and distal two-thirds of metatarsi I, II, and palpal tarsus scopulate ventrally and laterally (Fig. 10G, H). Paired tarsal claws: leg I p2 (1 large, 1 small) r0; leg II p2 (1 large, 1 small), r2 (1 large, 1 small); leg III p0, r0; right leg IV p2 (2 large), r0. Pedipalp claw with 2 large teeth.

Spination: Leg I: tibia p3, r4; metatarsus p2, r5; tarsus p1 r3. Leg II: tibia p2, r4; metatarsus p3, r7; tarsus p1, r3. Leg III: patella p3; tibia p6, metatarsus p7, r6; tarsus with ventral patch of 9 short spines. Right leg IV: metatarsus p2, r1; tarsus with ventral 16 short spines ventrally. Pedipalp: tibia p6, r6; tarsus p3, r3.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I femur 3.7, patella 2.5, tibia 2.1, metatarsus 1.7, tarsus 1.3, total = 11.3. Leg II femur 3.3, patella 2.3, tibia 2.0, metatarsus 2.6, tarsus 1.3, total = 11.5. Leg III femur 2.9, patella 2.1, tibia 1.8, metatarsus 2.8, tarsus 1.6, total = 11.2. Leg IV (right): femur 4.1, patella 2.9, tibia 3.6, metatarsus 3.1, tarsus 2.0, total = 15.7. Pedipalp: femur 3.1, patella 1.29 tibia 1.8, tarsus 2.2, total = 9.1.

Abdomen: Setose, oval, one pair of indistinct, unsclerotised dorsal sigilla; 8.4 long, 6.3 wide (Fig. 10A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, oval-shaped, covered in opaque mottled brown nodules, becoming more concentrated in median band.

Variation (n=2) Carapace 6.9–7.0 long, 5.2–5.6 wide, 3–11 labial cuspules. Spination: Leg I: tibia p3, r4; metatarsus p2–4, r4; tarsus p1, r2–3. Leg II: tibia p1–2, r4; metatarsus p3–4, r5–7; tarsus p2, r3–5. Leg III: patella p3, tibia p0–1, metatarsus p5–6, r4–6; tarsus with 8–9 spines ventrally. Leg IV: metatarsus p2–9, r1–2. Pedipalp: tibia p6, r5–5; tarsus p3–4, r 3–4.

Etymology. This species is named in honour of Nicholas Birks, for his generous efforts in collecting and photographing specimens for this project.

Distribution. *Blakistonia birksi* is known from Ngarkat Conservation Park in south-eastern South Australia, Cleland Conservation Park and Mark Oliphant Conservation Park in the Mount Lofty Ranges, and the Grampians National Park in Victoria (Fig. 32).

Remarks. The sandy habitat of Ngarkat Conservation Park is unusual for the genus, as most species of *Blakistonia* generally prefer to build burrows in clay. This species is further unusual in that it exists in two locations in the Mount Lofty Ranges, which have historically been well collected; however, this species was not found in the SAM collection. This could potentially be due to the cryptic nature and small size of the burrow lids.

***Blakistonia carnarvon*, sp. n.**
(Fig. 11A–L)

Type material. AUSTRALIA: *Queensland:* Holotype male, Carnarvon Station, 24°49'12.00"S, 147°44'31.20"E, 24 November–13 December 2010, malaise trap, A. Zwick (QMB S96934).

Diagnosis. Males of *B. carnarvon* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 11G–I); from those of *B. hortoni*, *B. plata*, *B. birksi*, and *B. newtoni* by the presence of two, rather than one, prolateral macrosetae on tibia I (Fig. 11G–I); from those of *B. parva* and *B. maryae* by an eye group that is wider than long (Fig. 11D); from those of *B. olea* and *B. tariae* by the combined presence of a distinctive ring of dark colour around the edge of the carapace (Fig. 11A) and the AME with a similar or smaller diameter to the ALE (Fig. 11D); and from those of *B. raveni* by an embolus that narrows and tapers before the midpoint (Fig. 11J–L). Females are unknown.

Description. *Holotype male* (QMB S96934). Small idiopid spider (total length 9.2).

Colour (in ethanol; Fig. 11A–C): Legs, pedipalp and carapace medium chestnut-brown, distinctly darker around lateral margins (Fig. 11A); labium, maxillae and sternum lighter medium brown, paler towards margins; chelicerae slightly darker (Fig. 11E, F); abdomen greyish-brown with distinct pattern of seven dark brown chevrons (Fig. 11A, C).

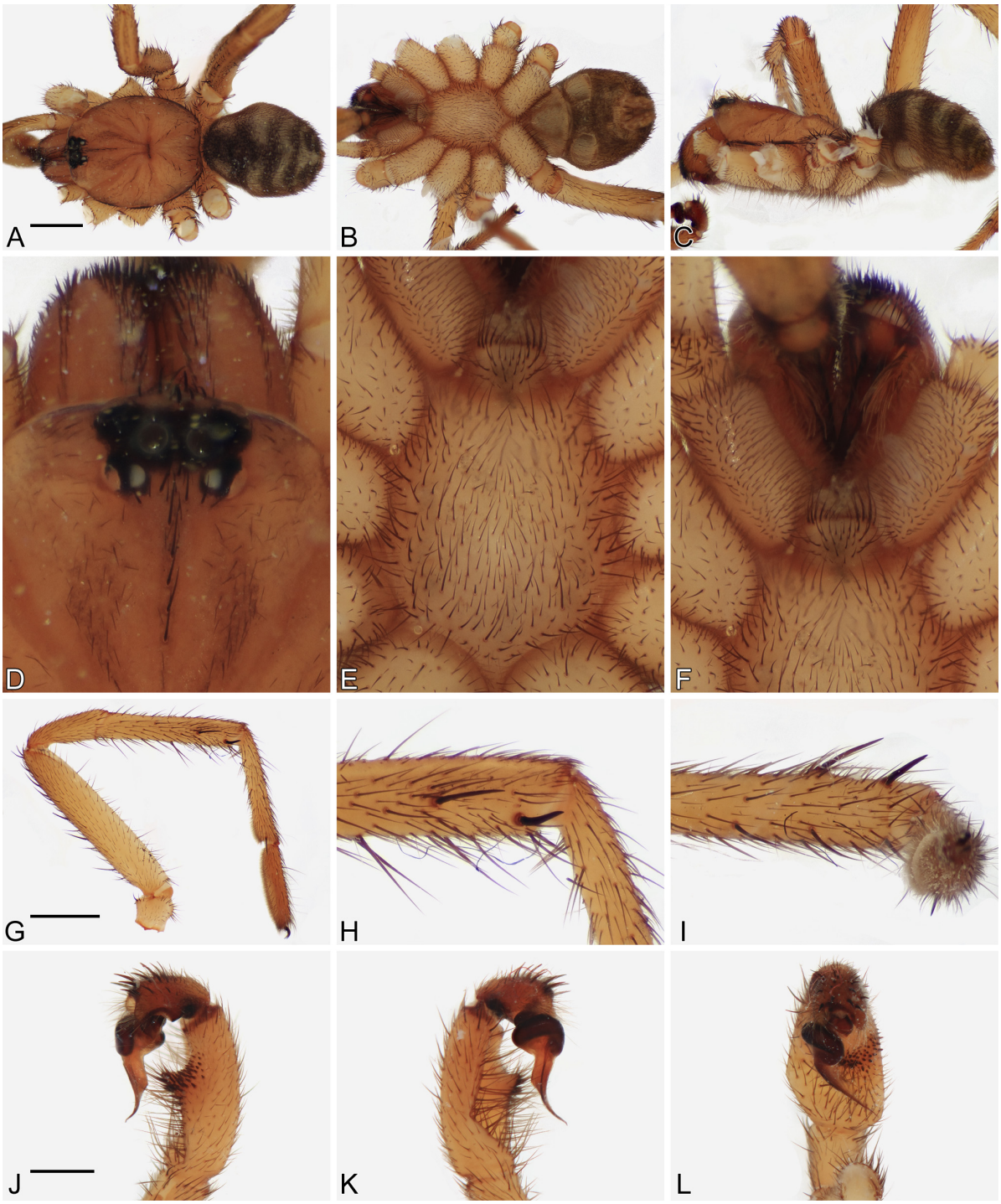


FIGURE 11. *Blakistonia carnarvon* **sp. n.**, holotype male (QMB S96934). A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macrosetae, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G).

Cephalothorax: Carapace 4.7 long, 4.2 wide, 3.4 high, 1.1 times longer than wide; oval (Fig. 11A), caput low, ocular area raised (Fig. 11C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of setae between fovea and eye group, and radiating outwards from fovea, with two distinctive patches of short, fine setae on sides of caput, carapace setae concentrated and form fringe on lateral margins; median clump of

thickened setae on clypeus (Fig. 11D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.3 wide, 2.2 long, 0.3 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 0.9; posterior eye row slightly recurved; AME slightly smaller than ALE and separated by less than AME; PLE about one-third the size of ALE and separated by about ALE diameter; PME pale, about two-thirds of PLE, and separated from PLE by less than its own diameter (Fig. 11D). Labium without cuspules (Fig. 11F). Sternum 2.2 long, 3.3 wide, evenly setose. Maxillae without cuspules (Fig. 11E, F).

Legs: diffusely setose and spinose; tarsi I, II slightly ventrally swollen; tarsi and distal metatarsi I, II scopulate (Fig. 11G–I). Paired tarsal claws: leg I p5 (5 large) r5 (5 large); leg II p4 (4 large), r6 (5 large, 1 small); leg III p3 (3 large), r2 (2 large); leg IV p5 (2 large, 3 small, r3 2 large, 3 small).

Spination: Tibia I with two prolateral macrosetae (Fig. 11G–I). All legs diffusely setose and spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 5.2, patella 2.4, tibia 4.1, metatarsus 5.3, tarsus 2.2, total = 19.2. Leg II: femur 5.0, patella 2.4, tibia 3.6, metatarsus 3.2, tarsus 2.2, total = 16.4. Leg III: femur 4.1, patella 1.9, tibia 3.0, metatarsus 3.7, tarsus 2.3, total = 15.0. Leg IV: femur 5.5, patella 2.3, tibia 4.8, metatarsus 5.1, tarsus 2.9, total = 20.6. Pedipalp: femur 2.8, patella 1.5, tibia 2.5, tarsus 1.2, total = 8.0.

Pedipalp: Femur with dorsal spines, patella with thickened ventral setae; tibia short and swollen, RTA short and pointed, covered in short, dense spinules for *ca.* half of distance between base of apophysis and distal tibia, becoming more sparse toward distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, just over length of bulb; cymbium with rows of spnules, becoming longer and denser distally (Fig. 11J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 4.5 long, 3.2 wide (Fig. 11A).

Variation: None.

Etymology. The specific name is a noun in apposition that refers to the type locality at Carnarvon Station Reserve, Queensland.

Distribution. This species is known only from Carnarvon Station, in central Queensland (Fig. 34).

Remarks. The specimen was caught in a Malaise trap in brigalow (*Acacia harpophylla*) woodland on a grassy hillside at Carnarvon Station Reserve, which is one of the largest remnants of native vegetation in inland Queensland.

***Blakistonia emmottorum*, sp. n.**
(Fig. 12A–L)

Type material. ***AUSTRALIA: Queensland****:* Holotype male, Noonbah Station, north of Jundah, 24°07'S, 143°11'E, 28 August 1993, hand collected, A.J. Emmott (QMB S29540).

Diagnosis. Males of *B. emmottorum* can be distinguished from those of *B. maryae*, *B. plata*, *B birksi*, *B. newtoni*, *B. hortoni*, *B. parva*, *B. maryae*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 12G–I); and from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. gemmelli*, and *B. aurea* by the subquadrate (wider than long) eye group (Fig. 12D). Females are unknown.

Description. *Holotype male* (QMB S29540). Small idiopid spider (total length 6.0).

Colour (in ethanol; Fig. 12A–C): Carapace, legs and pedipalp very pale yellow-brown, darker around caput (Fig. 12A); sternum, labium and maxillae lighter golden yellow; chelicerae slightly darker yellow-brown (Fig. 12E, F); abdomen even paler yellowish brown with faint chevron pattern posteriorly (Fig. 12A, C.)

Cephalothorax: Carapace 3.2 long, 2.5 wide, 2.0 high, 1.3 times longer than wide; oval (Fig. 12A), caput low, ocular area raised (Fig. 12C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea slightly procurved; row of setae between fovea and eye group; carapace sparsely setose, with indistinct lines of setae radiating outwards from fovea, concentrated and form fringe on lateral margins; median clump of thickened setae on clypeus (Fig. 12D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.7 wide, 0.4 long, 0.3 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 0.9; posterior eye row straight; AME about two-thirds of ALE and separated by less than AME diameter; PLE two-thirds size of ALE and separated by about ALE diameter; PME pale, just over half size of PLE, and separated from PLE by less than its own diameter (Fig. 12D). Labium without cuspules (Fig. 12F). Sternum 2.0 long, 1.3 wide, evenly setose. Maxillae with *ca*. 6 cuspules on both sides (Fig. 12E, F).

Legs: diffusely setose; tarsi I, II ventrally swollen; tarsi I, II weakly scopulate (Fig. 12G–I). Paired tarsal claws: leg I p4 (2 large, 2 small) r4 (2 large, 2 small); leg II p5 (2 large, 3 small), r4 (2 large, 2 small); leg III p4 (3 large, 1 small), r4 (2 large, 2 small); leg IV p8 (7 large, 1 small, r4 (2 large, 2 small).

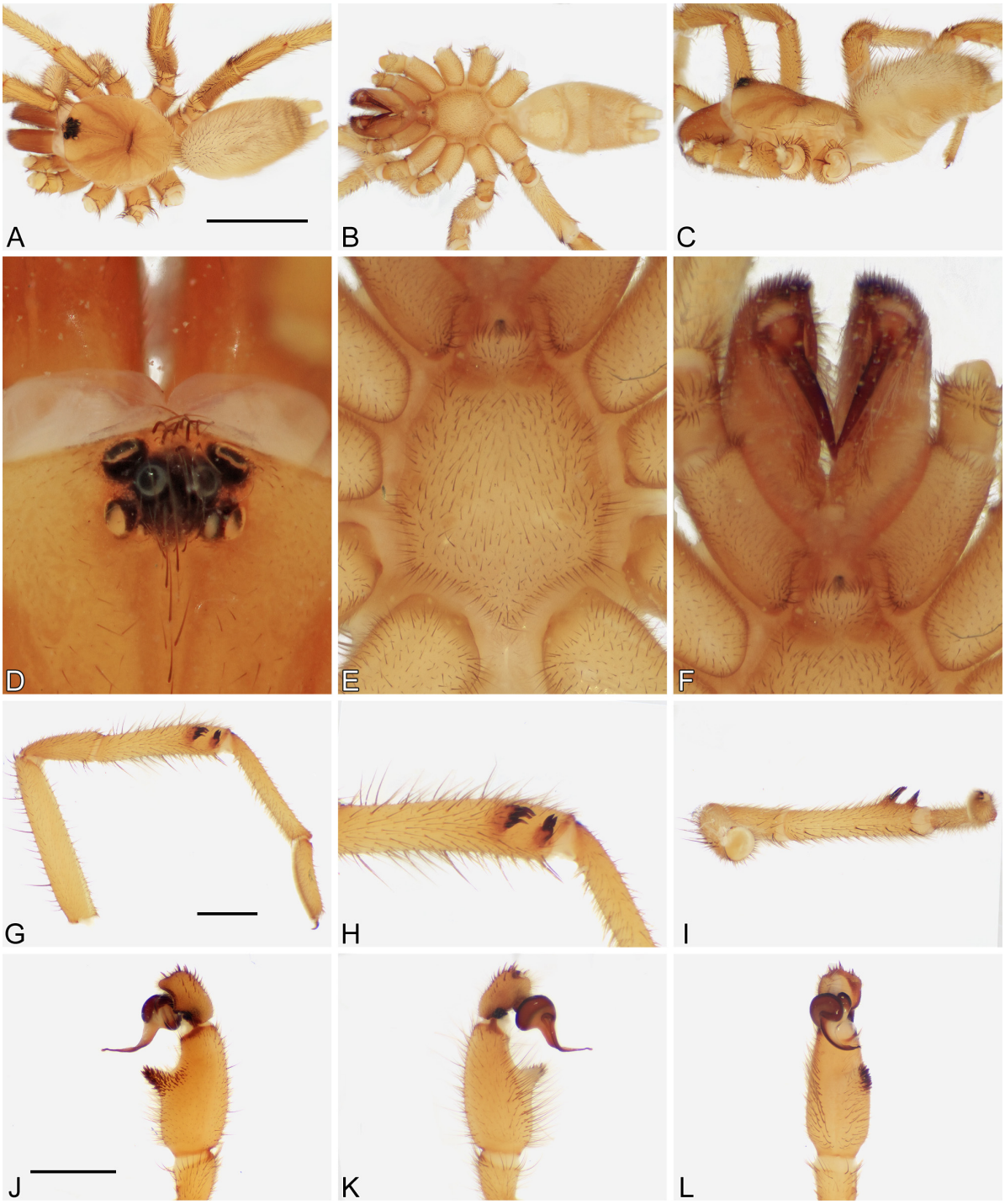


FIGURE 12. *Blakistonia emmottorum* **sp. n.**, holotype male (QMB S29540): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, clasping spurs, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 5 mm (A), 2 mm (G, J).

Spination: Tibia I with prolateral clasping spurs, distal-most spur with 2 terminal peg-like macrosetae, proximal-most with 3 terminal peg-like macrosetae (Fig. 12G–I). Leg II: metatarsus p1, r5. Leg III: tibia p1, r1; metatarsus p4, r10; tarsus p1, r1. Leg IV: metatarsus p11, r7; tarsus p3, r4.

Leg and pedipalp measurements: Length of legs IV > II > I > III. Leg I: femur 3.3, patella 1.5, tibia 2.5, metatarsus 2.2, tarsus 1.5, total = 11.0. Leg II: femur 3.0, patella 1.0, tibia 2.2, metatarsus 3.0, tarsus 1.1, total = 10.3. Leg III: femur 2.3, patella 1.0, tibia 2.0, metatarsus 2.3, tarsus 1.4, total = 9.0. Leg IV (right): femur 3.8, patella 1.4, tibia 3.4, metatarsus 3.6, tarsus 1.9, total = 14.1. Pedipalp: femur 1.7, patella 1.0, tibia 1.6, tarsus 0.8, total = 5.1.

Pedipalp: Femur with thickened dorsal setae; tibia short and swollen, RTA short, stout, pointed, covered in short, dense spinules that continue for *ca*. half distance between base of apophysis and distal tibia, becoming more sparse toward distal tibia; long, erect setae ventrally on tibia; bulb uniform, globular; embolus simple, slender, tapering, twisted, slightly longer than bulb; cymbium with sparse rows of short spinules, becoming longer and denser distally (Fig. 12J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 3.0 long, 2.0 wide (Fig. 12A).

Variation: None.

Etymology. This species is named in honour of Angus and Karen Emmott, the owners of Noonbah Station and the collectors of the only known specimen of this species.

Distribution. *Blakistonia emmottorum* is known only from Noonbah Station in central Queensland (Fig. 34).

Remarks. The specimen was found in a passage between houses at Noonbah Station, in August during rain.

***Blakistonia gemmelli*, sp. n.**
(Fig. 13A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Weetootla Well, Flinders Ranges, 30°30'00"S, 139°15'00"E, 9 May 1989, pitfall trap, D. Hirst (SAM NN20097). Paratypes: 1 male, same data (SAM NN20098); 1 male, same data except 30°29'00"S, 139°13'00"E, 8 May 1989.

Diagnosis. Males of *B. gemmelli* can be distinguished from those of *B. maryae*, *B. plata*, *B. birksi*, *B. newtoni*, *B. hortoni*, *B. parva*, *B. maryae*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 13G–I); from those of *B. bella* by the lack of a dorsal abdominal cardiac stripe (Fig 13A); from those of *B. pidax* by the thick spine-like spinules on the cymbium (Fig. 13J–L); from those of *B. tunstilli* by the spinules on the palpal tibia being similar in size or only slightly shorter compared to those on the RTA (Fig. 13J, L); from those of *B. emmottorum* by the square eye group (Fig. 13D); and from those of *B. aurea* by the short and stout RTA, with the field of RTA spinules extending only slightly onto the tibia (Fig. 13J), and by the strong abdominal pattern (Fig 13A). Females are unknown.

Description. *Holotype male* (SAM NN20097)**.** Small idiopid spider (total length 7.8).

Colour (in ethanol; Fig. 13A–C): Carapace, legs and pedipalp uniform pale golden orange-brown (Fig. 13A); sternum, labium and maxillae very similar; chelicerae darker golden-brown (Fig. 13E, F); abdomen same golden orange-brown with pattern of seven mottled chevrons; first chevron large and triangular second chevron about half width of first, remaining five chevrons split in centre, not continuous (Fig. 13A, C).

Cephalothorax: Carapace 3.6 long, 2.9 wide, 2.5 high, 1.2 times longer than wide; oval (Fig. 13A), caput low, ocular area raised (Fig. 13C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of sparse setae between fovea and eye group; carapace otherwise with few smaller fine setae, concentrated and form fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 13D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.1 wide, 0.7 long, 0.4 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 0.9; posterior eye row slightly procurved; AME only slightly smaller than ALE and separated by about ALE diameter; ALE and PLE separated by about twice PLE diameter; PME pale, less than half of AME and only slightly smaller than PLE, and separated from PLE by less than its own diameter (Fig 13D). Labium without cuspules (Fig. 13F). Sternum 1.9 long, 1.7 wide, evenly setose (Fig. 13E). Maxillae with 6 (left) and 4 (right) cuspules (Fig. 13E, F).

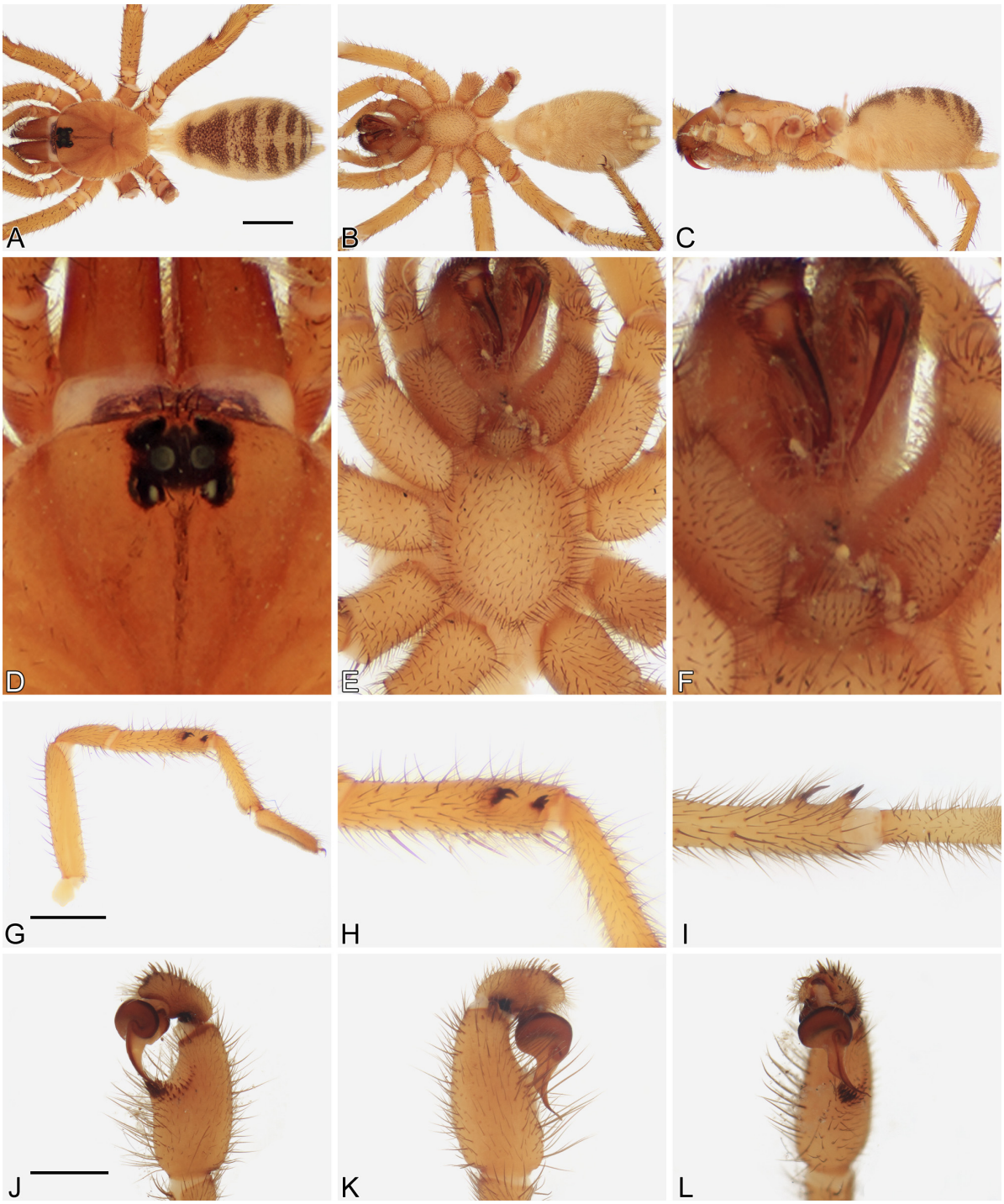


FIGURE 13. *Blakistonia gemmelli* **sp. n.**, holotype male (SAM NN20097): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, mating spur, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Legs: setose and spinose; tarsi I, II ventrally swollen; tarsi and distal metatarsi I, II weakly scopulate only ventrally (Fig. 13G–I). Paired tarsal claws: leg I p5 (2 large, 3 small) r5 (3 large, 2 small); leg II p2 (2 large), r2 (2 large); leg III p4 (2 large, 2 small), r5 (1 large, 4 small); leg IV p3 (3 large), r4 (3 large, 1 small).

Spination: Tibia I with prolateral clasping spurs, both spurs with 2 terminal peg-like macrosetae (Fig. 13G–I), r2; metatarsus p1. Leg II: tibia p1, r4; metatarsus p1, r5. Leg III: (right) patella r3; tibia p3, r1; metatarsus p7, r7; tarsus p4. Leg IV: tibia p3, r4; metatarsus p4, r6; tarsus p4, r6.

Leg and pedipalp measurements: Length of legs IV > II > I > III. Leg I: femur 3.1, patella 1.5, tibia 2.3, metatarsus 2.0, tarsus 1.5, total = 10.4. Leg II: femur 3.3, patella 1.6, tibia 2.4, metatarsus 2.1, tarsus 1.5, total = 10.9. Leg III: femur 2.8, patella 1.2, tibia 2.0, metatarsus 2.2, tarsus 1.6, total = 9.8. Leg IV (right): femur 3.6, patella 1.6, tibia 3.5, metatarsus 3.2, tarsus 2.0, total = 13.9. Pedipalp: femur 1.9, patella 0.7, tibia 1.7, tarsus 0.9, total = 5.2.

Pedipalp: Patella with thickened ventral setae; tibia short, swollen, RTA very short,pointed, with several setae and covered in short, dense spinules from just over half of the distance between base of apophysis and distal tibia, becoming very sparse towards dstal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, only slightly longer than length of bulb; cymbium covered in rows of short spinules, becoming longer closer to distal edge (Fig. 13J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 4.2 long, 2.9 wide (Fig. 13A).

Variation (n=3): Carapace 3.1–3.6 long, 2.8–2.9 wide, no labial cuspules. Spination: Leg I: tibia r2–5; metatarsus p0–1, r0–3. Leg II: tibia p1–2, r3–4; metatarsus p1–2, r 3–5; tarsus r0–1. Leg III: patella p3; tibia p1–3, r2–3; metatarsus p3–8, r6–8; tarsus p2–4, r0–3. Leg IV: tibia p0–3, r0–4; metatarsus p4–11, r3–6; tarsus p3–8, r2–6.

Etymology. This species is named in honour of Mike Gemmell, for his long-term interest in trapdoor spiders.

Distribution. *Blakistonia gemmelli* is known only from Weetootla Well, in the Flinders Ranges (Fig. 31).

Remarks. One specimen of *B. aurea* has also been found at Weetootla Well (SAM NN20096).

***Blakistonia hortoni*, sp. n.**
(Fig. 14A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Mount Crawford Forest Reserve, Mount Lofty Ranges, 34°42'S, 138°58'E, 27 May–9 September 1988, pitfall, R. Tuckwell (SAM NN20090). Paratypes: 8 males, same data (SAM NN20089, NN20091, NN20092, NN20095, NN20100, NN20101, NN20102, NN20103).

Other material examined. AUSTRALIA: ***South Australia:*** 1 male, Padthaway Conservation Park, 36°36'S, 140°31'E, May 1982, pitfall, B. Guerin (SAM NN20076).

Diagnosis. Males of *B. hortoni* can be distinguished from *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 14G–I); from *B. parva*, *B. maryae*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the presence of one, rather than two, prolateral macroseta on tibia I (Fig. 14G–I); from those of *B. birksi* and *B. plata* by the square eye group (Fig. 14D); and from those of *B. newtoni* and *B. maryae* by the field of spinules on the palpal tibia being broad and not in a rounded crescent-shape (Fig. 14J). Females are unknown.

Description. *Holotype male* (SAM NN20090)**.** Medium idiopid spider (total length 10.0).

Colour (in ethanol; Fig. 14A–C): Carapace uniform pale golden orange-brown (Fig. 14A); sternum, labium and maxillae very similar, chelicerae slightly darker red-brown (Fig. 14E, F); abdomen same golden orange-brown with pattern of seven mottled chevrons, dark, with darker mottling also between chevrons (Fig. 14A, C); legs and pedipalp same colour as cephalothorax (Fig. 14G–L).

Cephalothorax: Carapace 4.9 long, 3.9 wide, 3.3 high, 1.3 times longer than wide; oval (Fig. 14A), caput moderately raised, ocular area raised (Fig. 14C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of thick setae between fovea and eye group; carapace quite setose, with smaller fine setae distributed evenly across carapace, concentrated and forming fringe around lateral margins; clump of thickened setae on clypeus (Fig. 14D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.9 wide, 0.8 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–APLE/ALE–ALE ratio 1.0; posterior eye row slightly procurved; AME approximately half the size of ALE and separated by about the diameter of AME; ALE and PLE separated by about twice the diameter of PLE; PME pale, similar in size to AME and about two-thirds size of PLE, and separated from PLE by about its own diameter (Fig. 14D). Labium with 5 cuspules (Fig. 14F). Sternum 2.8 long, 2.1 wide, evenly setose (Fig. 14E). Maxillae with *ca.* 20 cuspules on both sides (Fig. 14E, F).

FIGURE 14. *Blakistonia hortoni* **sp. n.**, holotype male (SAM NN20090): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macroseta, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G, J).

Legs: setose and spinose; tarsi I, II ventrally swollen; tarsi and distal metatarsi I, II weakly scopulate (Fig. 14G–I). Paired tarsal claws: leg I p7 (7 large) r6 (6 large); leg II p6 (6 large), r6 (6 large); leg III p6 (2 large, 4 small), r4 (1 large, 3 small); leg IV p5 (2 large, 3 small), r5 (2 large, 3 small).

Spination: Tibia I with single prolateral macroseta (Fig. 14G–I). All other legs heavily setose and spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 4.6, patella 2.3, tibia 3.3, metatarsus 3.3, tarsus 2.1, total = 15.6. Leg II: femur 4.4, patella 2.0, tibia 3.2, metatarsus 3.4, tarsus 2.1, total = 15.1. Leg III: femur 3.6, patella 1.8, tibia 2.6, metatarsus 3.2, tarsus 2.2, total = 13.4. Leg IV: femur 4.4, patella 2.2, tibia 4.5, metatarsus 4.4, tarsus 2.6, total = 18.1. Pedipalp: femur 2.7, patella 1.3, tibia 2.5, tarsus 1.1, total = 7.6.

Pedipalp: Patella with thickened ventral setae; tibia short and swollen, RTA short, pointed, with thick clump of setae on tip, and covered in short, dense spinules for two-thirds distance between base of apophysis and distal tibia, becoming only slightly sparser towards distal dibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, just under twice the length of bulb; cymbium covered in rows of short spinules, becoming longer closer to distal edge (Fig. 14J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 5.1 long, 3.2 wide (Fig. 14A).

Variation (n=10): Carapace 3.0–5.0 long, 3.0–3.3 wide, 5 labial cuspules.

Etymology. This species is named in honour of Benjamin Horton, for his commitment to wildlife education and conservation, and for his efforts in saving the lives of countless animals during the Sampson Flat bushfires of 2015.

Distribution. *Blakistonia hortoni* is known only from Mount Crawford Conservation Park and Padthaway Conservation Park in the Mount Lofty Ranges (Fig. 31).

Remarks. Further specimens of this species, including females, could not be located at the type locality by one of the authors (SEH). Mount Crawford is now mostly covered in plantation forests and is quite sandy, which is an unusual habitat for *Blakistonia*. *Blakistonia aurea* is also found in roadside banks just outside the forest reserve, but has not been found within the reserve itself.

***Blakistonia mainae*, sp. n.**
(Figs 15A–I, 16A–F)

Type material. AUSTRALIA: ***Western Australia:*** Holotype female, Mount Ragged, Cape Arid National Park, 33°26'47"S, 123°28'15"E, 27 August 2014, hand collected from burrows, S.E. Harrison, M.S. Harvey (WAM T141137^{DNA}). Paratypes**:** 1 female, same data except 33°26'43"S, 123°28'07"E (WAM T141136^{DNA}); 1 female, same data except 33°26'44"S, 123°28'08"E (WAM T141138^{DNA}).

Other material examined. AUSTRALIA: ***Western Australia:*** 1 male (in fragments), Mount Ragged, Cape Arid National Park, 33°27'S, 123°28'E, 2 November 1986, hand collected from redback spider web, B. Main (WAM T141143).

Diagnosis. Males of *B. mainae* can be distinguished from those of *B. maryae*, *B. plata*, *B birksi*, *B. newtoni*, *B. hortoni*, *B. parva*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni*, by the prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 16B–C); and from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the presence of four thick, evenly spaced setae between the eye group and the fovea (16A). Females of *B. mainae* can be distinguished from those of other species by the book lungs being brown or dark brown, in contrast to the paler abdomen (Fig. 15C), and also by the presence of four thick, evenly spaced setae between the eye group and fovea (Fig. 15A, D).

All life stages of *B. mainae* can also be distinguished from those of other species with sequence data by the following nucleotide substitutions (*n*=3 specimens): G(132), A(216), C(300), A(453), A(482), T(507); and by the following unique motifs: TG(42–43), TA(66–67), AT(90–91).

Description. *Holotype female* (WAM T141137) Medium-sized idiopid spider (total length 14.6).

Colour (in ethanol; Fig. 15A–C): Carapace, legs and pedipalp medium to dark golden-brown, carapace slightly darker around fovea (Fig. 15A); sternum medium golden-brown, darker towards anterior and lateral margins; labium and maxillae golden-brown, chelicerae dark brown (Fig. 15E, F); abdomen grey-brown with 7 chevrons of uniform width spaced over length of abdomen, becoming more closely spaced towards posterior abdomen; anterior-most chevrons connected by medial patch (Fig. 15A, C).

Cephalothorax: Carapace 6.7 long, 4.9 wide, 5.5 high, 1.1 times longer than wide; oval (Fig. 15A), caput high, ocular area very slightly raised (Fig. 15C); cuticle uniformly smooth; fovea procurved; four prominent, evenly

spaced setae located between fovea and eye area, cluster of setae directly posterior to eye areas, and very small, fine setae also scattered across carapace, forming indistinct fringe around lateral margins; median clump of thickened setae on clypeus. Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.1 wide, 1 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row straight; AME *ca.* half size of ALE and separated by about diameter of ALE; ALE equal in size to PLE, and separated by their diameter; PME pale, *ca*. 0.25 of PLE, and separated from PLE by less than its own diameter (Fig. 15D). Labium with two cuspules (Fig. 15F). Sternum 4.1 long, 2.9 wide, moderately setose with setae becoming denser and longer around margins; one pair of sigilla located *ca*. halfway down abdomen, and separated from lateral margins of abdomen by about their own diameter (Fig. 15E). Maxillae with *ca*. 30 cuspules on both sides (Fig. 15E, F).

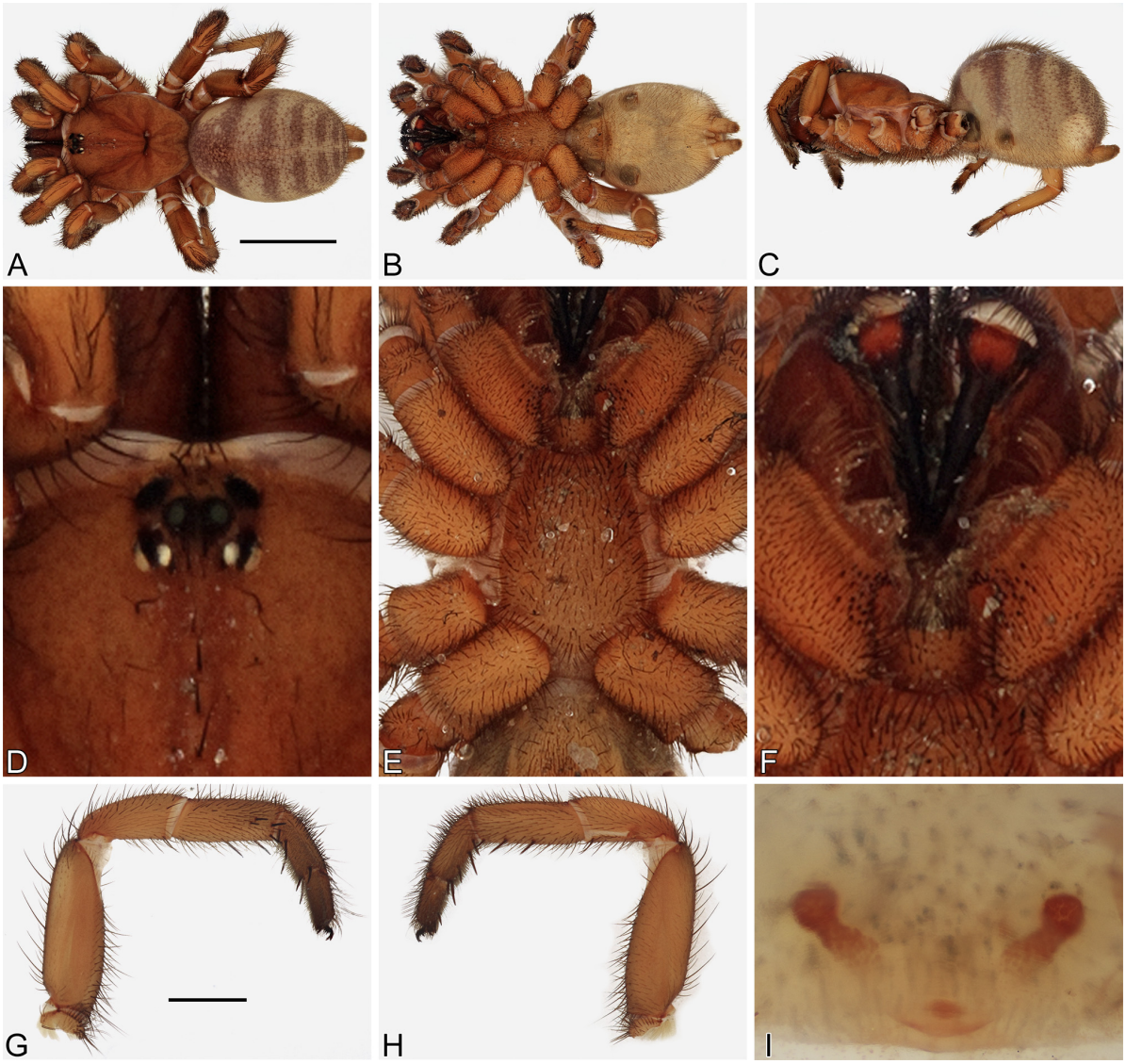


FIGURE 15. *Blakistonia mainae* **sp. n.**, holotype female (WAM T141137): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 2 mm (G).

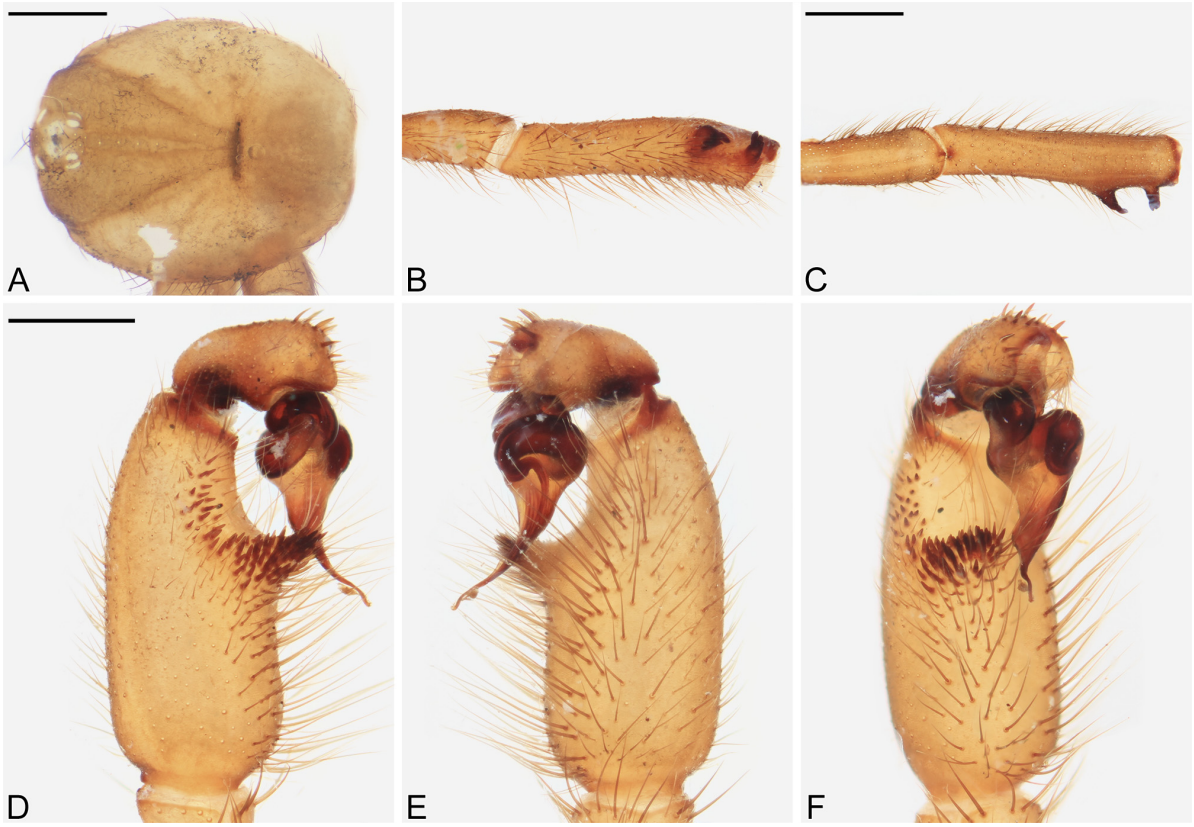


FIGURE 16. *Blakistonia mainae* **sp. n.**, male (WAM T141143): A, carapace, dorsal view; B, left leg I, clasping spurs, prolateral view; C, left leg I, dorsal view; D, right pedipalp, prolateral view; E, left pedipalp, retrolateral view; F, left pedipalp, proventral view. Scale bars = 2 mm (A, B), 1 mm (D).

Legs: moderately setose and spinose, with exception of retrolateral leg IV, which is mostly asetose; distinct erect setae on metatarsi and distal tibiae I, II; femora I, II, and pedipalp laterally bowed; tarsi and metatarsi I, II, and palpal tarsus heavily scopulate (Fig. 15G, H). Paired tarsal claws: p2 (2 large) r3 (1 large, 2 small); leg II p3 (2 large, 1 small), r2 (1 large, 1 small); right leg III p2 (2 large), r2 (1 large, 1 small); leg IV p2 (2 large) r3 (3 large); median claw without teeth. Pedipalp with 2 (1 large, 1 small) teeth.

Spination: Leg I: tibia p4, r3; metatarsus p4, r4; tarsus r2. Leg II: tibia p2, r3; metatarsus p4, r7; tarsus p1, r5. Right leg III: patella p3, metatarsus p5, r4; tarsus with 7 short spines ventrally. Leg IV: metatarsus p4, r1, tarsus with 7 short spines ventrally. Pedipalp: tibia p7, r6; tarsus p3, r3.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 3.7, patella 2.8, tibia 2.4, metatarsus 1.6, tarsus 1.3, total = 11.8. Leg II: femur 3.7, patella 2.5, tibia 2.2, metatarsus 1.7, tarsus 1.3, total = 11.4. Leg III: femur 3.1, patella 2.4, tibia 2.1, metatarsus 1.9, tarsus 1.4, total = 10.9. Leg IV (right): femur 4.2, patella 3.4, tibia 3.8, metatarsus 3.5, tarsus 1.8, total = 16.7. Pedipalp: femur 3.7, patella 2.2, tibia 2.3, tarsus 2.3, total = 10.4.

Abdomen: Setose, oval, one pair of unsclerotised dorsal sigilla evident; book lungs dark brownish-grey, distinctly darker than lateral abdomen; 8.2 long, 5.9 wide (Fig. 15A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, circular, covered in opaque mottled brown nodules, becoming more concentrated towards distal spermathecae (Fig. 15I).

Variation (n=3): Carapace 6.4–7.1 long, carapace 5.4–5.9 wide, 2–4 labial cuspules. Spination: leg I tibia p4, r3–4; metatarsus p4, r4–5; tarsus p0–1, r2–4. Leg II tibia p2, r2–3; metatarsus p3–4, r6–7; tarsus p1, r5–7. Leg III patella p3; metatarsus p3–5, r3–5; tarsus with 5–8 short spines ventrally. Leg IV metatarsus p4–6, r1; tarsus with 7–12 short spines ventrally. Pedipalp: tibia p7–9, tarsus r3–6.

Male (WAM T141143). Total size unknown.

Colour (in ethanol; Fig. 16A–F): Carapace, legs and pedipalp uniform pale golden orange-brown.

Cephalothorax: Carapace 5.8 long, 4.3 wide, 1.3 times longer than wide; oval (Fig. 16A), caput low, ocular area slightly raised; cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; four prominent setae located between fovea and eye area, cluster of setae also directly posterior to eye areas, and very small, fine setae also scattered across carapace, forming indistinct fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 16A). Eye group 0.8 wide, 1.0 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row slightly procurved; AME similar in size to ALE and separated by less than the diameter of AME; ALE and PLE separated by just over the diameter of PLE; PME oval, 0.75 of PLE, and separated from PLE by less than its own diameter (Fig. 16A).

Spination: Tibia I with prolateral clasping spurs, both spurs with 2 terminal peg-like macrosetae (Fig. 16B, C).

Pedipalp: Tibia short, swollen, RTA short and pointed, with thick clump of setae on tip, and covered in short, dense spinules almost to distal tibia, becoming sparser; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, twisted, and just under twice the length of bulb; cymbium covered in rows of short spinules, becoming longer distally (Fig. 16D–F).

Variation: None.

Etymology. This species is named in honour of Dr Barbara York Main, for first collecting *Blakistonia* specimens from Mount Ragged in 1986, and for her lifelong commitment to improving our knowledge of Australian trapdoor spiders.

Distribution. *Blakistonia mainae* is known only from Mount Ragged, Cape Arid National Park, Western Australia (Fig. 33).

Remarks. The burrows of *B. mainae* are round with a narrow hinge, and slightly indented (Fig. 2G). The male specimen on which this description was based was collected dead from a *Latrodectus* web and is incomplete. The female description is based on a complete specimen (WAM T141137) and also has molecular data available thus it has been designated as the holotype.

***Blakistonia maryae*, sp. n.**
(Fig. 17A–L)

Type material. AUSTRALIA: *South Australia:* Holotype male, South Middleback Ranges, 33°14'S, 137°07'E, 6 June 1984, pitfall trap, B. Guerin (SAM NN20077). Paratype: 1 male, South Middleback Ranges, 33°14'S, 137°07'E, 6 June 1984, pitfall trap, B. Guerin (SAM NN20075).

Other material examined. AUSTRALIA: *South Australia:* 1 female, Scrubby Peak, Gawler Ranges, 33°03'23"S, 136°19'40°0"E, 17–26 September 2007, dug up, SEG/DEH Survey 587 (SAM NN26663^{DNA}); 1 female, Kolay Hut, Gawler Ranges, 32°33'24"S, 135°35'20"E, 11 November 2013, dug up from bank, M. Rix, S.E. Harrison (SAM NN29604^{DNA}); 1 female, Tumby Bay, Eyre Peninsula, 34°22'27"S, 136°05'18"E, 1 May 2013, dug from grassy verge, S.E. Harrison, M. Harrison (SAM NN29565^{DNA}); 1 juvenile, same data (NN29566^{DNA}); 1 male, same data except 5 June 1984 (SAM NN20071); 3 males, Kimba, Eyre Peninsula, 32°29'40.9"S, 135°21'52.0"E, 25–28 November, from pitfall trap, Eyre Peninsula Survey (SAM NN26633–5).

Diagnosis. Males of *B. maryae* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli* and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 17G–I); from those of *B. plata*, *B. parva*, *B. birksi*, *B. olea*, *B. tariae*, *B. carnarvon*, and *B. raveni* by the square eye group (Fig. 17D); and from those of *B. newtoni* and *B. hortoni* by the field of spinules on the palpal tibia being relatively narrow and not in a rounded crescent shape (Fig. 17J, L). Females of *B. maryae* can be distinguished from those of *B. wingellina* and *B. nullarborensis* by having a square or slightly subquadrate eye group (Fig. 18D); from those of *B. bassi* and *B. mainae* by the combined absence of fine golden hairs on the carapace (Fig. 18A) and the absence of dark brown on the book lungs (in contrast to a paler abdomen) (Fig. 18C); from those of *B. birksi* by abdominal chevrons being dark golden-brown, with abdomen golden-brown between chevrons (as opposed to chevrons that are dark brown to almost black, with abdomen dark brown between chevrons (Fig. 18A); and from those of *B. aurea* by the absence of cuspules on the labium (Fig. 18F).

All life stages of *B. maryae* can also be distinguished from those of other species with sequence data by the following nucleotide substitutions (n=4 specimens): C(276), G(354); and by the following unique motifs: GAA(482–484).

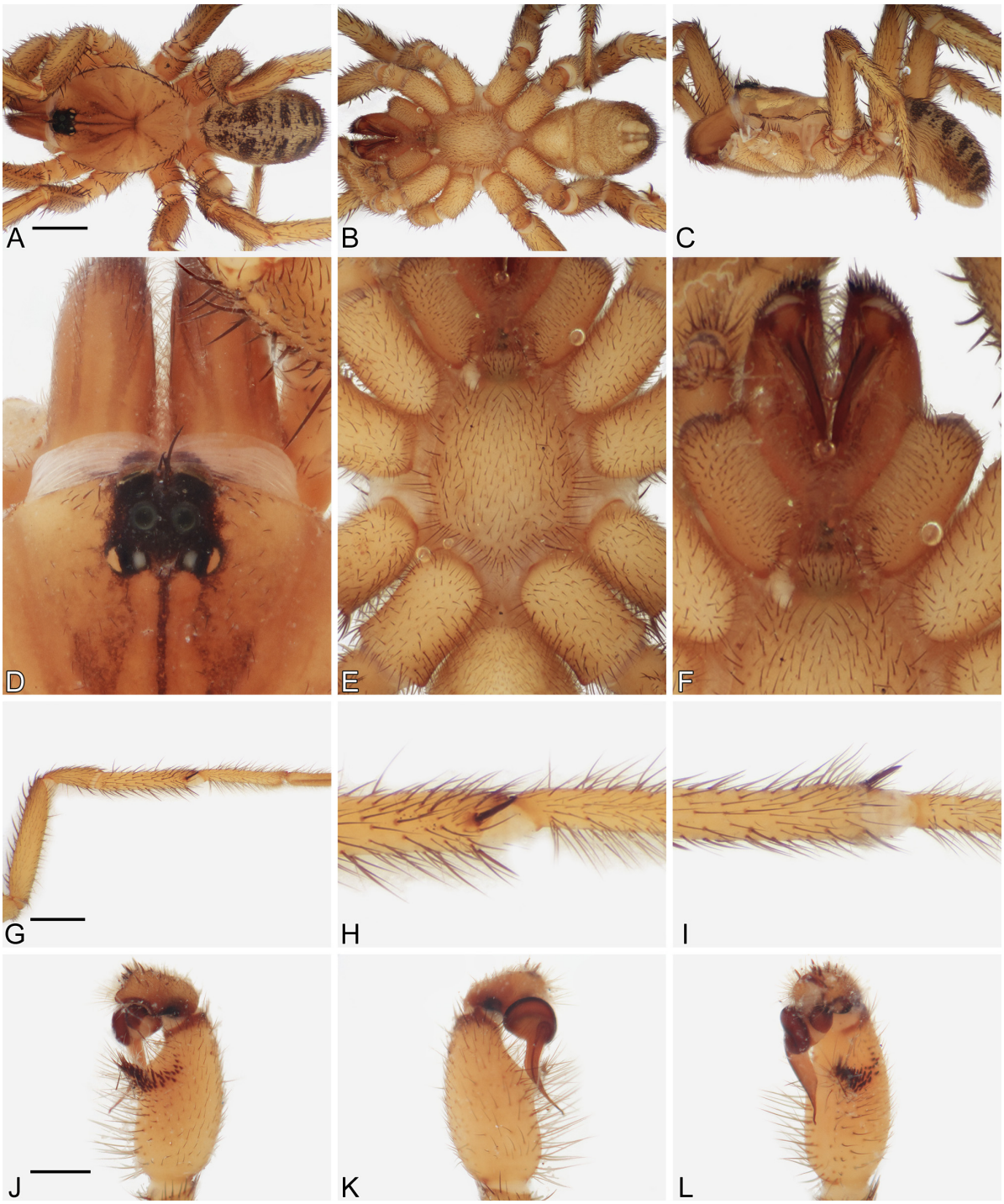


FIGURE 17. *Blakistonia maryae* **sp. n.**, holotype male (SAM NN20077): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macroseta, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Description. *Holotype male* (SAM NN20077). Small idiopid spider (total length 9.4).

Colour (in ethanol; Fig. 17A–C): Carapace, legs and pedipalp pale golden orange-brown, with darker lines on caput, radiating backwards from fovea, and around edges of carapace (Fig. 17A, G–L); sternum, labium and

maxillae very similar colour; chelicerae darker red-brown (Fig. 17E, F); abdomen orange golden-brown with pattern of *ca.* seven mottled, indistinct chevrons, all divided (Fig. 17A, C).

Cephalothorax: Carapace 4.8 long, 3.7 wide, 3.2 high, 1.3 times longer than wide; oval (Fig. 17A), caput low, ocular area raised (Fig. 17C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; carapace very sparsely setose, concentrated and forming fringe around edge of carapace; line of setae between fovea and eye group absent, however, few setae on lateral sides of eye area; median clump of thickened setae on clypeus (Fig. 17D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.7 wide, 0.7 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE /ALE–ALE ratio 1.1; posterior eye row straight to very slightly procurved; AME only slightly smaller than ALE and separated by about the diameter of AME; ALE and PLE separated by about twice the diameter of ALE; PME pale, less than half size of AME and about half size of PLE, and separated from PLE by just less than its own diameter (Fig. 17D). Labium with five cuspules near anterior margin (Fig. 17F). Sternum 2.5 long, 2.1 wide, evenly setose (Fig. 17E). Maxillae with 12 (left) and 21 (right) cuspules (Fig. 17E, F).

Legs: setose and diffusely spinose; tarsi I, II ventrally flattened; metatarsi and distal tarsi I, II weakly scopulate (Fig. 17G–I). Paired tarsal claws: leg I p6 (6 large) r6 (6 large); leg II p8 (3 large, 5 small), r8 (3 large, 5 small); leg III p7 (3 large, 4 small), r5 (3 large, 2 small); leg IV p9 (9 large), r7 (3 large, 4 small).

Spination: Tibia I with single prolateral macroseta (Fig. 17G–I). All legs without clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 4.5, patella 2.1, tibia 3.4, metatarsus 3.1, tarsus 1.6, total = 15.3. Leg II: femur 4.4, patella 2.0, tibia 3.3, metatarsus 2.2, tarsus 2.1, total = 14.0. Leg III: femur 3.1, patella 1.6, tibia 2.6, metatarsus 3.2, tarsus 2.3, total = 12.3. Leg IV (right): femur 4.7, patella 2.6, tibia 4.5, metatarsus 4.5, tarsus 2.6, total = 18.4. Pedipalp: femur 2.5, patella 1.2, tibia 2.2, tarsus 1.2, total = 7.2.

Pedipalp: Femur dorsally spinose; patella with thickened ventral setae; tibia short and swollen, RTA very short, pointed, with clump of setae and covered in short, dense spinules and for just over half of distance between base of apophysis and distal tibia, becoming more sparse towards distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, only slightly longer than bulb; cymbium covered in rows of short spinules, becoming longer closer to distal edge (Fig. 17J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 4.6 long, 2.7 wide (Fig. 17A).

Variation (n=6): Carapace 3.0–4.8 long, 2.5–2.7 wide, 5-6 labial cuspules.

Female (SAM NN29565)**.** Medium-sized idiopid spider (total length 18.5).

Colour (in ethanol; Fig. 18A–C): Carapace medium golden-brown, slightly darker around fovea and lateral margins of caput; sternum lighter golden-brown, darker towards anterior and lateral margins; labium and maxillae same golden-brown as margins of sternum, chelicerae dark brown (Fig. 18E, F); abdomen grey-brown with 6 mottled chevrons of uniform width spaced over length of abdomen, anterior-most chevron divided by pale medial patch (Fig. 18A, C); legs and pedipalps medium golden-brown (Fig. 18G, H).

Cephalothorax: Carapace 8.2 long, 6.3 wide, 5.9 high, 1.3 times longer than wide; oval (Fig. 18A); caput moderately raised, ocular area very slightly raised (Fig. 18C); cuticle uniformly smooth; fovea procurved; two parallel rows of large setae from fovea to eye group, with smaller setae located laterally to these rows; smaller fine setae also scattered across carapace, concentrated and forming fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 18D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.4 wide, 0.9 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row straight; AME *ca*. two-thirds the size of ALE and separated by less than diameter of AME; ALE and PLE separated by about diameter of AME; PLE and PME contiguous, oval (Fig. 18D). Labium without cuspules (Fig. 18F). Sternum 4.3 long, 3.5 wide, moderately setose with setae becoming denser and longer around margins; 3 pairs of sigilla, anterior-most pair at lateral margins, middle pair at half length, posterior pair slightly less than twice their width from edge (Fig. 18E). Maxillae with 22 (left) and 32 (right) cuspules (Fig. 18E, F).

Legs: moderately setose and diffusely spinose, leg III more heavily setose; distinct upright setae on metatarsi and of tibiae I, II; femora I, II, and pedipalp laterally bowed; tarsi and metatarsi I, II, and palpal tarsus heavily scopulate (Fig. 18G, H). Paired tarsal claws: p1 (1 large) r2 (2 large); leg II p3 (2 large, 1 small), r1 (large); right leg III r2 (1 large, 1 small), r2 (2 small); right leg IV p0, r4 (1 large, 4 small). Pedipalp claw with 2 large teeth.

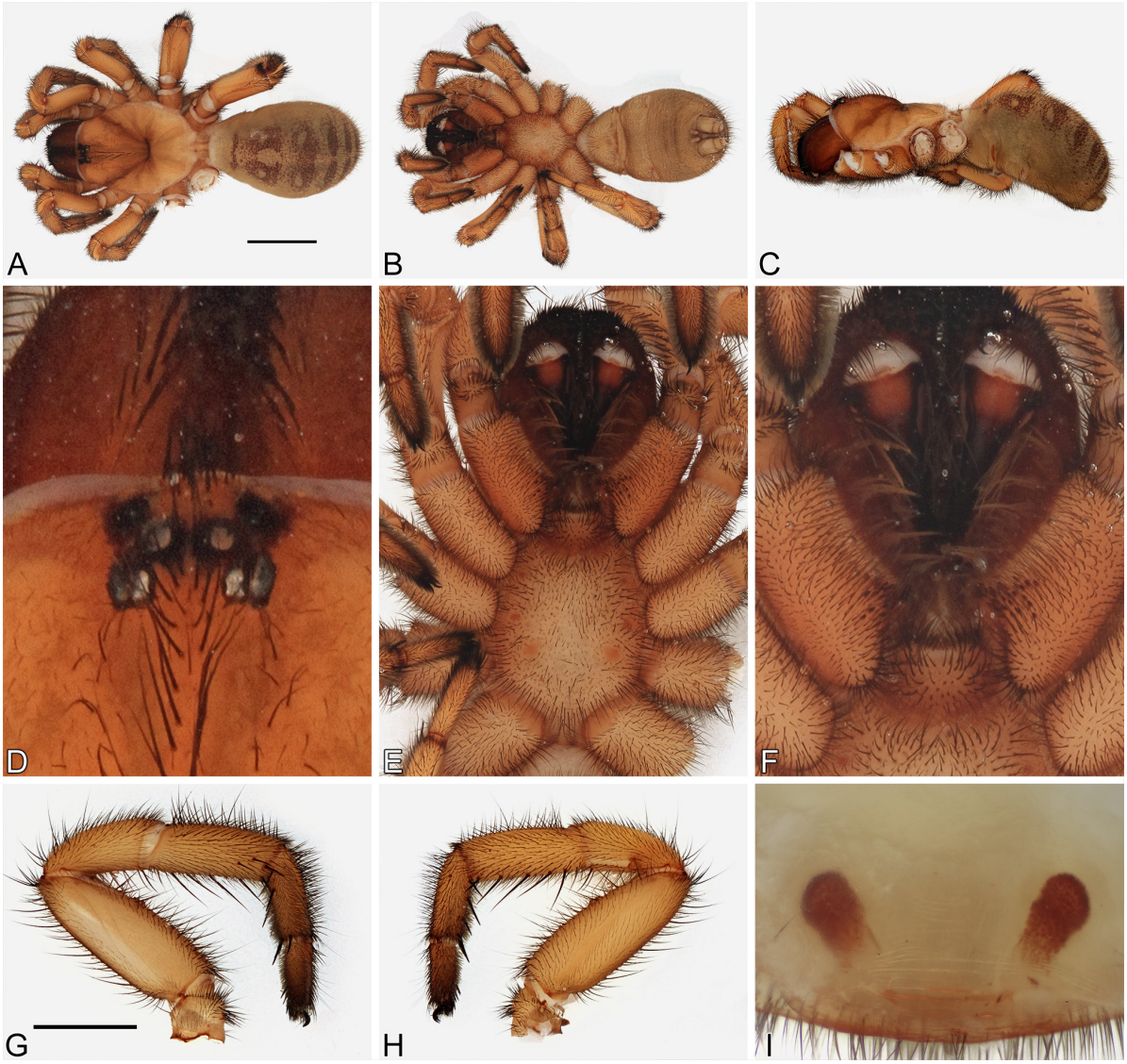


FIGURE 18. *Blakistonia maryae* **sp. n.**, female (SAM NN29565): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 2 mm (G).

Spination: Leg I: tibia p1, r5; metatarsus p4, r7; tarsus p3, r8. Leg II: tibia p4, r5; metatarsus II p4, r5; tarsus II p2, r4. Right leg III: patella p7; metatarsus III p6, r10; tarsus with 11 short spines ventrally. Right leg tibia IV: p8, r3; tarsus with *ca.* 23 short spines ventrally. Pedipalp: tibia p8, r5; tarsus p3, r3.

Leg and pedipalp measurements: Length of legs IV > II > I > III. Leg I: femur 3.7, patella 2.7, tibia 2.4, metatarsus 2.0, tarsus 1.7, total = 12.5. Leg II: femur 4.2, patella 2.9, tibia 2.7, metatarsus 2.0, tarsus 1.8, total = 13.6. Leg III (right): femur 3.4, patella 2.5, tibia 2.1, metatarsus 1.5, tarsus 1.5, total = 11.8. Leg IV (right): femur 5.2, patella 3.7, tibia 4.6, metatarsus 3.8, tarsus 4.1, total = 21.4. Pedipalp: femur 3.6, patella 2.3, tibia 2.2, tarsus 2.8, total = 10.9.

Abdomen: Setose, oval, three pairs of non-sclerotised, irregular dorsal sigilla on anterior three chevrons; 10.3 long, 6.8 wide (Fig. 18A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, with lobe of epigyne ca. same width as stalk, covered in opaque mottled brown nodules, becoming more concentrated towards distal spermathecae (Fig. 18I).

Variation (n=3): Carapace 6.7–10.3 long, 6.2–7.7 wide, no labial cuspules. Spination: Leg I: tibia p1–3, r4–6; metatarsus r3–4, r5–7; tarsus p2–3, r3–8. Leg II: tibia p1–4, r5–7: metatarsus p4 r5–7; tarsus p2–3, tarsus r4–11. Leg III: patella p5–7, tibia p0–2, r0–1; tarsus with 11–17 short spines ventrally. Leg IV: tibia p0–1, r0–1; metatarsus p6–11, r2–4; tarsus with 20–28 spines ventrally. Pedipalp: tibia p2–9, r4–7; tarsus p3–5, r3–4.

Etymology. This species is named in honour of the senior author's mother, Mary Harrison, for her invaluable assistance on numerous collecting trips.

Distribution. *Blakistonia maryae* is found on the Eyre Peninsula, and is known from Tumby Bay, the Middleback Ranges, Kimba, and two localities in the Gawler Ranges (Fig. 32).

Remarks. The burrow lid of *B. maryae* is D-shaped and slightly indented (Fig. 2H–K). The rim of the burrow is usually lined with twigs and small leaves (Fig. 2H–K), which although common in other idiopid genera such as *Idiosoma* and *Gaius*, has not been previously documented in *Blakistonia*. These twigs are used as 'feeling lines' to increase the area of foraging (Main 1962). Twig-lining was not observed in the specimen from Kolay Hut, Gawler Ranges (Fig. 2K), however, it is likely that the absence of twig-lining was a result of the burrow being built on an unconsolidated bank, with erosion and no leaf litter available. We have tentatively linked the females from Tumby Bay and Gawler Ranges with the males from Kimba and Mount Crawford, due to their distributions on the Eyre Peninsula, and no conflicting differences in other morphological features, such as eye group shape.

***Blakistonia newtoni*, sp. n.**
(Fig. 19A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Hiltaba, Gawler Ranges National Park, 32°09'51"S, 135°03'09"E, 13–22 November 2012, pitfall, N. Birks, BushBlitz survey (SAM NN28064).

Diagnosis. Males of *B. newtoni* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, *B. aurea*, *B. parva*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the presence of one, rather than two, prolateral macroseta on tibia I, and by the absence of prolateral clasping spurs on tibia I (Fig. 19G–I); from those of *B. plata* and *B. birksi* by the square eye group (Fig. 19D); and from those of *B. maryae* and *B. hortoni* by the field of spinules on the palpal tibia being in a rounded crescent shape, and by the ventral margin of the palpal tibia distal to the RTA being strongly concave in prolateral view (Fig. 19J–L). Females are unknown.

Description. *Holotype male* (SAM NN28064)**.** Medium-sized idiopid spider (total length 10.4).

Colour (in ethanol; Fig. 19A–C): Carapace bright golden orange-brown, with darker, indistinct lines of colour both sideson both sides of caput, and between fovea and eye group (Fig. 19A); sternum, labium and maxillae very similar colour, chelicerae darker red-brown (Fig. 19E, F); abdomen same golden orange-brown as sternum and carapace with pattern of seven dark, broad, mottled chevrons, down entire side of abdomen (Fig. 19A, C); legs and pedipalp same colour as of carapace (Fig. 19G–L).

Cephalothorax: Carapace 5.1 long, 4.4 wide, 3.8 high, 1.2 times longer than wide; oval (Fig. 19A), caput low, ocular area raised (Fig. 19C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea slightly procurved; carapace very sparsely setose, slightly more concentrated behind and both sides of eye group, and forming fringe around edge of carapace; median clump of thickened setae on clypeus (Fig. 19D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.8 wide, 8.9 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row straight; AME only slightly smaller than ALE and separated by about one and a half times the distance of AME; ALE and PLE separated by about three times the diameter of ALE; PME pale, less than half the size of AME and about half the size of PLE, and separated from PLE by about its own diameter (Fig. 19D). Labium with five cuspules (Fig 19F). Sternum 2.8 long, 2.1 wide, evenly setose (Fig. 19E). Maxillae with 25 (left) and 19 (right) cuspules (Fig. 19E, F).

Legs: Moderately setose and sparsely spinose; tarsi I, II ventrally flattened; tarsi and distal metatarsi I, II weakly scopulate. Paired tarsal claws: leg I p9 (3 large, 3 small) r8 (6 large, 2 small); leg II p9 (8 large, 1 small), r8 (6 large, 2 small); leg III p7 (6 large, 1 small), r6 (3 large, 3 small); leg IV p6 (6 large), r8 (7 large, 1 small).

Spination: Leg I: Tibia with single prolateral macroseta (Fig. 19G–I), r1; metatarsus p1 r1. Leg II: tibia r1; metatarsus p2, r3. Leg III: tibia p1, r3; tibia p1, r3; metatarsus p7, r10; tarsus p7, r6. Leg IV: moderately setose and sparsely spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > II > I > III. Leg I: femur 5.0, patella 2.5, tibia 3.8,

metatarsus 3.2, tarsus 2.0, total = 16.5. Leg II: femur 4.9, patella 2.5, tibia 3.6, metatarsus 3.0, tarsus 2.3, total = 16.3. Leg III: femur 4.2, patella 2.2, tibia 3.2, metatarsus 3.4, tarsus 2.2, total = 15.2. Leg IV (right): femur 5.0, patella 2.3, tibia 5.3, metatarsus 5.4, tarsus 2.7, total = 20.7. Pedipalp: femur 2.8, patella 1.3, tibia 2.2, tarsus 1.2, total = 7.5.

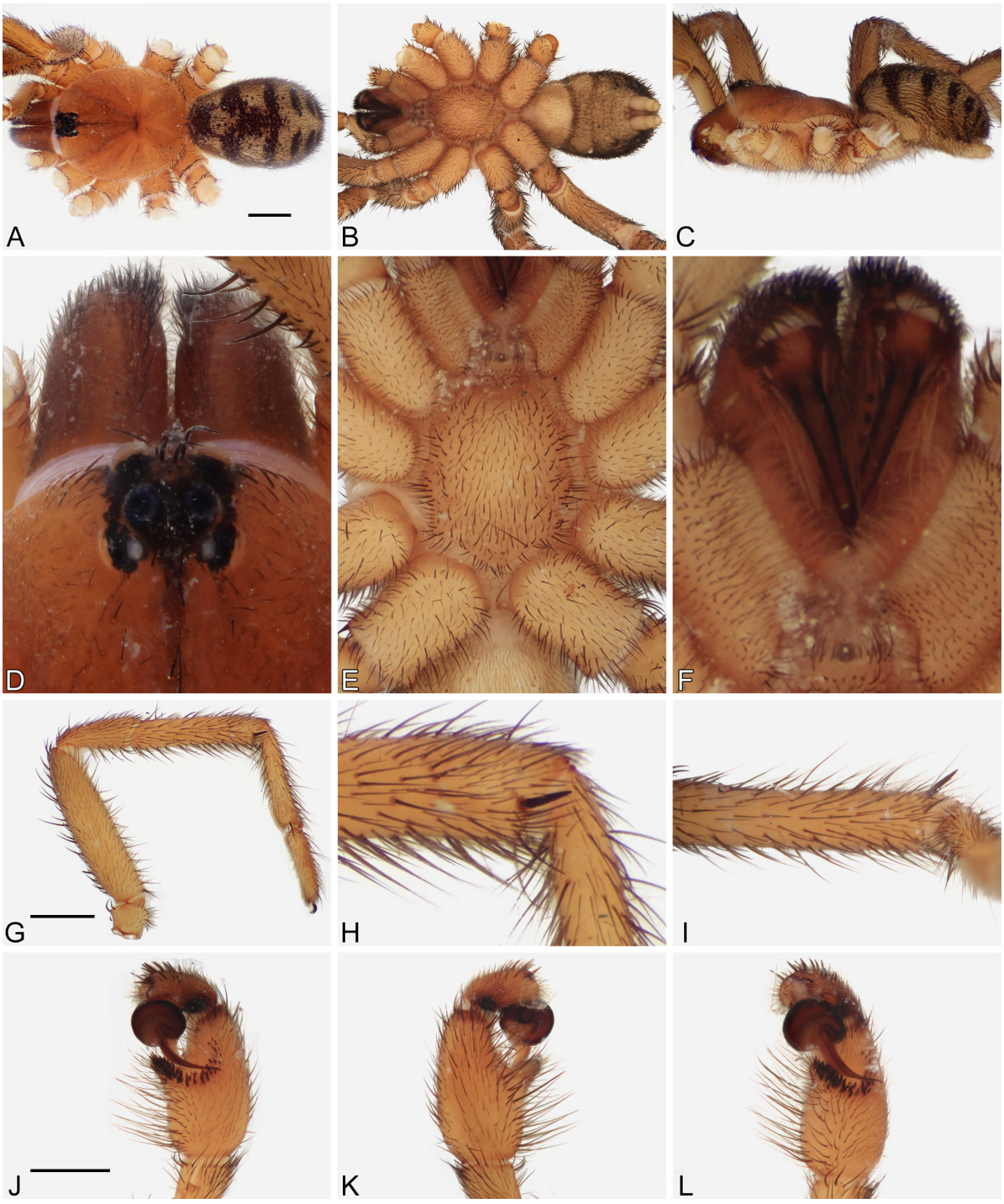


FIGURE 19. *Blakistonia newtoni* **sp. n.**, holotype male (SAM NN28064): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macroseta, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G, J).

Pedipalp: Femur spinose on dorsal surface; patella with thickened ventral setae; tibia short and swollen, RTA short, pointed, densely covered in short, stout spinules in narrow line to just over two-thirds of distance between base of apophysis and distal tibia, becoming more sparse towards distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, curved but not twisted, only slightly longer than bulb; cymbium covered in rows of short spinules, becoming longer distally (Fig. 19J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 5.3 long, 3.2 wide (Fig. 19A).

Variation: None.

Etymology. This species is named in honour of Mark Newton, for his work in making South Australia's invertebrate fauna more readily identifiable to the general public, and for supplying specimens and images for this study.

Distribution. *Blakistonia newtoni* is known only from Hiltaba Reserve in the Gawler Ranges (Fig. 32).

Remarks. Specimens of this species were collected in a pitfall trap, 1.8 km WSW. of Hiltaba Station, under *Triodia* vegetation on a rocky hill slope.

***Blakistonia nullarborensis*, sp. n.**
(Fig. 20A–I)

Type material. AUSTRALIA: ***Western Australia:*** Holotype female, east of Madura, Nullarbor Plain, 32°24'57"S, 124°20'34"E, 29 March 2014, dug from burrow in degraded roadside habitat, M.S. Harvey, S.E. Harrison (WAM T141142^{DNA}).

Other material examined. AUSTRALIA: ***Western Australia:*** 1 female, east of Balladonia, Nullarbor Plain, 31°53'54"S, 126°54'30"E, 29 March 2014, dug from burrow in remnant native vegetation, M.S. Harvey, S.E. Harrison (WAM T141139^{DNA}); 1 female, Cocklebiddy, 32°02'12"S, 126°05'28"E, 29 March 2014, dug from burrow in highly degraded roadside habitat, M.S. Harvey, S.E. Harrison (WAM T141140^{DNA}); 1 female, Moonera, 31°59'17"S, 126°33'11"E, 29 March 2014, dug from burrow in native vegetation, M.S. Harvey, S.E. Harrison (WAM T141141^{DNA}).

Diagnosis. Females of *B. nullarborensis* can be distinguished from those of all other species of *Blakistonia*, except *B. wingellina*, by the strongly trapezoidal eye group (Fig. 20D); however, *B. wingellina* and *B. nullarborensis* are unable to be reliably distinguished using morphology alone. Males are unknown.

All life stages of *B. wingellina* can also be distinguished from those of other species with sequence data by the following nucleotide substitution (*n*=4 specimens): G(171).

Description. *Holotype female* (WAM T141142)**.** Large idiopid spider (total length 23.0).

Colour (in ethanol; Fig. 20A–C): Carapace, legs and pedipalp medium golden-brown, slightly darker around fovea and lateral margins of caput (Fig. 20A); sternum a lighter golden-brown, darker towards anterior margins; labium and maxillae same golden-brown as anterior margins of sternum, chelicerae dark brown (Fig. 20E, F); abdomen grey-brown with eight pale mottled chevrons of uniform width spaced over length of abdomen, more closely spaced at posterior abdomen (Fig. 20A, C).

Cephalothorax: Carapace 9.3 long, 7.5 wide, 7.5 high, 1.2 times longer than wide; oval (Fig. 20A); caput high, ocular area flat (Fig. 20C); cuticle uniformly smooth; fovea procurved; one large patch of thick setae posterior to eye area; smaller fine setae also scattered across the carapace, concentrated and forming fine, indistinct fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 20D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.9 wide, 1.4 long, 0.3 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.3; posterior eye row slightly recurved; AME slightly larger than half ALE and separated by the diameter of AME; ALE and PLE separated by about diameter of PLE; PME pale, *ca*. 0.25 of PLE, and separated from PLE by about its own diameter (Fig. 20D). Labium without cuspules (Fig. 20F). Sternum 4.9 long, 3.7 wide, moderately setose with setae becoming denser and longer around margins; 3 pairs of sigilla, anterior-most pair *ca*. in margins, close to anterior margin; second pair at one-third length; third pair at *ca*. twice their width from edge (Fig. 20E). Maxillae with 21 (left) and 24 (right) cuspules, becoming denser near inner margins (Fig. 20E, F).

Legs: moderately setose and diffusely spinose, with retrolateral side of all legs being least setose and dorsal sides of III, IV with thick, dense, spine-like setae; distinct upright setae on tarsi, metatarsi and distal tibiae I and II;

femora I, II, and pedipalp laterally bowed; tarsi and metatarsi I, II, and palpal tarsus heavily scopulate (Fig. 20G–H). Paired tarsal claws: leg I p2 (1 large, 1 small) r3 (2 large, 1 small); leg II p3 (2 large, 1 small), r2 (2 large); right leg III p2 (1 large, 1 small), r2 (1 large, small); right leg IV p0, r2 (2 small). Pedipalp claw with 1 large and 2 small teeth.

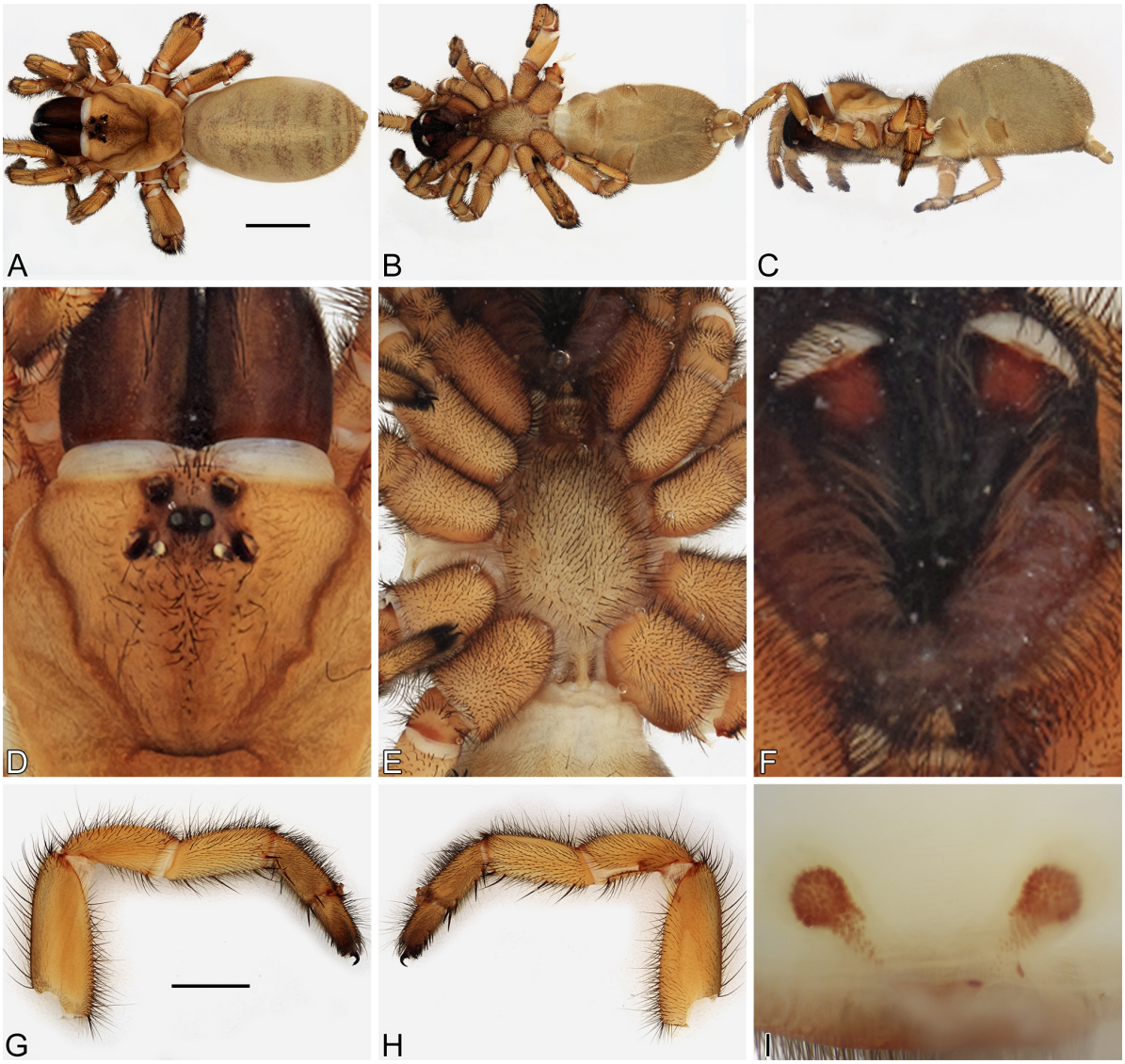


FIGURE 20. *Blakistonia nullarborensis* **sp. n.**, holotype female (WAM T141142): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 2 mm (G).

Spination: Leg I: tibia p2, r4; metatarsus p5, r4; tarsus with 10 short spines ventrally. Leg II: tibia p2, r4; metatarsus p4, r5; tarsus p0, r10. Leg II: tibia p2, r4; metatarsus p5, r5; tarsus p0, r10. Right leg III: patella p7; tibia p2, r0; metatarsus p5, r7. Right leg IV: metatarsus p2, r5; tarsus with 19 short spines ventrally. Pedipalp: tibia p5, r7; tarsus p2, r5.

Leg and pedipalp measurements: Length of legs IV > I > III > II. Leg I: femur 4.2, patella 2.6, tibia 2.4, metatarsus 2.8, tarsus 2.6, total = 14.6. Leg II: femur 4.2, patella 3.1, tibia 2.7, metatarsus 1.9, tarsus 1.8, total = 13.7. Leg III: femur 4.2, patella 3.0, tibia 2.5, metatarsus 2.5, tarsus 2.2, total = 14.4. Leg IV (right): femur 4.4, patella 2.4, tibia 3.8, metatarsus 3.0, tarsus 1.9, total = 15.5. Pedipalp: femur 4.7, patella 3.4, tibia 2.7, tarsus 2.2, total = 15.0.

Abdomen: Setose, oval, dorsal sigilla not evident; 16.0 long, 10.1 wide (Fig. 20A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, circular, covered in opaque mottled brown nodules, more concentrated on lobe of spermathecae (Fig. 20I).

Variation (n=4): Carapace 6.2–9.3 long, 6.2–7.5 wide, no labial cuspules. Spination: Leg I: tibia p2, r3–6; metatarsus p3–5, r5–6; tarsus p0, r3–10. Leg II: tibia p1–3, r2–4; metatarsus p2–5, r5 tarsus p0, r10–12. Leg III: patella 3–7, tibia p0–2, r0; metatarsus p4–6, r5–7, tarsus with 5–13 short spines ventrally. Leg IV: metatarsus p3–6, r1–2; tarsus with 7–9 short spines ventrally. Pedipalp: p0-2, tibia p2–6, r4–7; tarsus p2, r3–5.

Etymology. The specific name refers to the Nullarbor Plain, where this species is found.

Distribution. *Blakistonia nullarborensis* is known only from the Nullarbor Plain (Fig. 33).

Remarks. The burrow of *B. nullarborensis* is D-shaped and slightly indented. When collecting specimens, SEH and MSH were unable to locate burrows of juveniles, and many habitats near the Eyre Highway were highly degraded.

***Blakistonia olea*, sp. n.**
(Fig. 21A–L)

Type material. AUSTRALIA: ***Western Australia:*** Holotype male, Peak Charles National Park, site LH9, 32°54'34.3"S, 121°10'19.3"E, 26 March 2012, *Allocasuarina* woodland, S. Comer, E. Adams (WAM T127864).

Diagnosis. Males of *B. olea* can be distinguished from those of all other *Blakistonia* species by the AME being significantly larger than the ALE (Fig. 21D). Females are unknown.

Description. *Holotype male* (WAM T127864)**.** Small idiopid spider (total length 11.6).

Colour (in ethanol; Fig. 21A–C): Carapace and chelicerae olive-brown, darker around lateral margins (Fig. 21A); sternum, labium and maxillae uniformly yellow; abdomen darker mottled olive-brown with lighter pattern of four thin chevrons, joined by pale, oblong medial patch (Fig. 20A, C); legs and pedipalp lighter than carapace, with dorsal femora the darkest (Fig. 21G–L).

Cephalothorax: Carapace 5.4 long, 4.2 wide, 3.9 high, 1.3 times longer than wide; oval (Fig. 21A), caput moderately raised, ocular area raised (Fig. 21C); cuticle smooth, with pits outward from fovea and each side of caput; fovea straight; row of four thick setae between fovea and eye group, culminating in several longer, thickened setae directly posterior to eye group; carapace sparsely setose, with indistinct lines of setae radiating outwards from fovea, slightly more concentrated on lateral margins; median clump of thickened setae on clypeus (Fig. 21D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.0 wide, 0.6 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row slightly recurved; AME *ca.* twice the size of ALE and separated by about half of ALE; PLE *ca.* half of ALE and separated by about ALE diameter; PME pale, about half of PLE, and separated from PLE by less than its own diameter (Fig. 21D). Labium without cuspules (Fig. 21F). Sternum 2.9 long, 2.4 wide, evenly setose; sigilla indistinct (Fig. 21E). Maxillae with 8 (left) and 4 (right) cuspules (Fig. 21E, F).

Legs: diffusely setose and spinose; tarsi I, II ventrally swollen; tarsi I, II weakly scopulate (Fig. 21G–I). Paired tarsal claws: leg I p2 (2 large) r6 (6 large); leg II p5 (5 large), r5 (2 large, 3 small); leg III p3 (1 large, 2 small), r3 (3 large); leg IV prolateral claw missing, r3.

Spination: Tibia I with two prolateral macrosetae (Fig. 21G–I). All other legs diffusely setose and spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 5.3, patella 2.4, tibia 3.8, metatarsus 4.0, tarsus 2.2, total = 17.7. Leg II: femur 4.8, patella 2.2, tibia 3.5, metatarsus 3.9, tarsus 2.2, total = 16.6. Leg III: femur 3.9, patella 2.0, tibia 2.9, metatarsus 3.8, tarsus 2.5, total = 15.1. Leg IV: femur 5.1, patella 2.5, tibia 4.9, metatarsus 5.6, tarsus 3.0, total = 21.1. Pedipalp: femur 2.9, patella 1.5, tibia 2.6, tarsus 1.2, total = 8.2.

Pedipalp: Femur with dorsal spines, patella with thickened ventral setae; tibia short and swollen, RTA short and pointed, with thick clump of setae on tip, and covered in short, dense spinules for *ca.* half of distance between base of apophysis and distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slightly longer than bulb, slender, tapering, tip slightly twisted; cymbium covered in fine setae (Fig. 21J–L).

Abdomen: Setose, oval, three pairs of indistinct, unsclerotised dorsal sigilla; 6.2 long, 3.4 wide (Fig. 21A).

Variation: None.

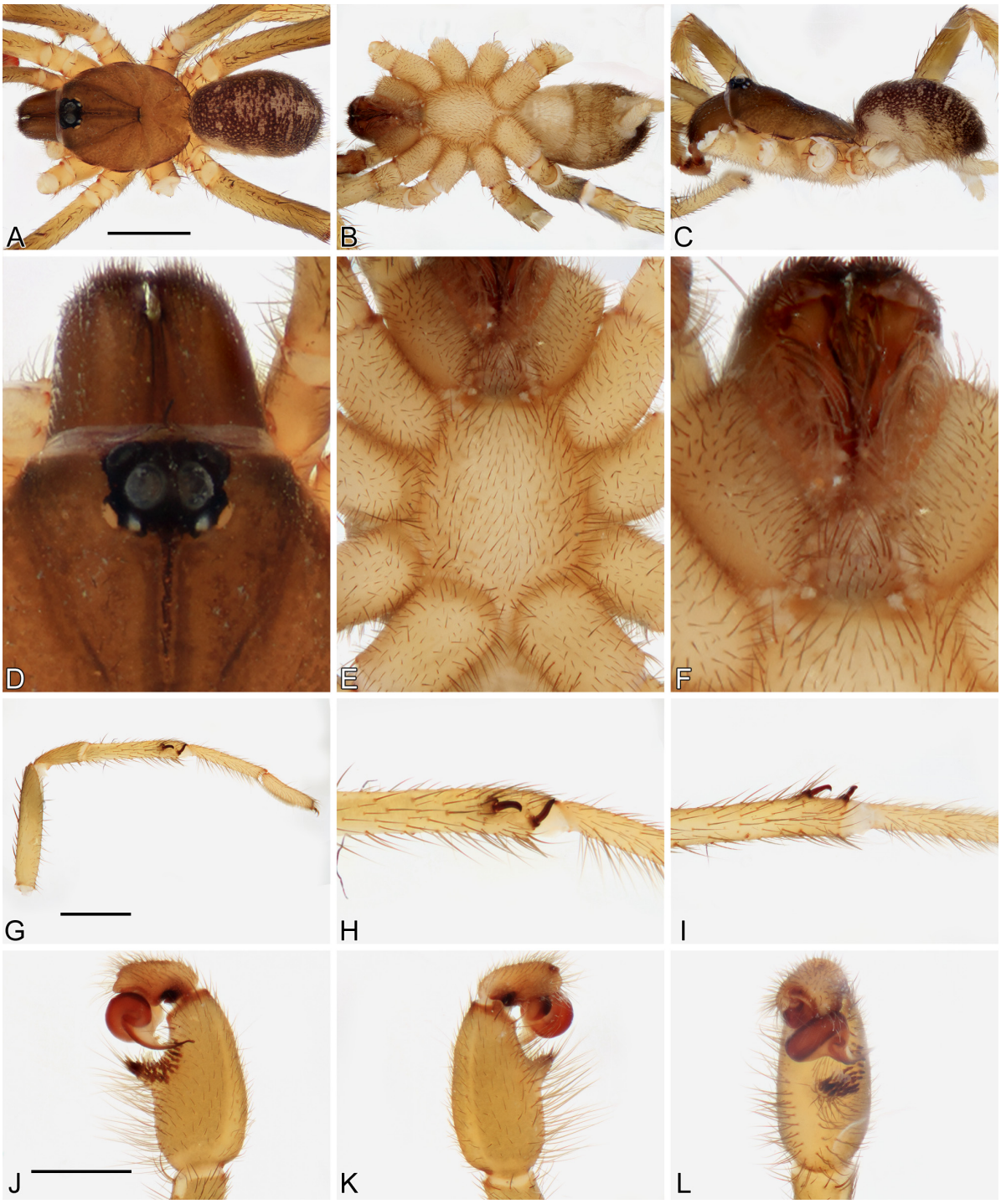


FIGURE 21. *Blakistonia olea* **sp. n.**, holotype male (WAM T127864): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macrosetae, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Etymology. The specific name is taken from the Latin *olea* (meaning 'olive'), in reference to the olive-green the colour of this species.

Distribution. *Blakistonia olea* is known only from Peak Charles National Park, in Western Australia (Fig. 33).

Remarks. Although females of *Blakistonia* have been found from this location, we cannot link them with certainty to this male due to lack of genetic data from the male and females, the conservative morphology of female specimens and the significantly larger size of females compared to the male.

***Blakistonia parva*, sp. n.**
(Fig. 22A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Beresford Railway Station, 29°18'15"S, 136°39'00"E, 25–30 September 1995, pitfall trap, D.E.H. Stony Deserts Survey (SAM NN20066).

Diagnosis. Males of *B. parva* can be distinguished from those of all other species of *Blakistonia* by the absence of prolateral clasping spurs on tibia I and by the presence of two, rather than one, prolateral macrosetae on leg I (Fig. 22G–I), and an eye group that is distinctly longer than wide (Fig. 22D). Females are unknown.

Description. *Holotype male* (SAM NN20066)**.** Very small idiopid spider (total length 7.2).

Colour (in ethanol; Fig. 22A–C): Carapace, legs, pedipalp, sternum, labium and maxillae uniformly yellow, chelicerae slightly darker (Fig. 22A–F); abdomen yellow with seven mottled brown chevrons cover only dorsal abdomen, not laterally (Fig. 22A, C)

Cephalothorax: Carapace 3.3 long, 2.3 wide, 2.0 high, 1.4 times longer than wide; oval (Fig. 22A), caput low, ocular area raised (Fig. 22C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; three rows of sparse setae longways behind eye group, additional setae in sparse rows radiating outwards from fovea, fine setae scattered very sparsely across carapaceforming indistinct fringe around lateral margins; 3 setae around eye group and clypeus (Fig. 22D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.5 wide, 0.7 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.1; posterior eye row straight; AME only slightly smaller than ALE and separated by about diameter of AME; ALE and PLE separated by just over ALE diameter; PME about half of AME, slightly less than half of PLE and almost directly adjacent to PLE (Fig. 22D). Labium without cuspules (Fig. 22F). Sternum 1.5 long, 1.4 wide, evenly setose; three pairs of very small sigilla, evenly spaced, all very small (Fig. 22E). Maxillae without cuspules, with shorter thickened setae in proximal corner (Fig. 22E, F).

Legs: sparsely setose; legs II, III and IV without spines; tarsi I and II ventrally swollen; metatarsi and distal tarsi I, II scopulate on ventral surface only (Fig. 22G–H). Paired tarsal claws: leg I p4 (4 large), r4 (4 large); leg II p4 (4 large), r4 (4 large); leg III p3 (2 large, 1 small), r4 (4 large); leg IV p3 (3 large), r3 (2 large, 1 small).

Spination: Tibia I with two prolateral macrosetae (Fig. 22G–I). All other legs without spines.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 2.9, patella 1.4, tibia 2.3, metatarsus 1.5, tarsus 1.8, total = 9.9. Leg II: femur 2.7, patella 1.3, tibia 2.1, metatarsus 1.6, tarsus 1.4, total = 9.1. Leg III: femur 2.1, patella 1.1, tibia 1.4, metatarsus 1.6, tarsus 1.2, total = 7.4. Leg IV (right): femur 2.9, patella 1.3, tibia 2.7, metatarsus 2.6, tarsus 1.6, total = 11.1. Pedipalp: femur 1.6, patella 0.9, tibia 1.6, tarsus 0.9, total = 5.0.

Pedipalp: All segments without spines; tibia short, incrassate, RTA slender, pointed, covered in long setae and thick, short, dense spinules, latter organised in rough 'rows' on apophysis and continue in line about as wide apophysis about halfway toward distal edge of tibia, becoming sparser towards distal edge of tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, only twisted distally, *ca.* 1.5 times the length of bulb; cymbium covered in rows of short, sparse spinules, becoming longer closer to distal edge (Fig. 22J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 3.9 long, 2.7 wide (Fig. 22A).

Variation: None.

Etymology. The specific name is taken from the Latin *parvus* (meaning 'small'), as it is the smallest of all known *Blakistonia* species.

Distribution. *Blakistonia parva* is known only from Beresford Railway Station, off the Oodnadatta Track in northern South Australia (Fig. 32).

Remarks. The male was collected in 1995 as part of the South Australian Department for Environment and Heritage's 'Stony Deserts Biological Survey' (see Brandle 1998).

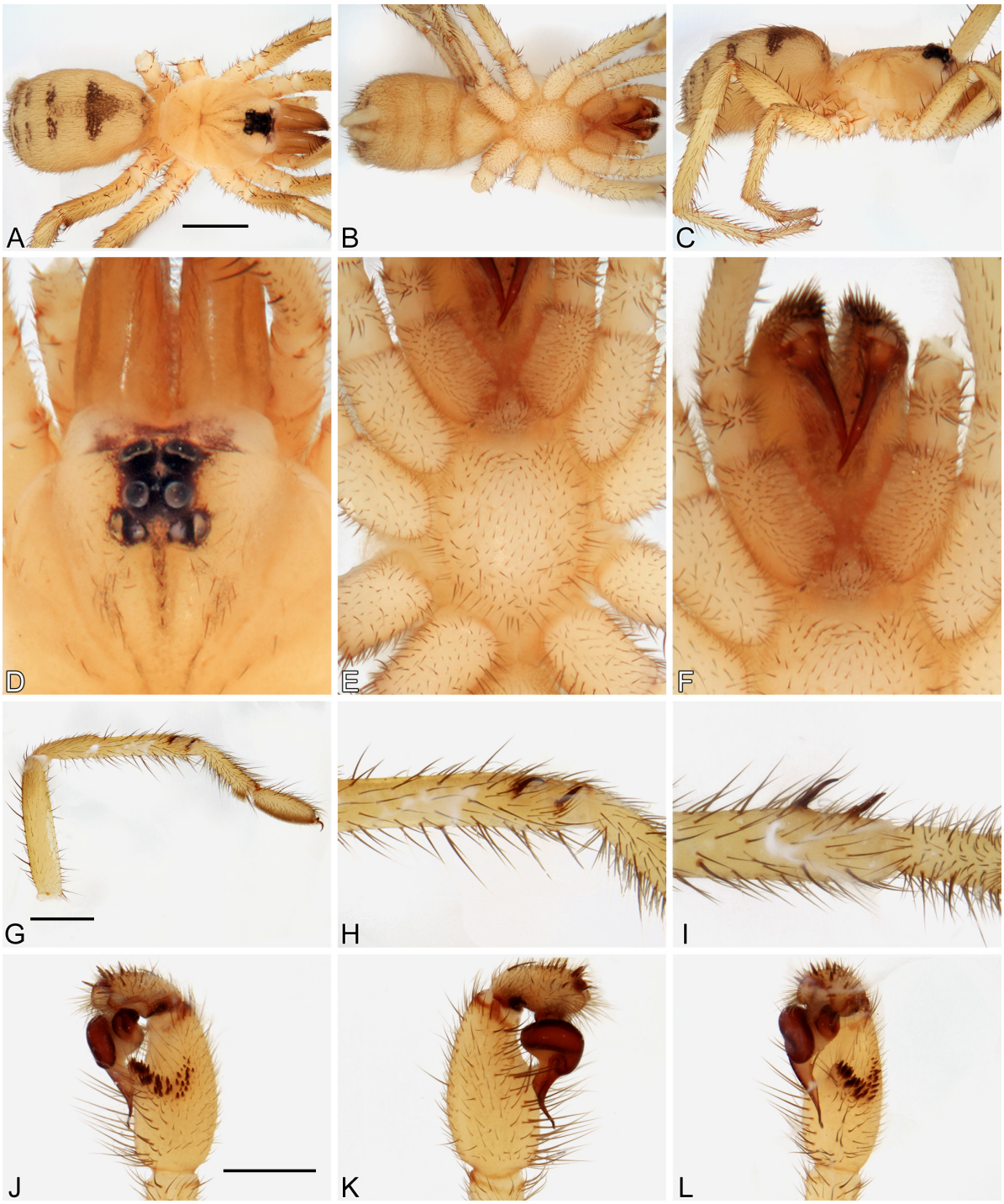


FIGURE 22. *Blakistonia parva* **sp. n.**, holotype male (SAM NN20066): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macrosetae, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

***Blakistonia pidax*, sp. n.**
(Fig. 23A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Strangways Springs, 29°08'14"S, 136°34'00"E, 25–30 September 1995, pitfall trap, D.E.L.M. Stony Deserts Survey (SAM NN20064^{DNA}). Paratype: 1 male, same data (SAM NN20065).

Diagnosis. Males of *B. pidax* can be distinguished from those of *B. maryae*, *B. plata*, *B. birksi*, *B. newtoni*, *B. hortoni*, *B. parva*, *B. maryae*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the presence of prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 23G–I); and from those of *B. bella*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli* and *B. aurea* by the absence of spinules on the cymbium (Fig. 23J–L). Females are unknown.

All life stages of *B. pidax* can also be distinguished from those of other species with sequence data by the following nucleotide substitutions (*n*=1 specimen): G(128), T(198), T(327), T(378), C(459), T(519), A(538) and the following unique motif: TA(321–322).

Description. *Holotype male* (SAM NN20064)**.** Medium idiopid spider (total length 10.2).

Colour (in ethanol; Fig. 23A–C): Carapace, legs and pedipalp uniform pale golden orange-brown (Fig. 23A); sternum, labium and maxillae very similar, sternum darker towards anterior margins; chelicerae slightly darker than carapace (Fig. 23E, F); abdomen golden orange-brown with distinctive pattern of seven mottled dark chevrons dorsally not laterally (Fig. 23A, C).

Cephalothorax: Carapace 4.6 long, 3.9 wide, 3.3 high,1.2 times longer than wide; oval (Fig. 23A), caput low, ocular area raised (Fig. 23C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; distinct row of setae from halfway between fovea and eye group to eye group, culminating in a group of longer, thickened setae directly posterior to eye group; smaller fine setae also scattered very sparsely across the carapace, concentrated and form fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 23D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.8 wide, 0.7 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.1; posterior eye row straight; AME *ca*. two-thirds of ALE and separated by about AME diameter; ALE and PLE separated by about twice ALE diameter; PME about two-thirds of the size of AME and only slightly smaller than PLE, and separated from PLE by about its own diameter (Fig. 23D). Labium without cuspules (Fig. 23F). Sternum 2.9 long, 2.2 wide, evenly setose; three pairs of small sigilla (Fig. 23E). Maxillae without cuspules (Fig. 23E, F).

Legs: moderately setose and very sparsely spinose; tarsi I, II ventrally swollen; tarsi I II weakly scopulate (Fig. 23G–I). Paired tarsal claws: leg I p8 (8 large) 75 (6 large, 1 small); leg II p8 (8 large), r5 (4 large, 1 small); leg III p4 (3 large, 1 small), r5 (4 large, 1 small); leg IV p5 (4 large, 1 small), r5 (2 large, 3 small).

Spination: Tibia I with prolateral clasping spurs, distal-most spur with 2 terminal peg-like macrosetae, proximal-most with 3 terminal peg-like macrosetae (Fig. 23G–I). Leg II without spines. Leg III: patella p4; metatarsus p2, r2; tarsus p4, r1. Leg IV: metatarsus p5, r2.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 4.3 patella 2.0, tibia 3.1, metatarsus 3.1, tarsus 1.7, total = 14.2. Leg II: femur 4.3, patella 2.1, tibia 3.0, metatarsus 3.0, tarsus 1.7, total = 14.1. Leg III: femur 3.7, patella 1.6, tibia 2.1, metatarsus 1.9, tarsus 1.9, total = 13.0. Leg IV: femur 4.2, patella 2.3, tibia 4.1, metatarsus 4.9, tarsus 2.4, total = 18.1. Pedipalp: femur 2.3, patella 1.0, tibia 2.2, tarsus 1.1, total = 6.6.

Pedipalp: All segments without spines; patella with thickened ventral setae distally; tibia short and swollen, RTA short, thin and pointed, covered in dense spinules in line *ca.* as wide as apophysis halfway to distal tibia, becoming only slightly sparser; long, erect setae ventrally; bulb uniform, globular; embolus simple, slender, tapering, slightly twisted with a flanged tip, slightly longer than length of bulb; cymbium covered in rows of sparse, thickened setae, becoming longer closer to distal edge (Fig. 23J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 5.6 long, 3.2 wide (Fig. 23A).

Variation (n=2): Carapace 4.4–4.6 long, 3.5–3.9 wide, no labial cuspules. Spination: leg III patella p4, metatarsus p2, r1-3. Leg IV: metatarsus p4-5, r1-2.

Etymology. The specific name is taken from the Greek *pidax* (meaning 'spring'), and refers to the location where the species was found.

Distribution. *Blakistonia pidax* is known only from Strangways Springs, south-west of Lake Eyre in central South Australia (Fig. 32).

Remarks. This male was collected in a pitfall trap during the 'Stony Deserts Biological Survey', which was conducted between 1994 and 1997 (see Brandle 1998).

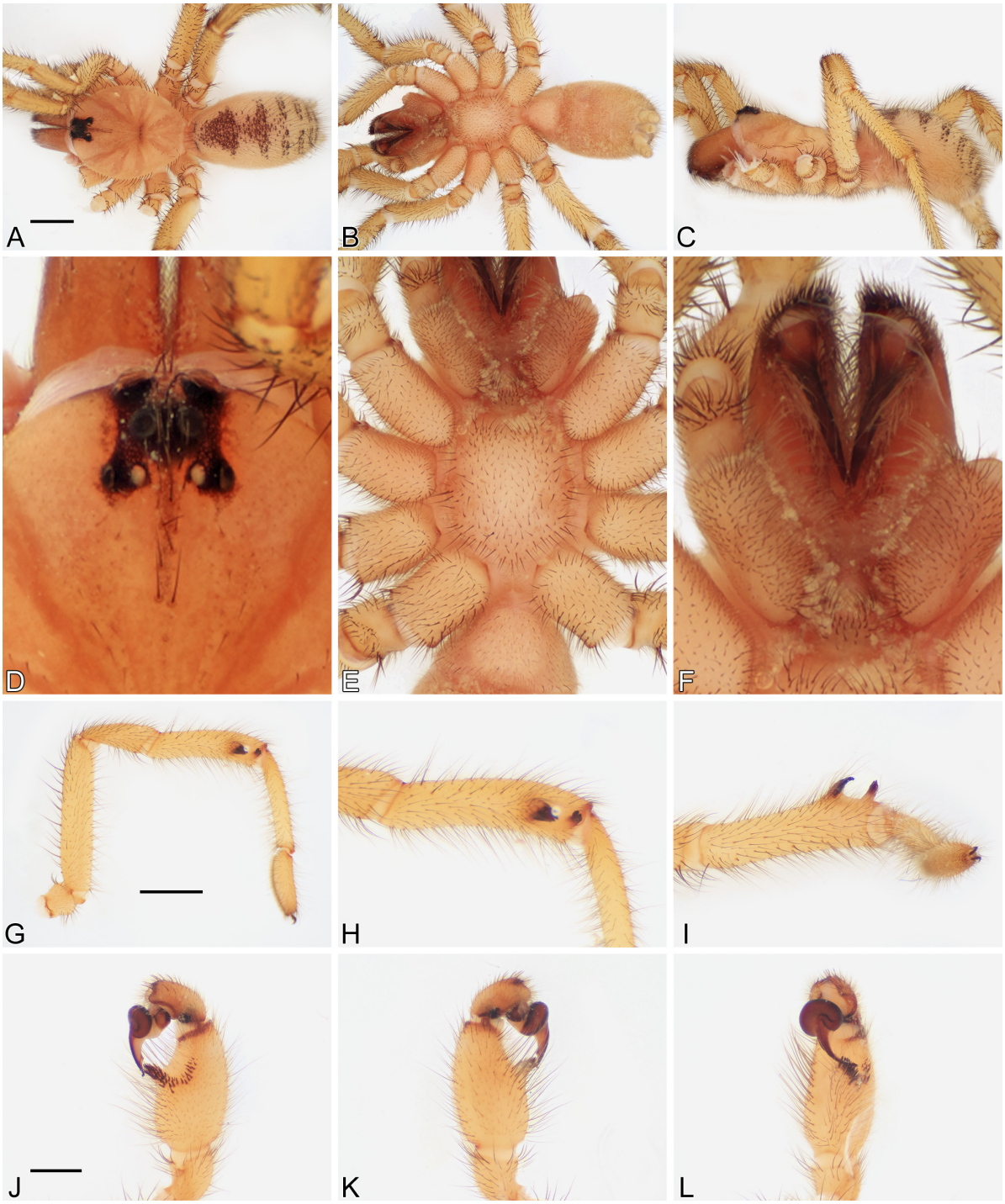


FIGURE 23. *Blakistonia pidax* **sp. n.**, holotype male (SAM NN20064): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, clasping spurs, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

***Blakistonia plata*, sp. n.**
(Fig. 24A–L)

Type material. AUSTRALIA: ***Queensland:*** Holotype male, Texas, 28°52’0.01”S, 151°10’0.12”E, 24 November 1996, found in tree clearing, T.B. Churchill (QMB S48356).

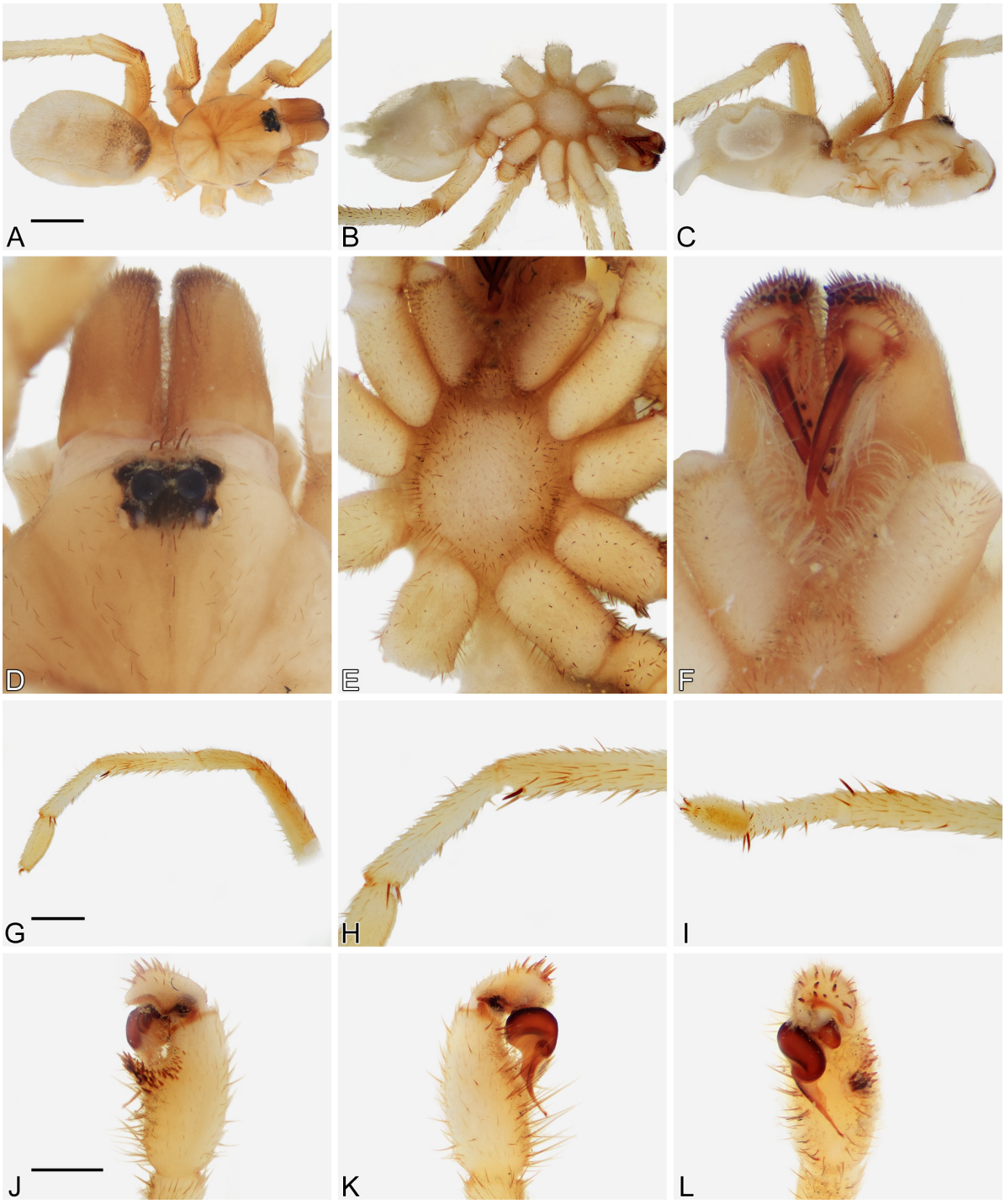


FIGURE 24. *Blakistonia plata* **sp. n.**, holotype male (QMB S48356): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, right leg I, macroseta, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Diagnosis. Males of *B. plata* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 24G–I); from those of *B. parva*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the presence of one, rather than two, prolateral macroseta on tibia I (Fig. 24G–I); from those of *B. maryae*, *B. hortoni* and *B. newtoni* by a subquadrate eye group (Fig. 24D); and from those of *B. birksi* by the absence of cuspules on the maxillae (Fig. 24F) and by the absence of a strongly patterned abdomen (Fig. 24A). Females are unknown.

Description. *Holotype male* (QMB S48356). Small idiopid spider (total length 9.3).

Colour (in ethanol; Fig. 24A–C): Carapace very pale yellow-brown, darker around caput (Fig. 24A); sternum pale yellow, darker towards anterior and lateral margins; labium and maxillae pale yellow, chelicerae pale orange-brown (Fig. 24E, F); abdomen pale yellow-brown with only a faint chevron pattern towards anterior end (Fig. 24A, C); legs and pedipalp very pale yellow-brown (Fig. 24G–L).

Cephalothorax: Carapace 4.0 long, 3.5 wide, 3.1 high, 1.1 times longer than wide; oval (Fig. 24A), caput low, ocular area raised (Fig. 24C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of setae between fovea and eye group; carapace very sparsely setose, with indistinct lines of setae radiating outwards from fovea, concentrated and form fringe on lateral margins; median clump of thickened setae on clypeus (Fig. 24D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.9 wide, 2.2 long, 0.3 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row straight; AME equal in size to ALE and separated by less than the diameter of AME/ALE; PLE two-thirds of ALE and separated by about ALE diameter; PME pale, just over half the size of PLE, and separated from PLE by less than its own diameter (Fig. 24D). Labium without cuspules (Fig. 24F). Sternum 2.2 long, 1.6 wide, evenly setose; sigilla indistinct (Fig. 24E). Maxillae without cuspules (Fig. 24E, F).

Legs: diffusely setose and spinose on all surfaces, more setose on ventral tibiae, metatarsi and tarsi III, IV; tarsi I, II slightly ventrally swollen; tarsi I, II weakly scopulate (Fig. 24G–I). Paired tarsal claws: right leg I p5 (4 large, 1 small) r6 (3 large, 3 small); right leg II p4 (3 large, 1 small), r4 (2 large, 2 small); right leg III p3 (2 large, 1 small), r4 (2 large, 2 small); right leg IV p5 (3 large, 2 small, r5 2 (3 large, 2 small).

Spination: Tibia I with single prolateral macroseta (Fig. 24G–I). All legs diffusely setose and spinose, without clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 4.2, patella 2.1, tibia 3.2, metatarsus 4.5, tarsus 1.7, total = 15.7. Leg II: femur 4.0, patella 2.0, tibia 2.9, metatarsus 4.5, tarsus 1.7, total = 15.7. Leg III: femur 3.4, patella 1.7, tibia 2.3, metatarsus 2.8, tarsus 1.7, total = 11.9. Leg IV: femur 4.4, patella 1.9, tibia 4.1, metatarsus 4.7, tarsus 2.1, total = 17.2. Pedipalp: femur 2.1, patella 1.2, tibia 1.9, tarsus 0.9, total = 6.1.

Pedipalp: Femur with dorsal spines, patella with thickened ventral setae; tibia very short and swollen, RTA short and very pointed, covered in short, dense spinules for *ca*. half distance between base of apophysis and distal tibia, becoming more sparse towards distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, just over the length of bulb; cymbium covered in rows of spinules of moderate length, becoming longer and denser towards distal edge (Fig. 24J–L).

Abdomen: Abdomen setose, oval, dorsal sigilla not evident; 5.3 long, 3.4 wide (Fig. 24A).

Variation: None.

Etymology. The specific name is taken from the Latin *plata* (meaning 'silver'), in reference to the silver mining industry in Texas, Queensland.

Distribution. *Blakistonia plata* is known only from Texas, in south-eastern Queensland (Fig. 34).

Remarks. This male specimen was found in a tree clearing.

***Blakistonia raveni* sp. n.**
(Fig. 25A–L)

Type material. AUSTRALIA: ***Queensland:*** Holotype male, Drummond Ranges Summit, 23°32'00"S, 147°18'00"E, 25 October–17 December 2000, open forest, pitfall trap, D. Cook, G. Monteith (QMB S57760).

Diagnosis. Males of *B. raveni* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 25G–I); from those of *B. plata*, *B birksi*, *B. newtoni*, and *B. hortoni* by the presence of two, rather than one, prolateral macrosetae

on tibia I (Fig. 25G–I); from those of *B. parva* and *B. maryae* by an eye group that is wider than long (Fig. 25D), and from those of *B. olea*, *B. tariae* and *B. carnarvon* by the AME that are not significantly larger than the ALE (Fig. 25D), a distinctive ring of dark colour around the carapace edge (Fig. 25A), and an embolus that narrows/tapers before its midpoint (Fig. 25L). Females are unknown.

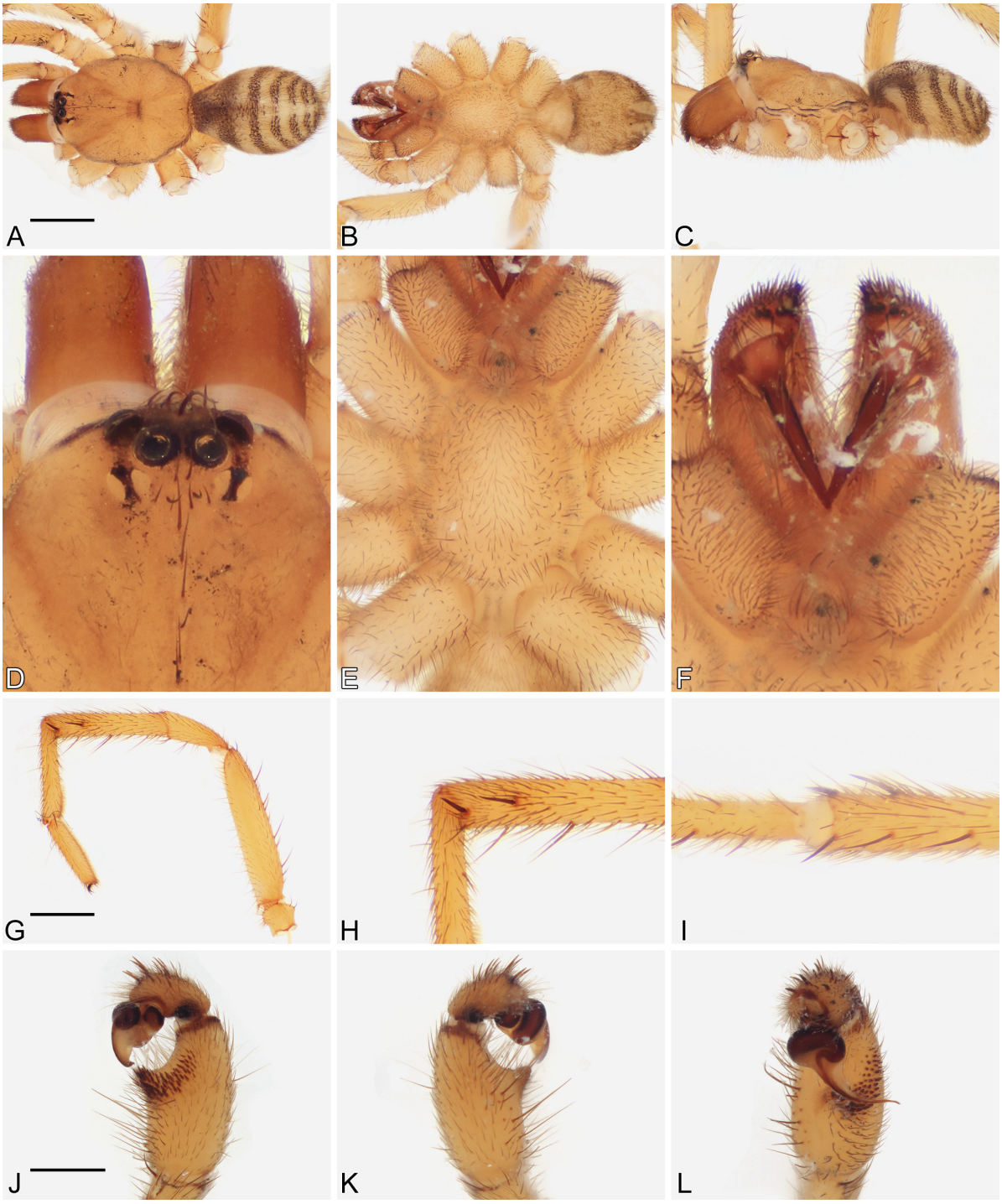


FIGURE 25. *Blakistonia raveni* **sp. n.**, holotype male (QMB S57760).): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macroseta, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Description. *Holotype male* (QMB S57760)**.** Small idiopid spider (total length 9.2).

Colour (in ethanol; Fig. 25A–C): legs, pedipalp and carapace yellow-brown, darker around lateral margins (Fig. 25A); sternum yellow-brown, paling towards margins; labium and maxillae same medium brown as sternum; chelicerae slightly darker yellow-brown (Fig. 25E); abdomen grey-brown with a distinct pattern of seven dark brown chevrons, anterior two chevrons connected by dark brown median patch, posterior three chevrons separated by pale medial patch (Fig. 25A, C).

Cephalothorax: Carapace 3.6 long, 2.8 wide, 2.8 high, 1.3 times longer than wide; oval (Fig. 25A), caput moderately raised, ocular area raised (Fig. 25C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of setae between fovea and eye group, culminating in clump of setae directly posterior to eye group; setae radiating outwards in lines from fovea, concentrated and form fringe on lateral margins; median clump of thickened setae on clypeus (Fig. 25D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.8 wide, 0.5 long, 0.3 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row slightly recurved; AME slightly smaller than ALE and separated by less than AME diameter; PLE about one-third of ALE and separated by about ALE diameter; PME pale, about two-thirds of PLE, and separated from PLE by less than its own diameter (Fig. 25D). Labium without (Fig. 25F). Sternum 1.9 long, 1.7 wide, evenly setose; sigilla indistinct (Fig. 25E). Maxillae without cuspules (Fig. 25E, F).

Legs: diffusely setose and spinose; tarsi I and II ventrally slightly swollen; tarsi and distal metatarsi I, II scopulate. Paired tarsal claws: leg I p5 (5 large) r6 (5 large, 1 small); leg II p5 (5 large), r5 (5 large); leg III p5 (5 large), r5 (5 large); leg IV p6 (5 large, 1 small, r6 5 large, 1 small).

Spination: Tibia I with two prolateral macrosetae (Fig. 15G–I). All legs diffusely setose and spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 3.6, patella 1.8, tibia 2.6, metatarsus 2.3, tarsus 1.6, total = 11.9. Leg II: femur 3.2, patella 1.5, tibia 2.4, metatarsus 2.1, tarsus 1.7, total = 9.2. Leg III: femur 2.8, patella 1.3, tibia 2.1, metatarsus 2.3, tarsus 1.7, total = 8.5. Leg IV: femur 3.7, patella 1.8, tibia 3.4, metatarsus 3.4, tarsus 1.9, total = 14.2. Pedipalp: femur 2.0, patella 1.0, tibia 1.7, tarsus 0.9, total = 8.0.

Pedipalp: Femur with dorsal spines, patella with thickened ventral setae; tibia short and swollen, RTA very short and stout, covered in short, dense spinules for more than half distance between base of apophysis and distal tibia, becoming more sparse towards distal end; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, just over length of bulb; cymbium with rows of long spinules, becoming longer and denser distally (Fig. 25J–L).

Abdomen: Abdomen setose, oval, dorsal sigilla not evident; 3.5 long, 2.4 wide (Fig. 25A).

Variation: None.

Etymology. This species is named in honour of Dr Robert Raven, for his unparalleled contributions to arachnid taxonomy.

Distribution. *Blakistonia raveni* is known only from the Drummond Ranges, Queensland (Fig. 34).

Remarks. This specimen was caught in a pitfall trap in open forest.

***Blakistonia tariae*, sp. n.**
(Fig. 26A–L)

Type material. AUSTRALIA: ***Western Australia:*** Holotype male, Coolinup Nature Reserve, 33°43'53"S, 122°17'50"E, 2 May–29 November 2000, pitfall, P. Van Heurck, Salinity Action Plan Survey (WAM T139466). Paratype: 1 male, same data (WAM T142374).

Other material examined. AUSTRALIA: ***Western Australia:*** 1 male, Durokoppin Nature Reserve, 31°24'S, 117°45'E, 11 August–9 September 1990, pitfall, B. Main (WAM T139467).

Diagnosis. Males of *B. tariae* can be distinguished from those of *B. bella*, *B. pidax*, *B. tunstilli*, *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the absence of prolateral clasping spurs on tibia I (Fig. 26G–L); from those of *B. plata*, *B birksi*, *B. newtoni*, and *B. hortoni* by the presence of two, rather than one, prolateral macrosetae on tibia I (Fig. 26G–I); from those of *B. parva* and *B. maryae* by an eye group that is wider than long (Fig. 26D), and from *B. olea*, *B. carnarvon* and *B. raveni* by the combined presence of AME that are similar or smaller in diameter relative to the ALE (Fig. 26D), and a carapace that is fairly uniform in colour, with no distinct ring of dark colour around edge of carapace (Fig. 26A). Females are unknown.

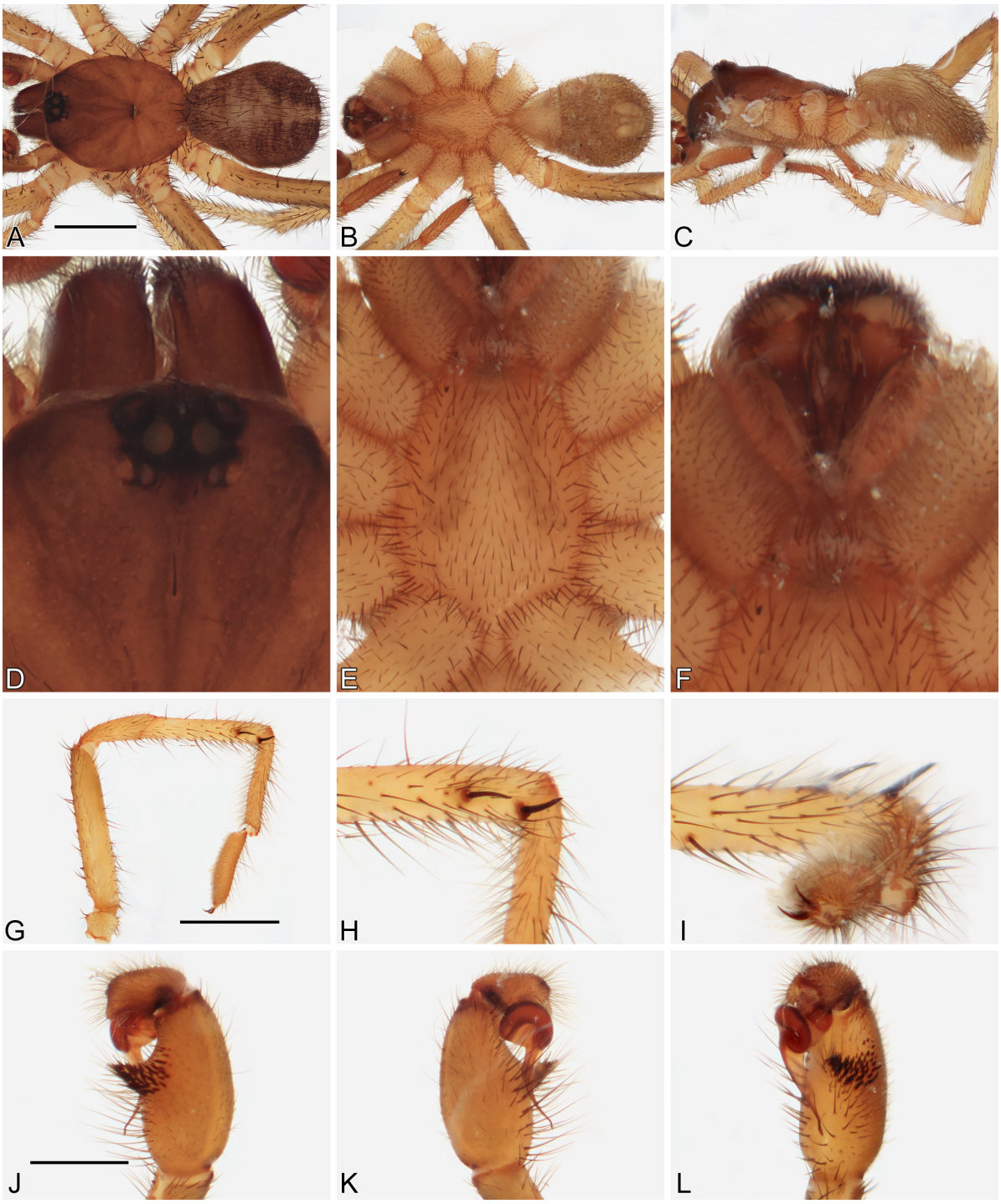


FIGURE 26. *Blakistonia tariae* **sp. n.**, holotype male (WAM T139466): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, macrosetae, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Description. *Holotype male* (WAM T139466)**.** Small idiopid spider (total length 6.7).

Colour (in ethanol; Fig. 26A–C): Legs, pedipalp and carapace dark red-brown, darker around caput and anterior margin (Fig. 26A); sternum light golden-yellow; labium and maxillae same yellow as sternum, chelicerae

similar dark red-brown as anterior end of carapace (Fig. 26E, F); abdomen medium brown with no noticeable chevron pattern (Fig. 26A, C).

Cephalothorax: Carapace 3.5 long, 2.5 wide, 1.8 high, 1.4 times longer than wide; oval (Fig. 26A), caput low, ocular area raised (Fig. 26C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; row of three thick setae between fovea and eye group, culminating in several longer, thickened setae directly posterior to eye group; carapace very sparsely setose, with indistinct lines of setae radiating outwards from fovea, concentrated and form fringe on lateral margins; median clump of thickened setae on clypeus (Fig. 26D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.6 wide, 1.6 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.0; posterior eye row straight; AME similar in size to ALE and separated by about half ALE diameter ALE; PLE just over half of ALE and separated by about ALE diameter; PME pale, about half of PLE, and separated from PLE by less than half its own diameter (Fig. 26D). Labium without cuspules (Fig. 26F). Sternum 1.6 long, 2.0 wide, evenly setose; sigilla indistinct (Fig. 26E). Maxillae without cuspules (Fig. 26E, F).

Legs: diffusely setose and spinose on all surfaces; tarsi I, II slightly ventrally swollen; tarsi I, II weakly scopulate (Fig. 26G–I). Paired tarsal claws: leg I p5 (5 large) r5 (5 large); leg II p4 (4 large), r6 (5 large, 1 small); leg III p3 (3 large), r2 (2 large); leg IV p5 (2 large, 3 small, r3 2 large, 3 small).

Spination: Tibia I with two prolateral macrosetae (Fig. 26G–I). All other legs diffusely setose and spinose, with no clear demarcation between lanceolate setae and smaller spine-like setae.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 3.4, patella 1.6, tibia 2.4, metatarsus 2.2, tarsus 1.5, total = 11.1. Leg II: femur 3.1, patella 1.4, tibia 2.3, metatarsus 1.9, tarsus 1.3, total = 10.0. Leg III: femur 2.6, patella 1.3, tibia 1.8, metatarsus 2.1, tarsus 1.5, total 1.5. Leg IV: femur 3.2, patella 1.7, tibia 3.5, metatarsus 3.2, tarsus 1.7, total = 13.4. Pedipalp: femur 1.9, patella 1.0, tibia 1.6, tarsus 0.7, total = 5.2.

Pedipalp: Femur with dorsal spines, patella with thickened ventral setae; tibia short and swollen, RTA short and pointed, covered in short, dense spinules for *ca.* half distance between base of apophysis and distal tibia, becoming more sparse towards distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, tip slightly twisted, *ca.* twice length of bulb; cymbium covered in fine setae, without spinules (Fig. 26J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 3.2 long, 2.0 wide (Fig. 26A).

Variation (n=2): Carapace 3.4–3.6 long, 2.7 wide, 0–2 labial cuspules.

Etymology. This species is named in honour of Tari Pawlyk, for her environmental work in the Western Australian Goldfields and her love of the Esperance beaches.

Distribution. *Blakistonia tariae* is known from Coolinup National Park (near Esperance), and Durokoppin Nature Reserve, both in south-western Australia (Fig. 33).

Remarks. The spiders found in Coolinup Nature Reserve (WAM T139466 and T142374) were collected as part of the 'Salinity Action Plan Survey' (see Keighery 2004). The spider from Durokoppin Nature Reserve was found in 'Transect F'.

***Blakistonia tunstilli,* sp. n.**
(Fig. 27A–L)

Type material. AUSTRALIA: ***South Australia:*** Holotype male, Relief Bore, Tallaringa Conservation Park, Great Victoria Desert, 28°13'S, 133°22'E, 2–7 October 1993, pitfall, Australian and New Zealand Scientific Exploration Society (SAM NN20068). Paratype: 1 male, same data (SAM NN20069); 1 male, same data except 28°14'S, 133°20'E (SAM NN20080).

Diagnosis. Males of *B. tunstilli* can be distinguished from those of *B. maryae*, *B. plata*, *B birksi*, *B. newtoni*, *B. hortoni*, *B. parva*, *B. maryae*, *B. olea*, *B. tariae*, *B. carnarvon* and *B. raveni* by the presence of prolateral clasping spurs on tibia I, each with raised cuticular bases and bearing multiple terminal peg-like macrosetae (Fig. 27G–I); from those of *B. bella* by the absence of a dark dorsal cardiac stripe (Fig. 27A); from those of *B. pidax* by the presence of spinules on the cymbium (Fig. 27J–L); and from those of *B. emmottorum*, *B. gemmelli*, and *B. aurea* by the spinules on the palpal tibia being much shorter than those on the RTA (Fig. 27A). Females are unknown.

Description. *Holotype male* (SAM NN20080). Medium-sized idiopid spider (total length 11.6).

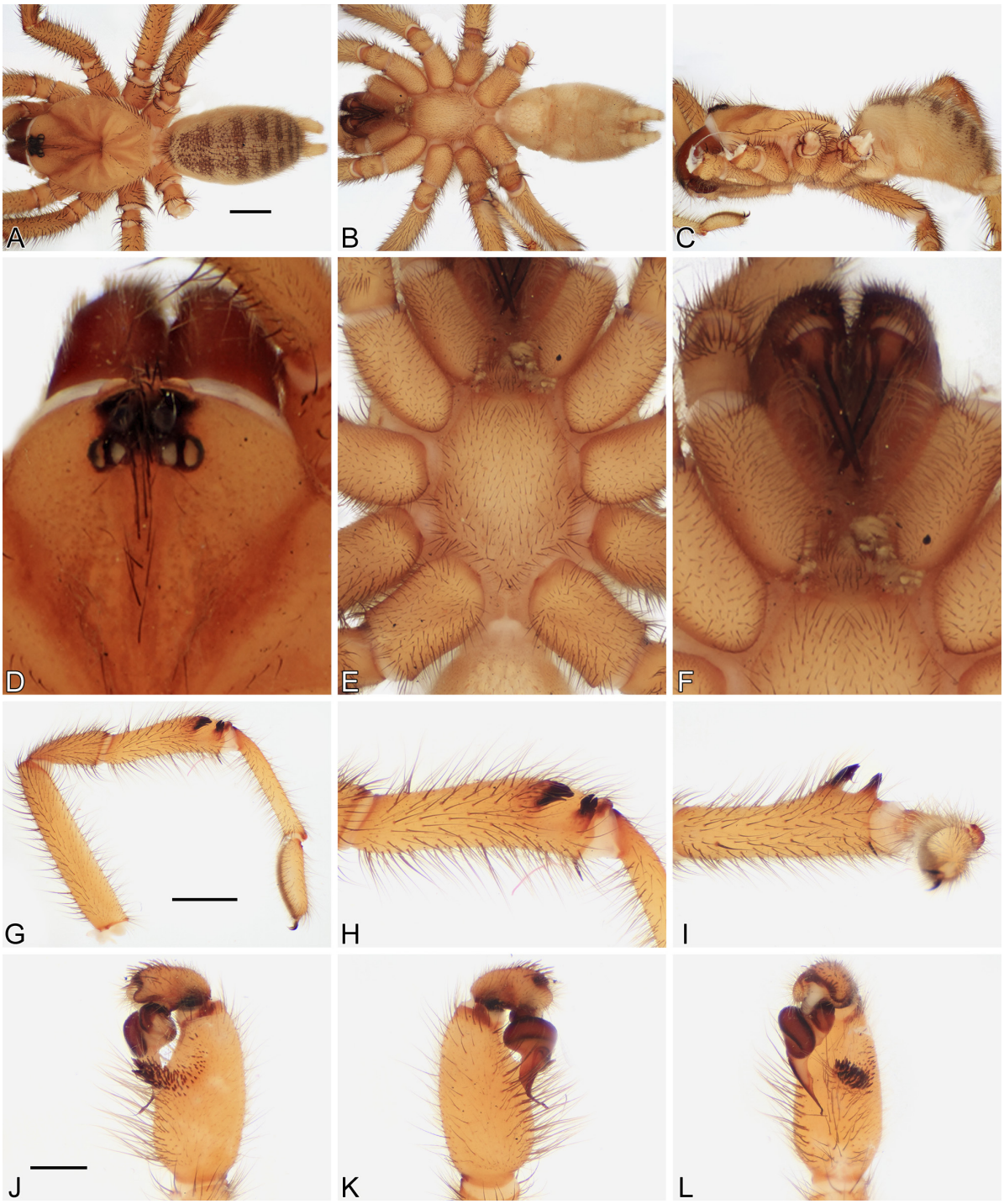


FIGURE 27. *Blakistonia tunstilli* **sp. n.**, holotype male (SAM NN20068): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, clasping spurs, prolateral view; I, left leg I, ventral view; J, left pedipalp, prolateral view; K, left pedipalp, retrolateral view; L, left pedipalp, proventral view. Scale bars = 2 mm (A, G), 1 mm (J).

Colour (in ethanol; Fig. 27A–C): Carapace, legs and pedipalp uniform pale golden orange-brown (Fig. 27A); sternum, labium and maxillae very similar colour, chelicerae slightly darker orange-brown (Fig. 27E, F); abdomen same golden orange-brown, covered by seven greyish brown mottled chevrons along entire dorsum (Fig. 27A, C.

Cephalothorax: Carapace 5.5 long, 4.4 wide, 3.4 high, 1.3 times longer than wide; oval (Fig. 27A), caput low, ocular area slightly raised (Fig. 27C); cuticle smooth, with pits outward from fovea and both sides of caput; fovea straight; defined row of setae from behind eye group to about one-third of distance between fovea and eye group; two lines of setae also diagonally backwards and outwards from fovea, with setae concentrated and forming fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 27D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 0.9 wide, 0.7 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE–PLE/ALE–ALE ratio 1.2; posterior eye row straight; AME *ca.* two-thirds of ALE and separated by about half ALE; ALE and PLE separated by about ALE diameter; PME about two-thirds of AME and about half of PLE. PLE and PME both pale and directly adjacent (Fig. 27D). Labium without cuspules (Fig. 27F). Sternum 3.2 long, 2.0 wide, evenly setose (Fig. 27E). Maxillae without cuspules (Fig. 27E, F).

Legs: moderately setose; I and II without macrosetae or spines, legs III and IV with few spines; tarsi I, II ventrally swollen; tarsi I, II weakly scopulate (Fig. 27G–I). Paired tarsal claws: leg I p7 (7 large) r5 (5 large); leg II p5 (5 large), r5 (5 large); leg III p5 (5 large), r5 (4 large, 1 small); leg IV p4 (4 large), r5 (5 large).

Spination: Spination: Tibia I with prolateral clasping spurs, distal-most spur with 2 terminal peg-like macrosetae, proximal-most with 4 terminal peg-like macrosetae (Fig. 27G–I). Leg II without spines. Leg III: patella p5; metatarsus p1, r3. Leg IV: metatarsus p4, r1.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 5.2, patella 2.4, tibia 3.5, metatarsus 3.5, tarsus 2.2, total = 16.6. Leg II: femur 4.5, patella 2.3, tibia 3.3, metatarsus 3.4, tarsus 2.0, total = 15.5. Leg III: femur 4.0, patella 1.8, tibia 2.9, metatarsus 3.7, tarsus 2.2, total = 14.6. Leg IV (right): femur 5.5, patella 2.7, tibia 4.9, metatarsus 5.4, tarsus 2.2, total = 20.6. Pedipalp: femur 3.2, patella 1.6, tibia 2.6, tarsus 1.3, total = 10.2.

Pedipalp: All segments without spines; patella with thickened ventral setae; tibia short and swollen, RTA short and pointed, covered in short, dense spinules almost to distal tibia, becoming sparser towards distal tibia; long, erect setae on ventral tibia; bulb uniform, globular; embolus simple, slender, tapering, slightly twisted with flanged tip, slightly longer than length of bulb; cymbium covered in rows of short spinules, becoming longer closer to distal edge (Fig. 27J–L).

Abdomen: Setose, oval, dorsal sigilla not evident; 6.1 long, 3.5 wide (Fig. 27A).

Variation (n=3): Carapace 5.3–6.1 long, 4.3–4.8 wide, no labial cuspules. Spination: leg III: patella p4–6, metatarsus p0–1, r3–4. Leg IV: metatarsus p3–4, r0–1, tarsus p0–1.

Etymology. This species is named in honour of Guy Tunstill, for his dedication to preserving and teaching indigenous languages, as well as for his knowledge of Australian wildlife.

Distribution. *Blakistonia tunstilli* is known only from Tallaringa Conservation Park, south-west of Lake Eyre in central South Australia (Fig. 32).

Remarks. The specimens of this species were pitfall trapped in vegetation including *Acacia aneura*, *Eucalyptus*, *Waitzia* and *Eremophila*.

***Blakistonia wingellina*, sp. n.**
(Fig. 28A–I)

Type material. AUSTRALIA: ***Western Australia:*** Holotype female, Wingellina Community, 26°02’22.2”S, 128°58’32.9”E, 12 April 2008, dug from burrow, P. Boulton, Outback Ecology (WAM T132917). Paratypes: 1 female, same data except 13 April 2008 (WAM T132914); 1 female, same data except 9 April 2008 (WAM T132915); 1 female, same data except 12 April 2008 (WAM T132916^{DNA}); 1 female, same data except 16 April 2008 (WAM T132919).

Other material examined: 1 juvenile, Wingellina Community, 26°02’22.2”S, 128°58’32.9”E, 15 April 2008 (WAM T132918).

Diagnosis. Females of *B. wingellina* can be distinguished from all other species of *Blakistonia*, except *B. nullarborensis*, by the strongly trapezoidal eye group (Fig. 28D). *Blakistonia wingellina* and *B. nullarborensis* are unable to be reliably distinguished using morphology alone. Males are unknown.

All life stages of *B. wingellina* can also be distinguished from those of other species with sequence data except *B. aurea* by the following nucleotide substitution (*n*=1 specimen): C(90).

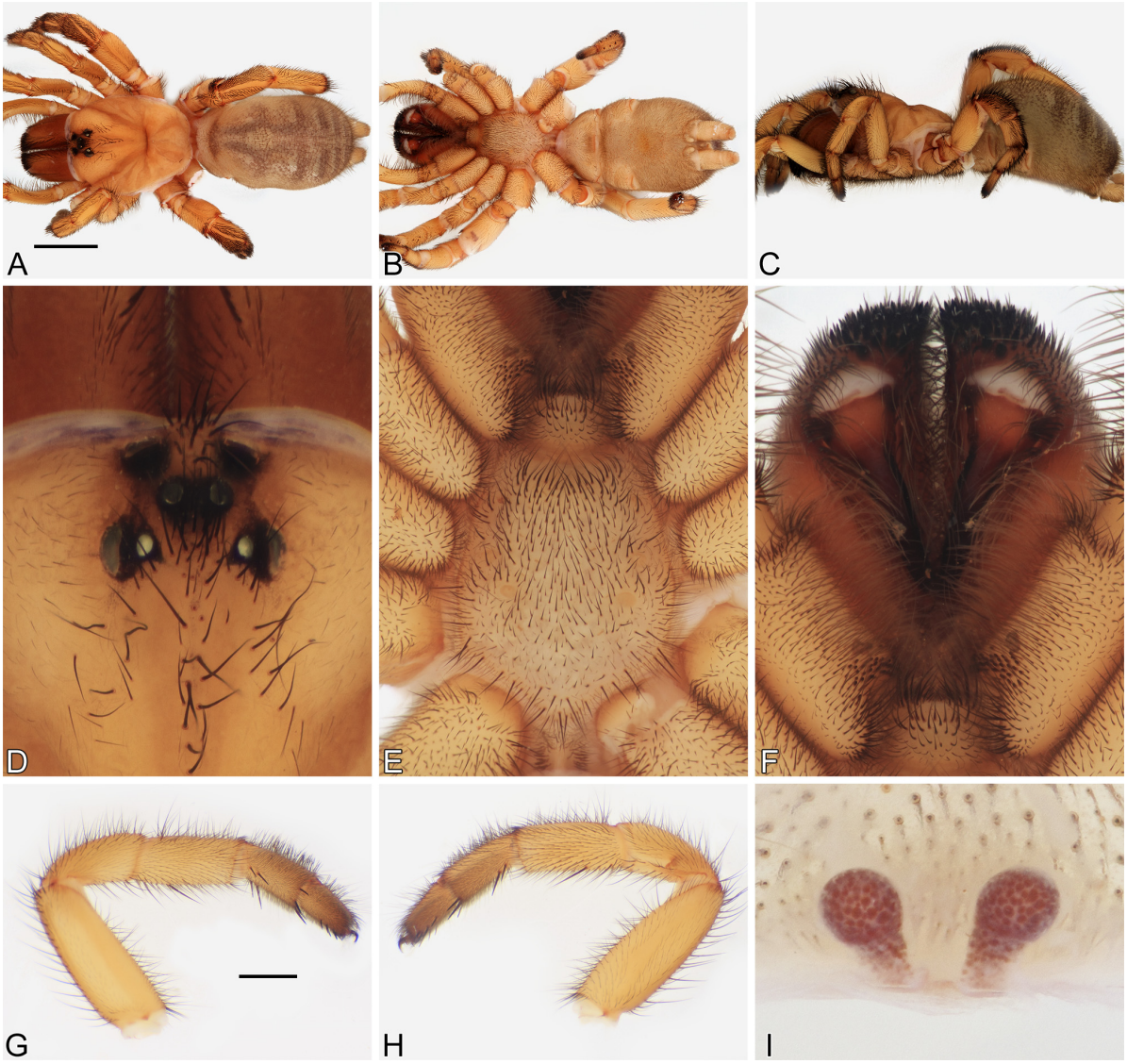


FIGURE 28. *Blakistonia wingellina* **sp. n.**, holotype female (WAM T132917): A, habitus, dorsal view; B, habitus, ventral view; C, habitus, lateral view; D, eye group, dorsal view; E, sternum, ventral view; F, maxillae and labium, ventral view; G, left leg I, prolateral view; H, left leg I, retrolateral view; J, spermathecae. Scale bars = 5 mm (A), 1 mm (G).

Description. *Holotype female* (WAM T132917)**.** Large idiopid spider (total length 17.7).

Colour (in ethanol; Fig. 28A–C): Legs, pedipalp and carapace golden orange-brown, slightly darker around fovea and lateral margins of caput (Fig. 28A); sternum, labium and maxillae golden-brown, chelicerae darker golden-brown (Fig. 28E, F); abdomen grey-brown with mottled chevron pattern for length, extending only slightly onto lateral surface, more closely spaced posteriorly (Fig. 28A, C).

Cephalothorax: Carapace 7.8 long, 6.1 wide, 5.6 high, 1.3 times longer than wide; oval (Fig. 28A); caput low, ocular area flat (Fig. 28C); cuticle uniformly smooth; fovea procurved; three rows of thick setae behind eye area, medial row extends furthest to fovea; smaller fine setae scattered very sparsely across carapace, concentrated and form very fine, indistinct fringe around lateral margins; median clump of thickened setae on clypeus (Fig. 28D). Length of median clypeus less than 1.0; anterior margin slightly convex. Eye group 1.5 wide, 1.4 long, 0.2 of carapace width; anterior eye row strongly procurved, PLE/ALE–ALE ratio 1.3; posterior eye row recurved; AME about 0.5 of ALE and separated by about ALE diameter; ALE and PLE separated by about 1.5 times PLE diameter; PME pale, *ca.* 0.25 of PLE, and separated from PLE by about its own diameter (Fig. 28D). Labium without

cuspules (Fig. 28E). Sternum 4.1 long, 3.4 wide, moderately setose with setae becoming denser and longer around margins; 3 pairs of sigilla, anterior-most pair in lateral margins near anterior margin; second pair at one-third length; third pair at *ca*. three times their width from margins (Fig. 28E). Maxillae with *ca*. 30 (left) and 27 (right) cuspules (Fig. 28E, F).

Legs: moderately setose and diffusely spinose, retrolateral sides least setose and dorsal III and IV with thick, dense, spine-like setae; distinct upright setae on tarsi and metatarsi I, II; femora I, II, and pedipalp laterally bowed; tarsi and metatarsi I, II, and palpal tarsus heavily scopulate (Fig. 28G, H). Paired tarsal claws: leg I p2 (1 large, 1 small) r3 (3 large); leg II p2 (1 large, 1 small), r2 (1 large, 1 small); right leg III p2 (1 large, 1 small), r1 (1 large); right leg IV p2 (2 large), r2 (1 large, 1 small). Pedipalp claw with 1 large and 1 small ventral tooth.

Spination: Leg I: tibia p2, r4; metatarsus p5, r6; tarsus p9. Leg II: tibia r3; metatarsus p4, r6; tarsus p2, r10. Right leg III: patella p4; metatarsus p5, r4; tarsus p4, r5. Right leg IV: metatarsus p9, r1; tarsus p8, r4. Pedipalp: tibia p4, r5; tarsus p2, r4.

Leg and pedipalp measurements: Length of legs IV > I > II > III. Leg I: femur 3.9, patella 2.6, tibia 2.5, metatarsus 2.2, tarsus 1.2, total = 12.4. Leg II: femur 3.6, patella 2.5, tibia 2.0, metatarsus 1.9, tarsus 1.7, total = 11.7. Leg III: femur 3.5, patella 2.6, tibia 2.0, metatarsus 2.3, tarsus 1.9, total = 12.3. Leg IV: femur 4.5, patella 3.7, tibia 4.0, metatarsus 3.4, tarsus 2.1, total = 17.7. Pedipalp: femur 3.8, patella 2.2, tibia 2.0, tarsus 2.7, total = 10.7.

Abdomen: Setose, oval, one pair of indistinct, unsclerotised dorsal sigilla on anterior-third of abdomen; 9.9 long, 5.8 wide (Fig. 28A).

Genitalia: Spermathecae paired, simple, unbranched, stout and outward facing, oval-shaped, covered in opaque mottled brown nodules, more concentrated on lobe of spermathecae (Fig. 28I).

Variation (n=5): Carapace 7.0–10.3 long, 5.6, 7.7 wide, no labial cuspules. Spination: Leg II tibia p0–2, r2–4; metatarsus p3–5, r4–9; tarsus p0–3, r4–14. Leg II tibia p0,. r2–3; metatarsus p3–4, r5–7; tarsus p2–4, r6–10. Leg III patella p3–4, r0 ; tibia p0–2, r0 ; metatarsus p3–5, r4–5; tarsus p4–8, r4–6. Leg IV metatarsus p5–9, r1–6; tarsus p8–10, r3–4. Pedipalp patella p0. r1; tibia p4–5, r3–5; tarsus p1–3, r1–4.

Etymology. The specific name is a noun in apposition, and refers to the community of Wingellina, where the specimens were collected.

Distribution. This species is known only from Wingellina, Western Australia (Fig. 33), near the Western Australian/South Australian border in the Goldfields region.

Remarks. The land surrounding the Wingellina community consists of prickly mallee and mulga country.

Blakistonia 'sp. 1'

Material examined. AUSTRALIA: ***Western Australia:*** One juvenile, Yamarna, 140 km E. of Laverton, 28°07'58"S, 123°41'22"E, 3 December 2011, hand collected, *Acacia* shrubland, V. Saffer (WAM T121587^{DNA}).

Diagnosis. As *Blakistonia* 'sp. 1' is known only from a juvenile specimen, it cannot be distinguished from other species by morphology. However, all life stages of this species can be distinguished from those of other species with sequence data by the following nucleotide substitutions (*n*=1 specimen): C(108), C(144), T(271), T(299), C(346), T(478); and by the following unique motifs: GAT(47–49), TC(57–58), TA(99–100), GC(210–211), CA(354–355), AGC(373–375), GTTA(414–418), GA(456–457), TTT(470–472), GT(477–478), AT(513–514).

Distribution. This species is known only from Yamarna, 140 km east of Laverton, in the Goldfields region of Western Australia (Fig. 33).

Remarks. As the only known specimen of *Blakistonia* 'sp. 1' is a juvenile, it is not formally described as a new species, although the molecular data clearly demonstrate it as new.

Unidentified *Blakistonia* specimens (females and juveniles)

Material examined. AUSTRALIA: ***South Australia:*** 1 juvenile, Kangaroo Island, 35°45'S, 137°37'E, 2 December 1965, A.R. Main (WAM T141084); 1 juvenile, about 11 km north of Tumby Bay, 34°16'S, 136°06'E, 14 December 1952, B.Y. Main (WAM T141088); 1 juvenile, Kappi Ki Homestead, 33°19'S, 120°58'E, 16 December

1952, B.Y. Main (WAM T141089); 1 female, 29 km from Lock on road to Elliston, 33°31'S, 135°44'E, 17 December 1952, B.Y. Main (WAM T141090); 1 juvenile, Ceduna, behind first line of sand hills-west of town, 32°07'S, 133°40'E, 21 December 1952, B.Y. Main (WAM T141091); 1 juvenile, Port Kenny, 7.5 km west of silo, 33°07'S, 134°37'E, 7 May 1986, B.Y. Main (WAM T141106); 1 female, 19 km east of Penong on Eyre Highway, 31°56'S, 133°08'E, 22 December 1952, B.Y. Main (WAM T141117); 1 female, Flinders Ranges, 33°06'S, 138°10'E, 24 March 1905, R.H. Pulleine (AM KS.10251); 1 juvenile, Oaklands, Yorke Peninsula, 34°59'15"S, 137°41'18"E, 11 October 1911, R.H. Pulleine (AM KS.119909); 1 female, Pichi Richi, 32°19'S, 138°06'E (AM KS.1626); 1 female, Bridgewater, Mount Lofty Ranges, 35°00'S, 138°43'E, 1 September 1972, D. Clyne (AM KS.1627); 1 female, Henley, 34°56'S, 138°31'E (AM KS.22872); 1 female, Adelaide, 34°56'S, 138°36'E (AM KS.43713); 1 female, Black Hill, 34°53'S, 138°42'E, 18 November 1917 (AM KS.43730); 1 juvenile, Mallala, 34°27'S, 138°31'E (AM KS.43731); 1 female, Yarcowie, 33°18'S, 138°54'E, 22 March 1905, R.H. Pulleine (AM KS.43733); 1 female, Mitcham, 34°59'S, 138°37'E, 26 October 1917, R.H. Pulleine (AM KS.43734) 1 female, Canowie, 33°25'S, 138°45'E, 1 April 1908 (AM KS.43838); 1 juvenile, Woolshed Flat, 32°27'S, 137°59'E, 1 July 1909 (AM KS.43839); 1 juvenile, Black Hill, 39°42'S, 139°28'E, 18 November 1917 (AM KS.43840); 1 female, Mt Lofty Ranges, 26°59'S, 138°43'E (AM KS.43841); 1 female, Kingswood, 32°34'S, 138°08'E, 22 March 1905, R.H. Pulleine (AM KS.43842); 1 female, Crystal Brook Golf Course, Mid-North, 33°21'S, 138°12'E, 31 March 1991, dug from burrow, D. Hirst (SAM NN20008); 1 female, Burra, Mid-North, 33°40'S, 138°56'E, 2 February 1993, M. Hutchinson (SAM NN20010); 1 female, Millbrook Reservoir, Mt Lofty Ranges, 34°58'S, 138°36'E, 2 April 1981, dug from burrow, D. Hirst (SAM NN20011); 1 female, Gawler, Adelaide Plains, 34°35'S, 138°44'E, March 1986, dug from short burrow in garden under pine bark, C. Read (SAM NN20012); 1 female, Mallala, Mid-North, 34°26'S, 138°30'E, 1905 (SAM NN20014); 1 female, Para Hills, Yuli Gully, Adelaide Plains, 34°48'S, 138°39'E, September 1991, L. Bebbington (SAM NN20018); 1 female, Brady Creek, Robertstown, Murray Mallee, 33°59'S, 139°04'E, May 1936, T. Honeychurch (SAM NN20019); 1 female, Ketchowla, Murray Mallee, 33°17'S, 139°13'E, 7 October 1989, dug from burrow, Strathalbyn Field Naturalists (SAM NN20020); 1 female, Para Hills, Adelaide Plains, 34°48'S, 138°39'E, 21 October 1984, dug from burrow in lawn, T. Morley (SAM NN20021); 1 female, Somerton Park, Adelaide Plains, 34°59'S, 138°31'E, 19 February 1975, B. Casanova (SAM NN20028); 1 female, Mitcham, Adelaide Plains, 34°58'S, 138°37'E, 17 May 1986, dug up in garden, R.V. Southcott (SAM NN20030); 1 female, Morialto Falls, Spring Gully Road, Mt Lofty Ranges, 34°54'S, 138°42'E, 23 July 1982, C.M. Krutls (SAM NN20036); 1 female, Adelaide, Adelaide Plains, 34°56'S, 138°36'E, 16 April 1905 (SAM NN20037); 1 female, Klemzig, Adelaide Plains, 34°52'S, 138°38'E, November 1976, dug from burrow, E. Rech (SAM NN20041); 1 female, Hope Valley, Adelaide Plains, 34°50'S, 138°42'E, April 2008 (SAM NN20042); 1 female, Glengowrie, 56 Barker Street, Adelaide, Adelaide Plains, 34°59'S, 138°31'E, 21 March 1971, K.R. Capps (SAM NN20045); 1 female, Colonel Light Gardens, Adelaide, Adelaide Plains, 34°58'S, 138°35'E, 29 October 1965, dug from burrows in garden, C. Luscombe (SAM NN20046); 1 female, Belair National Park, Mt Lofty Ranges, 35°00'S, 138°38'E, 19 April 1905 (SAM NN20048); 1 female, Clements Gap Conservation Park, near old school site, Mid-North, 33°30'S, 138°04'E, 14 June 1997, D. Hirst (SAM NN20049); 1 female, Black Hill, Mt Lofty Ranges, 34°54'S, 138°42'E, July 2007 (SAM NN20053); 1 female, Black Hill, Mt Lofty Ranges, 34°54'S, 138°42'E, July 2007 (SAM NN20054); 1 female, Black Hill, Mt Lofty Ranges, 34°54'S, 138°42'E, July 2007 (SAM NN20055); 2 females, Black Hill, Mt Lofty Ranges, 34°54'S, 138°42'E, July 2007 (SAM NN20056–7); 2 females, Athelstone, Adelaide Plains, 34°54'S, 138°42'E, 29 January 1971, dug from burrow, D.C. Lee (SAM NN20058–9); 1 female, Belair, Mt Lofty Ranges, 34°59'S, 138°37'E, December 1975 (SAM NN20062); 1 female, Middleback Station, Eyre Peninsula, 32°57'S, 137°23'E, September 1983, B. Guerin (SAM NN20067); 1 female, Middleback Station, Eyre Peninsula, 32°57'S, 137°23'E, July 1984, B. Guerin (SAM NN20070); 1 female, Bunyeroo Gorge, Heysen Range, Flinders Ranges, 31°25'S, 138°33'E, 17 May 1990, D. Hirst (SAM NN20072); 1 female, Middleback Station, Eyre Peninsula, 32°57'S, 137°23'E, July 1984, B. Guerin (SAM NN20073); 1 female, Middleback Station, Barber's paddock, Eyre Peninsula, 32°57'S, 137°23'E, July 1985, dug from burrow, B. Guerin (SAM NN20074); 1 female, Arcoona Creek Gammon Ranges, Flinders Rangers, 30°28'S, 138°58'E, 4 May 1989, dug from burrow in hard soil in creek bank, D. Hirst (SAM NN20081); 1 female, Bunyeroo Creek, ABC Range, Flinders Ranges, 31°25'S, 138°34'E, 16 May 1990, D. Hirst (SAM NN20083); 1 female, Bunyeroo Creek, ABC Range, Flinders Ranges, 31°25'S, 138°34'E, D. Hirst (SAM NN20084); 1 female, Bunyeroo Creek, ABC Range, Flinders Ranges, 31°25'S, 138°34'E, D. Hirst (SAM NN20085); 1 female, Welcome Well, Arcoona Station, Gairdner-Torrens Basin, 31°17'04"S, 137°04'21"E, pitfall

(SAM NN20088); 1 juvenile, Mt Ohlssen-Bagge peak, Wilpena Pound, Flinders Ranges, 31°32'S, 138°36'E, 23 April 1987, D. Hirst (SAM NN20093); 1 female, Mt Fairview, Paney Station, Gawler Ranges, 32°34'S, 135°35'E, 7 December 1989, Found amongst mallee near creek, D. Hirst (SAM NN20094), 1 female, Mt Ohlssen-Bagge peak, Wilpena Pound, Flinders Rangers, 31°32'S, 138°36'E, 23 April 1987, D. Hirst (SAM NN20099), 1 female, Kolay Hut, Paney Station, Gawler Rangers, 32°33'S, 135°36'E, 10 December 1989, D. Hirst (SAM NN20104), 1 female, Arcoona Creek, Flinders Rangers, 30°28'S, 139°01'E, 5 May 1989, dug from burrow on southern cliff face, door included, D. Hirst (SAM NN20105); 1 female, Kolay Hut, Paney Station, Gawler Ranges, 32°33'S, 135°36'E, 10 December 1989, D. Hirst (SAM NN20106); 1 female, Arcoona Creek Gammon Ranges, Flinders Ranges, 30°28'S, 138°58'E, 4 May 1989, D. Hirst (SAM NN20107); 1 female, Kolay Hut, Paney Stn, <20 m from creek, Gawler Ranges, 32°33'S, 135°36'E, 10 December 1989, dug from burrow near creek, D. Hirst (SAM NN20108) 1 female, Clements Gap Conservation Park, Mid-North, 33°29'S, 138°04'E, 4 October 1997, dug from burrow, D. Hirst (SAM NN20110); 4 females, Beetaloo Reservoir, Mid-North, 33°11'S, 138°16'E, 14 June 1997, dug from short burrow, D. Hirst (SAM NN20111–4); 1 female, Balcanoona, Flinders Ranges, 30°38'30"S, 139°31'10"E, July 1997, pitfall (SAM NN20115); 3 females, Mallala, Mid-North, 34°26'S, 138°30'E, April 2008 (SAM NN20663–5); 2 females, Mallala, Mid-North, 34°26'S, 138°30'E, April 2008 (SAM NN20664–5); 2 females, Pt Augusta, Eyre Peninsula, 32°29'S, 137°46'E (SAM NN20666–7); 9 females, Belair National Park, Mt Lofty Ranges, 35°01'S, 138°39'E, January 1936 (SAM NN20668–76); 1 female, Adelaide, Adelaide Plains, 34°56'S, 138°36'E (SAM NN20677); 1 female, Orroroo, Flinders Ranges, 32°44'S, 138°36'E, J.T. Gray (SAM NN20683); 1 female, Whyalla, Eyre Peninsula, 33°02'S, 137°34'E, 30 March 1976, P. Hudson (SAM NN20684); 1 female, Carappee Hill, Eyre Peninsula, 33°25'37"S, 136°15'56"E, pitfall, D. Hirst (SAM NN26636); 1 female, Wiawirra Station, Olary, 32°17'31"S, 140°23'38"E, 11 October 2006, N. Birks (SAM NN28999); 1 female, 5 km east of Olary, 32°17'S, 140°24'E, 11 October 2006, N. Birks (SAM NN29001); 1 female, 35.2 km north of Olary, 32°59'06"S, 140°10'41"E, Found in low chenopod shrubland (SAM NN29002); 3 juvenile, on road to Mount Middleback, off Port Lincoln Highway, south west of Whyalla, 33°11'16"S, 137°15'13"E, 2 May 2013, dug from burrow near paddock fence in saltbush paddock, S.E. Harrison, M.L. Harrison (SAM NN29569); 3 juveniles, Pichi Richi Park, Pichi Richi Pass, Flinders Ranges, 32°25'46"S, 137°58'16"E, 3 May 2013, dug from burrow in dry grass, S.E. Harrison, M.L. Harrison (SAM NN29572); 1 female, Pichi Richi Park, Pichi Richi Pass, Flinders Ranges, 32°25'46"S, 137°58'16"E, 3 May 2013, dug from burrow in dry grass, S.E. Harrison, M.L. Harrison (SAM NN29573); 1 female, Survey Road (dirt road between Melrose and Port Germein), 32°50'48"S, 138°10'53"E, 5 May 2013, dug from burrow on dry creek bank in paddock under gumtree, S.E. Harrison, M.L. Harrison (SAM NN29580); 3 juveniles, Lindsay Terrace, Kadina, 33°57'25"S, 137°43'07"E, 5 May 2013, dug from burrow on dry grassy verge, S.E. Harrison, M.L. Harrison (SAM NN29582); 3 juveniles, Hicky's Drive, Coobowie, 35°01'42"S, 137°45'42"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29585); 1 female, Saint Vincent Highway, Port Vincent, 34°46'44"S, 137°50'08"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29586); 3 juvenile, Arthurton Road, 34°21'58"S, 137°49'46"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29589); 3 juvenile, Maitland-Ardrossan Road, 34°23'21"S, 137°43'28"E, 6 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29591); 3 juveniles, on unnamed road from Port Moorowie toward Yorketown (extension of McEacherns Beach Road), 35°04'24"S, 137°32'01"E, 8 May 2013, dug from burrow on dry verge next to paddock, S.E. Harrison, M.L. Harrison (SAM NN29595); 1 female, McLaren Vale, Douglas Scrub, off Jackie's Trail, 35°11'07"S, 138°36'03"E, 24 September 2013, dug from burrow on compacted sand walking trail, S.E. Harrison, M.G. Rix, B. Parslow, E. Fagan-Jeffries (SAM NN29602); 1 female, McLaren Vale, Douglas Scrub, off Jackie's Trail, 35°11'07"S, 138°36'03"E, 24 September 2013, dug from burrow on compacted bank, S.E. Harrison, M.G. Rix, B. Parslow, E. Fagan-Jeffries (SAM NN29603); 1 female, Bailey Road, Echunga, 35°7'8.64"S, 138°48'9.93", 20 March 2015, dug from burrow in grassy roadside bank, S.E. Harrison, D. G. Bass (SAM NN29622); 1 female, Para Wirra Conservation Park, Humbug Scrub Road, Humbug Scrub, 34°42'05.322"S, 138°48'44.778", 1 April 2015, dug from burrow in clay soil near lake, S.E. Harrison, B. Horton (SAM NN29626); 1 female, Mark Oliphant Conservation Park, 35°01'46.44"S, 138°42'26.03", 20 August 2015, dug from burrow in roadside embankment, S.E. Harrison, D. Stringer and A. Lewis (SAM NN29636); 1 female, Mark Oliphant Conservation Park, 35°01'50.88"S, 138°42'26.58", 25 August 2015, dug from burrow in roadside embankment, S.E. Harrison, N. Birks (SAM NN29639); 1 female, Hallett, 33°20'09"S, 138°58'18"E, 18 July 2013, dug from burrow, J. Clayton

(SAM NN29805). ***Western Australia:*** 1 juvenile, 106 km east of Wigunda Tank, Eyre Highway, 31°33'S, 130°26'E, 23 December 1952, B.Y. Main (WAM T141092); 1 juvenile, 160 km west of Eucla, 21 km east of Madura, Eyre Highway, 31°54'S, 127°21'E, 24 December 1952, B.Y. Main (WAM T141093); 1 juvenile, Cocklebiddy Tank, 32°02'S, 126°05'E, 25 December 1952, B.Y. Main (WAM T141094); 1 juvenile, 331 km east of Norseman, 112 km east of Balladonia, 71 km west of Caiguna Tank, 32°14'S, 125°27'E, 25 December 1952, B.Y. Main (WAM T141095); 2 juveniles, 288 km east of Norseman, 69 km east of Balladonia, 32°15'38'S, 124°58'E, 25 December 1952, B.Y. Main (WAM T141096–7); 1 female, 2 km south of Peak Charles turnoff on 90 Mile Tank-Dowabi Track, 32°58'S, 121°38'E, 24 May 1955, B.Y. Main (WAM T141099); 2 juveniles, 8 km north of Peak Charles, 32°49'S, 121°14'E, 25 May 1955, B.Y. Main (WAM T141100–1); 1 juvenile, 14 km north east of Norseman, 32°6'S, 121°53'E, 8 July 1955, B.Y. Main (WAM T141102); 1 female, 8 km east of Moonera Tank, 31°58'S, 126°37'E, 8 August 1955, B.Y. Main (WAM T141103); 1 juvenile, same data (WAM T141104); 4 females, Moonera, 31°43'S, 126°35'E, 22 May 1986, B.Y. Main (WAM T141107–10); 1 female, 34.3 km east of Caiguna, 32°06'S, 125°35'E, 22 May 1986, B.Y. Main (WAM T141111); 1 female, Moonera, 43 km west of Madura, 31°43'S, 126°35'E, 22 May 1986, B.Y. Main (WAM T141112); 2 juveniles, Mt Ragged walking trail, 33°27'S, 123°28'E, 22 November 1986, B.Y. Main (WAM T141113–4). ***Northern Territory:*** 1 juvenile, Mt Olga, Valley of Winds, 25°18'S, 130°44'E, 10 September 1965, A.R. Main (WAM T141085); 1 juvenile, Maggie Springs, 25°23'S, 131°05'E, 11 September 1965, A.R. Main (WAM T141086); 1 specimen (fragments), Kings Creek walk, gorge, Kings Canyon National Park, 24°15'S, 131°30'E, 6 June 1995, B.Y. Main (WAM T141116).

Remarks. The female and juvenile specimens listed here could not be confidently identified due to the lack of diagnostic morphological features or molecular sequence data.

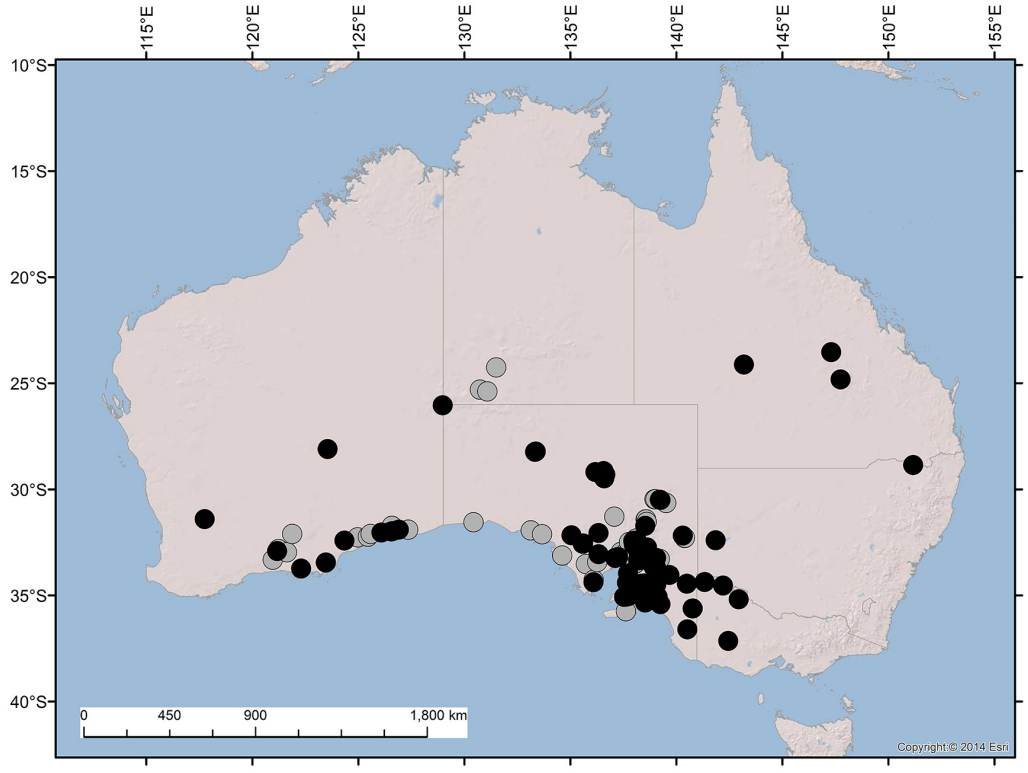


FIGURE 29. Distribution of *Blakistonia* across Australia, showing specimens belonging to identified species (black circles) and unidentified females (grey circles).

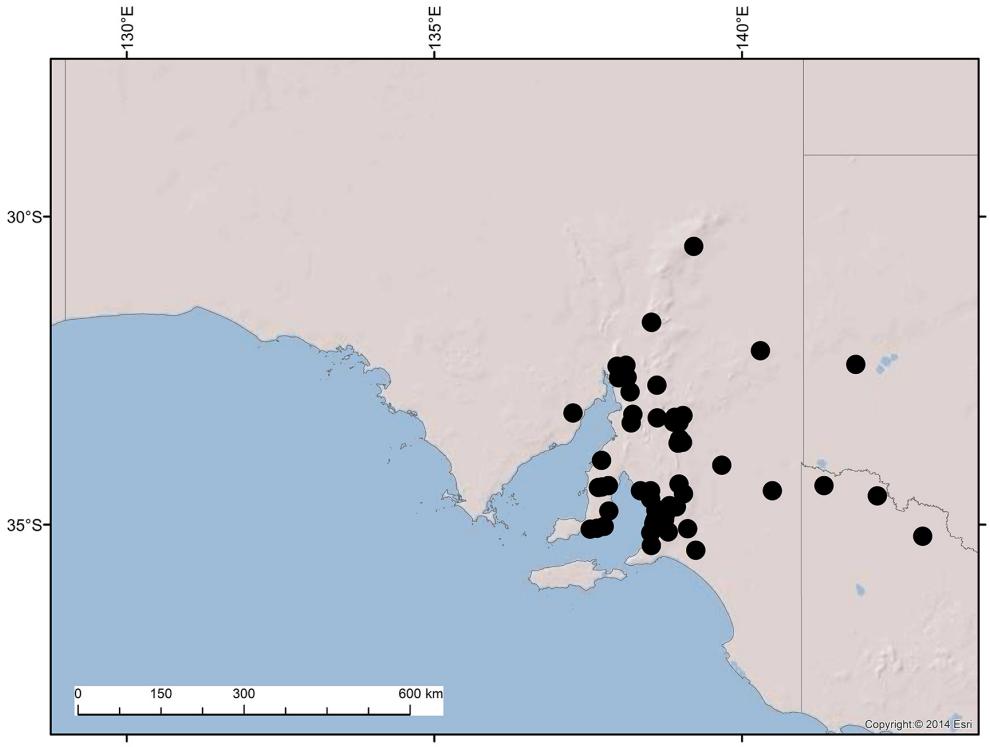


FIGURE 30. Distribution of *Blakistonia aurea* specimens across South Australia, western Victoria and western New South Wales.

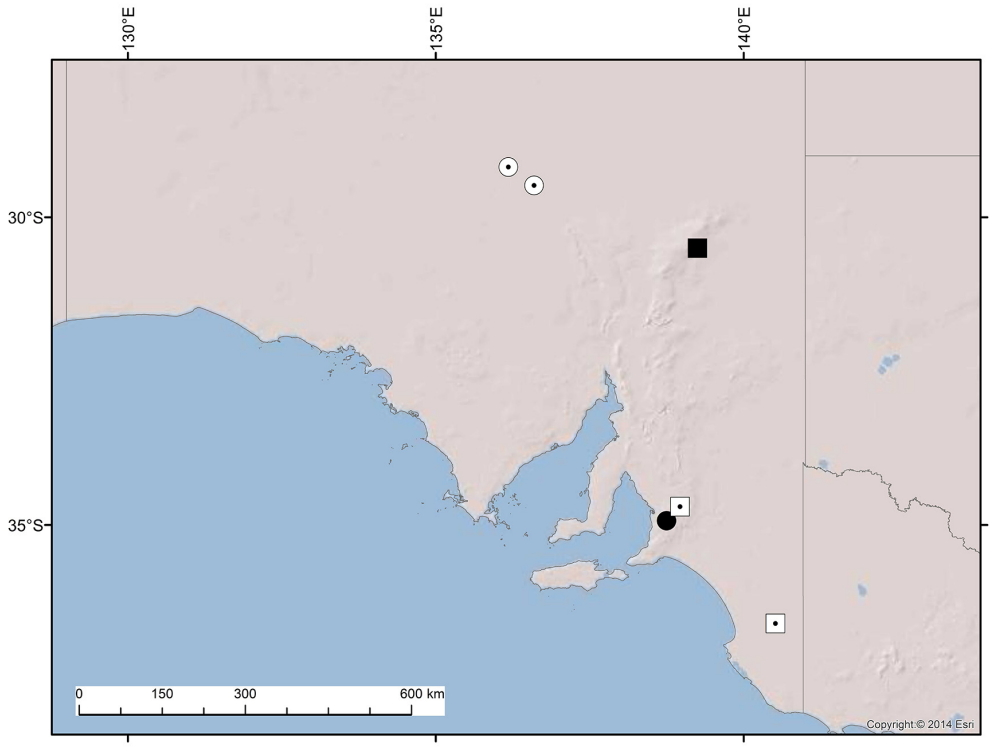


FIGURE 31. Distributions of *Blakistonia* species: *B. bassi* **sp. n.** (black circle), *B. hortoni* **sp. n.** (white squares), *B. bella* **sp. n.** (white circles), and *B. gemmelli* **sp. n.** (black square).

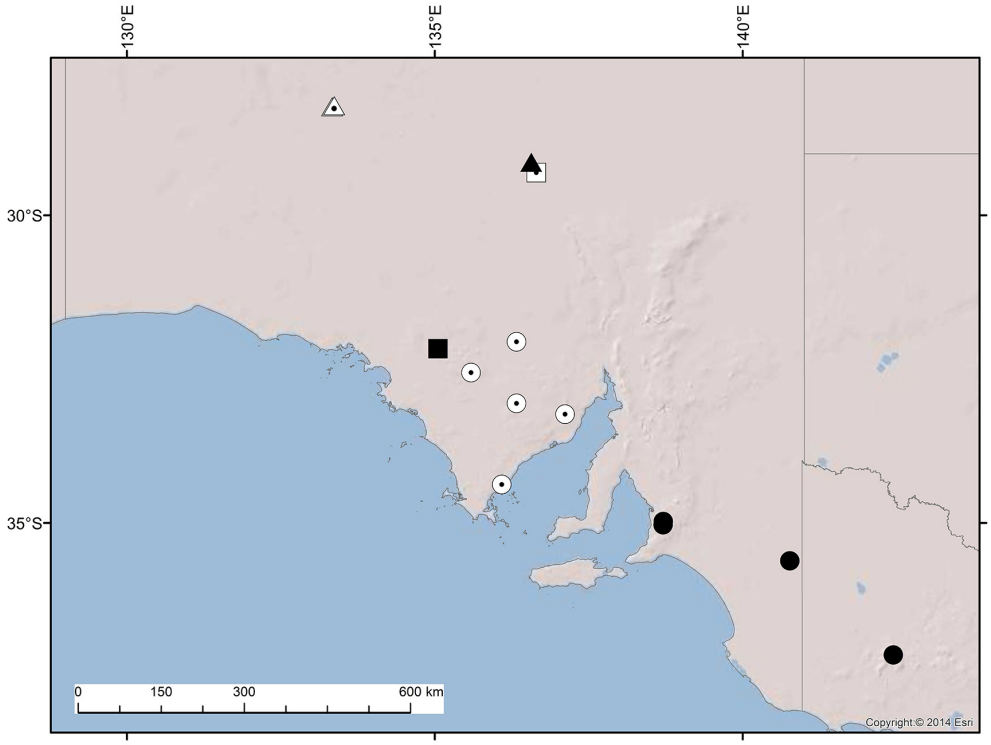


FIGURE 32. Distributions of *Blakistonia* species: *B. birksi* **sp. n.** (black circles), *B. maryae* **sp. n.** (white circles), *B. tunstilli* **sp. n.** (white triangle), *B. newtoni* **sp. n.** (black square), *B. pidax* **sp. n.** (black triangle) and *B. parva* **sp. n.** (white square).

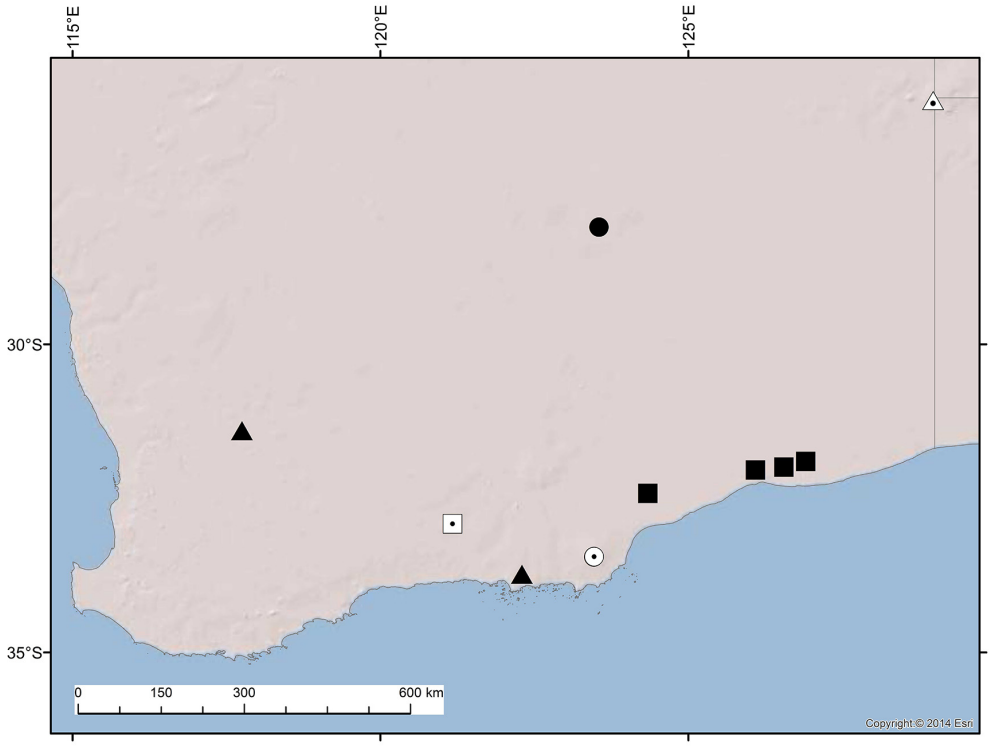


FIGURE 33. Distribution of *Blakistonia* species: *B. mainae* **sp. n.** (white circle), *B. wingellina* **sp. n.** (white triangle), *B. olea* **sp. n.** (white square), *B. nullarborensis* **sp. n.** (black squares), *Blakistonia* 'sp. 1' (black circle), and *B. tariae* **sp. n.** (black triangles).

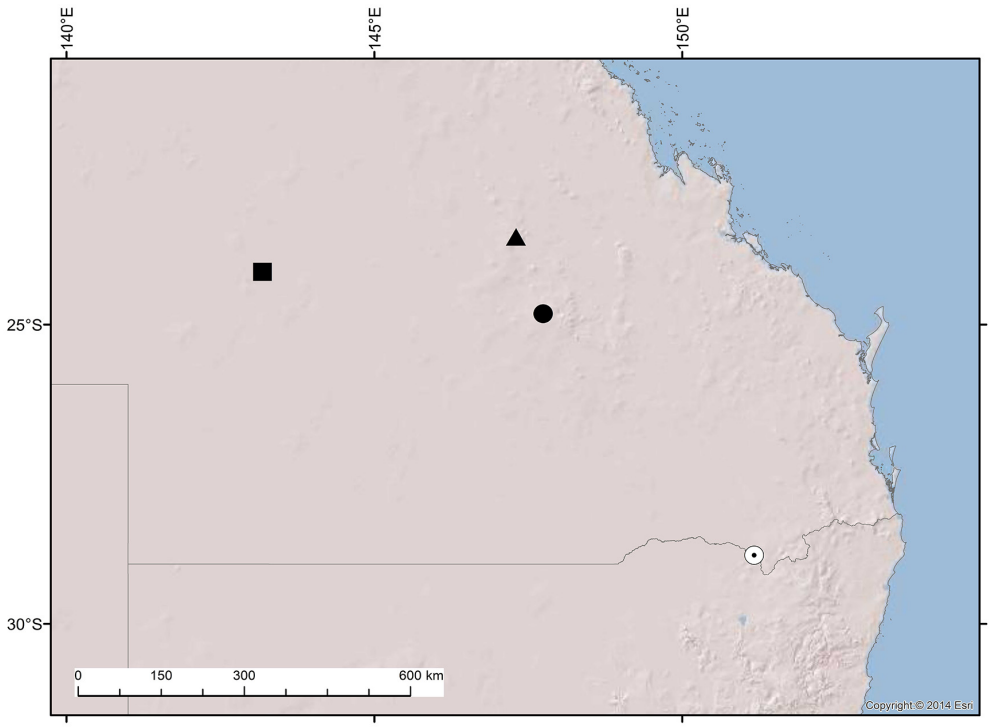


FIGURE 34. Distribution of *Blakistonia* species: *B. emmottorum* **sp. n.** (black square), *B. raveni* **sp. n.** (black triangle), *B. carnarvon* **sp. n.** (black circle), and *B. plata* **sp. n.** (white circle).

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CHAPTER V: General Discussion

5.1 Synthesis

This study set out to undertake a systematic revision of *Blakistonia*, using a combined molecular and morphological approach. Prior to the research incorporated in this thesis, the genus contained only the type species *Blakistonia aurea*, described in 1902, plus the enigmatic *B. rainbowi* and *B. exsiccata*. The genus now contains 19 newly described species from Western Australia, Victoria, New South Wales and South Australia, as well as the newly redescribed type species. In the process, '*B. exsiccata*' was designated a *nomen dubium*, and '*B.*' *rainbowi* was transferred to another family of Mygalomorphae.

The taxonomic history, reclassification, and biogeographic origins of '*B.*' *rainbowi* formed a major component of this thesis. The removal of the species from the Idiopidae and its placement into the family Migidae and the otherwise African genus *Moggridgea* posed a tantalising biogeographic question – how and when did this lineage arrive on Kangaroo Island, South Australia? To answer this, we tested three hypotheses which could explain the presence of this genus in Australia and concluded that a trans-oceanic dispersal scenario could not be rejected. In doing so, an explanation was forthcoming for the curious relationship of this species to its close African relatives, as first noticed by Cooper *et al*. (2011) and as clearly demonstrated by the morphological and molecular data analysed as part of this thesis. The vicariance versus dispersal debate has been a long-standing and controversial topic (e.g. Nelson & Platnick, 1981; Yoder & Nowak, 2006; Giribet & Boyer, 2010; de Queiroz, 2014) and this study has made a valuable contribution to piecing together the biogeographic history of a small but interesting component of Australia's biota.

This thesis also provided the first taxonomic revision of *Blakistonia*, a key taxon in the southern Australian idiopid fauna. To do this, a combination of molecular data and morphological characters from both male and female specimens were used, and an illustrated key for identifying both sexes was created. The unexpectedly diverse burrow morphology of the genus has also been described and documented with images to assist with identification in the field. Prior to this study, *Blakistonia* was only recorded to have a D-shaped trapdoor (such as *B. aurea* and *B. nullarborensis*), however, it is now known to also create a round, plug-like lid (e.g. *B. birksi* and *B. mainae*), which is similar to that of many species of *Euoplos*, and also a flap-like lid (e.g. *B. bassi*), similar to some *Idiosoma*. Interestingly, a single species, *B. maryae*, was also found to construct a twig-lined burrow entrance, which presumably acts to increase the foraging area of the species (Main, 1962). This is the first time twig-lining has been recorded for a species of *Blakistonia*, demonstrating that this foraging strategy has evolved multiple times within Australian idiopids.

This thesis also provided a better understanding of the distribution of the type and most abundant species, *B. aurea*. The molecular and morphological data demonstrate that rather than being a series of separate short-range endemic species, *B. aurea* is in fact broadly distributed, much more so than any of the newly described species within the genus. It can be found throughout the north-eastern Eyre Peninsula, the Yorke Peninsula, Flinders Ranges, Fleurieu Peninsula, Mount Lofty Ranges, and western Victoria (Chapter 4, Fig. 30), although it exhibits a pattern of phylogeographic genetic structuring throughout this range.

5.2 Conservation implications

This thesis is directly relevant to the conservation of mygalomorph spiders, given that numerous species of *Blakistonia* are short-range endemics (SREs). SREs are species with restricted geographic ranges (less than 10,000 km^2, *sensu* (Harvey, 2002). There are several factors which predispose species to becoming short-range endemics, which include low fecundity, slow growth, limited dispersal abilities, and restriction to fragmented habitats or niches. Although many invertebrates are too vagile to become SREs (Harvey, 2002), mygalomorph spiders, with their long life cycles and poor dispersal abilities, have an ideal combination of life-history traits to form restricted patterns of distribution. SREs are at high risk from a conservation perspective, as a small distribution correlates with rarity and a heightened chance of extinction (Rabinowitz, 1981).

Despite the fact that invertebrates comprise about 80% of Earth's species, they generate little conservation attention compared to the more 'charismatic' vertebrates such as birds and mammals (Braby, 2017). Evidence for limited distributions among invertebrates is sometimes regarded with suspicion and attributed to taxonomic ignorance (Harvey, 2002). While limited distributions can undoubtedly be the result of insufficient sampling effort, it must be acknowledged that some well-studied taxa are indeed in danger (Harvey, 2002), especially following comprehensive monography (e.g. Rix *et al*., 2018a). Conservation issues and declines of mygalomorph populations have been documented historically (Main, 1987, 1990, 2003), and are now starting to come further into focus with detailed systematic studies (e.g. Rix *et al*., 2018a) and demographic approaches aimed at understanding population dynamics (e.g. Rix *et al*., 2018c). Large declines in trapdoor spider populations have been recently documented by Rix *et al*. (2017c). Despite this, only a single spider in Australia is listed as threatened under the Commonwealth's *Environment Protection and Biodiversity Conservation Act 1999* (EPBC). The main processes that negatively affect trapdoor spider populations are those which go hand-in-hand with agricultural practices; that is, the clearing of native vegetation, presence of feral animals, and stocking of sheep and cattle (Rix *et al*., 2017c). The importance of a stable microclimate for burrowing spiders is well-known (e.g.

Coyle & Shear, 1981; Mason *et al*., 2013). Burrowing spiders rely heavily on an intact terrain, and activities such as landscaping and ploughing are particularly damaging (Rezac *et al.*, 2018). Such rapid alteration of the environment by humans can create severe selective pressures on species to either adapt to the altered habitat, leave, or persist in the remaining pockets of favourable habitat (Sih *et al*., 2011; Sih, 2013).These human-induced changes in the abundance and geographic range of species also contribute to the formation of SREs (Harvey, 2002) and in turn, the vulnerability of SREs is increased when combined with a limited capacity to adapt to or escape from human-induced environmental change (Sih *et al*., 2011) or relocate following disturbance (Mason *et al*., 2018a). In addition to the lack of available suitable habitat, highly disturbed environments also form 'landscape traps' (highly degraded areas) which are particularly threatening to SRE taxa (Mason *et al*., 2018a). Environmental cues (such as a certain temperature and relative humidity) usually associated with high-quality habitats may no longer be reliable in degraded habitats and may result in organisms entering such landscape traps. Habitat selection in sedentary, long-lived burrowing spiders is crucial to survival (Rezac *et al.,* 2018). The habitat created in these landscape traps may have poor prey diversity and abundance, which may negatively affect survival.

Species of *Blakistonia* may be especially vulnerable to habitat disturbance, given that all but two species, *B. aurea* and *B. birksi*, have very restricted distributions, and most are currently known from only single locations. In some instances, this may be a result of limited collecting in remote locations. However, this is not applicable for at least *B. bassi*, which is known from a single roadside cutting at Ashton, within the historically well-collected Mount Lofty Ranges. *Blakistonia maryae*, which is sparsely distributed on the Eyre Peninsula and is not found elsewhere, is likely to also be a particular conservation risk due to the amount of land used for primary production across this region. Population declines have recently been observed for *Blakistonia* by comparing historical collecting records on the Eyre and Yorke Peninsulas with field work conducted as part of this study (as per Rix *et al*. 2017b, Fig. 3). In contrast, the persistence of *B. aurea* in urban and peri-urban environments (pers. obs.) is also interesting from a conservation point of view. It is known that taxa with low mobility, low fecundity, poor dispersal abilities and a small geographical range distribution may persist in very small patches of remnant habitat in urban areas (Mason *et al*., 2016). These populations are referred to as 'urban engulfed' (Mason *et al*., 2018b). While *B. aurea* does not have a small geographical range, it does have low mobility and poor dispersal capabilities, and does appear to persist in urban environments. However, the degree of recruitment in these areas is questionable, as often only large, lone burrows of mature females are seen (pers. obs.) – so-called 'lone matriarchs' (see Rix *et al*. 2017b). Extensive clearing in urban areas may

leave SREs such as mygalomorph spiders more vulnerable to local extinction through predation in remaining small patches of habitat (Mason *et al*., 2018b). Male mygalomorph spiders may be particularly vulnerable to predation due to their mating behaviour, as wandering males are vulnerable to a suite of predators to which they would not normally be exposed when in their burrows (Mason *et al*., 2018b). Predation rates are known to be significantly affected by the amount of leaf-litter cover and proportion of surrounding parkland (Mason *et al*., 2018b), suggesting that the quality and quantity of remnant habitat are both important factors influencing population survival.

5.3 Evolution of *Blakistonia* in Australia

Many taxa with a high proportion of SREs appear to be so-called 'Gondwanan' relicts (Hopper *et al*., 1996), or more accurately, palaeo-endemic lineages with Austral or southern-temperate rather than tropical Asian origins (see Rix *et al*., 2015b; Harvey *et al*., 2017; Harvey *et al*., 2018) and *Blakistonia* is no exception. Aridification of Australia began around 15 Mya in the mid-Miocene and formed what is now one of the largest desert landforms in the world (Byrne *et al*., 2008). These aridification events played a major role in shaping Australia's biogeographic history by causing a large-scale contraction of previously mesic habitats. This, in turn, caused the extinction of some species, contraction of others, and range expansion in lineages that were able to evolve and adapt to widespread arid conditions (Rix *et al*., 2015b, 2017a). Large areas of remnant mesic habitat now only persist along the eastern and southwestern margins of the continent (Hill, 1994). As *Blakistonia* and other idiopid genera can be found in both temperate mesic areas and in Australia's arid zone, it is an ideal taxon to examine the evolutionary history of a group and its radiation in response to aridification. A dated, multi-gene phylogeny by Rix *et al*. (2017) showed that *Blakistonia*, along with *Euoplos* and *Idiosoma*, diversified in the arid zone during the mid-to-late Miocene. The most closely related species to arid-adapted *Blakistonia* is *B. bassi,* which is found at only a single location – a shady, mossy bank in the mesic Mount Lofty Ranges. Interestingly, this species is the only lineage that was found to build a flap-like lid, with all other species building plug-like doors. Therefore, an 'out-of-temperate-South-Australia' ancestral area hypothesis was suggested for *Blakistonia* (Rix *et al*., 2017a). Understanding these relationships between arid and mesic lineages is critical to improving our comprehension of the evolution of the Australian arid-zone biota.

5.4 Future directions

As species-level diversity is frequently underestimated in the absence of genetic analyses (Yoder *et al*., 2005), molecular data have played a vital role in improving our understanding of arachnid systematics. These data are usually obtained from a suite of a few standard

genes including the nuclear and mitochondrial rRNA genes 18S, 28S, 12S and 16S, as well as two protein-coding genes, nuclear histone H3 and mitochondrial COI (Benavides *et al*., 2017). These genes are often described as 'the usual suspects' (Dimitrov *et al*., 2017). Although data from these genes have undeniably played an important role in resolving phylogenetic relationships and species boundaries, future studies on idiopids and other spider families are likely to become less reliant on these 'usual suspects'. A range of novel genes are now starting to become available, as demonstrated in a recent study by Rix *et al.* (2017a), which included a baseline ortholog dataset of 149 genes. High-throughput sequencing technologies have revolutionised the questions that can be addressed and the taxa that can be studied (Wagner *et al*., 2013). A major advantage of the dramatic increase in available markers is that they can now be specifically selected for their level of 'informativeness' at the desired phylogenetic 'depth' (Rix *et al*., 2017a). Such genomic data have been useful in reconstructing relationships at both shallow (Wagner *et al*., 2013; Younger *et al*., 2018) and deep levels (Rokas *et al*., 2003; Prasad *et al*., 2008; Hejnol *et al*., 2009; Meusemann *et al*., 2010). In addition to generating massive amounts of data, parallel or high-throughput DNA sequencing platforms are also dramatically reducing the cost of sequencing (Shendure & Ji, 2008; Godwin *et al*., 2018) which is likely to make next-generation datasets increasingly common in the future (Wagner *et al*., 2013). This wider choice of genes and the reduced cost and time involved in generating these amounts of data provide an extensive toolkit for describing the vast molecular diversity evident in the Australian fauna at all levels.

Dating of multi-gene molecular phylogenies can also provide important insights about the evolutionary history of Australia's arid zone biota and the relationships between arid and mesic zone lineages. The basal divergence of the mesic *B. bassi* from all other arid-adapted *Blakistonia* has already been dated as mid-to-late Miocene, which is consistent with arid-zone expansion following the aridification of Australia in the mid-Miocene (Rix *et al*., 2017a). However, sampling of the arid-zone *Blakistonia* clade was otherwise sparse in that study, and a dated, multi-gene phylogeny with a more extensive range of specimens would be needed to thoroughly test the postulated 'out-of-South-Australia' ancestral area hypothesis. A more thorough sampling of some of the more genetically diverse *Blakistonia* lineages would also help to clarify inferences about the causes of genetic structuring across various landscapes. The molecular data in this thesis showed that several species had high levels of intraspecific genetic diversity, as evidenced by large pairwise distances, e.g. up to 12% within *B. birksi* and 15% within *B. maryae*. This is not uncommon in idiopid lineages, and indeed mean intraspecific divergences of 8.9% have been documented in species of *Idiosoma* (Rix *et al*., 2018a) and up to 15.6% in a widespread species of *Bungulla* (Rix *et al*.,

2018b). Larger taxon sampling is required to determine whether this pronounced genetic structuring is caused by insufficient sampling linked to cryptic speciation (Rix *et al*., 2018b) or is a reflection of pronounced habitat heterogeneity and recent isolation of populations. More thorough taxon sampling would also be helpful to fill in missing molecular and morphological data for species that are known from only one type of data. Unfortunately, many of the locations of arid-adapted lineages are very remote, making further collection costly and time-consuming. This is especially true for male specimens, where pitfall trapping is usually required after rainfall events which are sporadic at best across the arid zone.

Perhaps the most important advantage of improving the methods and knowledge in phylogenetics is the increased ability to quantify declines in populations of spiders. The ability to measure this decline is a critical component to future research if these iconic spiders are to be a conservation priority (Rix *et al*., 2017c). Identification of new species and documenting their distributions are critical for conservation purposes, so changes/decreases can be recorded through time. While the decline and lack of recruitment is often noticeable to experienced field researchers in a qualitative sense, it must be quantified if the information is to be used to inform management decisions by Rix *et al.* (2017c). Genetic information can be used to gather data relating to independently evolving lineages, whether gene flow is occurring through seemingly isolated populations due to wandering males, and to quantify the amount of genetic variation (as summarised in Rix *et al*., 2017c). However, the most crucial advantage to more rapid and accurate phylogenetic methods is the consequent improvement this will bring to taxonomic knowledge of the Idiopidae. Currently, in the majority of taxa, “most species – both described and undescribed – are known only to taxonomic specialists, and many of those known from only a handful of preserved specimens in museums and herbaria” (Harvey *et al*., 2011). The International Union for Conservation of Nature (IUCN) Red List criteria can only be used to assess the conservation status of species that are formally described. As the majority of the Australian terrestrial invertebrates remains undescribed (Yeates *et al*., 2003), a clear emphasis must be placed on the need for taxonomic studies of the Idiopidae and, indeed, of all invertebrates at risk of population declines through human-induced processes. The formal listing of species at risk is also important, with the listing of high-risk species (such as *B. bassi* and *B. maryae*) under the EPBC Act being a priority for future works.

6. APPENDICES

In addition to the core results chapters above, I was involved in a large collaborative and overarching research program within which my PhD work was nested. This larger program generated three key research outputs, of which I am a co-author, that directly relate to the

work I present for my PhD. The relevant papers are presented here as Appendices as follows:

APPENDIX 6.1: Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae: Arbanitinae) (2017, Molecular Phylogenetics & Evolution 109, 302–320).

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My contribution to this paper was 5%.

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Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae: Arbanitinae)

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ABSTRACT

The formation and spread of the Australian arid zone during the Neogene was a profoundly transformative event in the biogeographic history of Australia, resulting in extinction or range contraction in lineages adapted to mesic habitats, as well as diversification and range expansion in arid-adapted taxa (most of which evolved from mesic ancestors). However, the geographic origins of the arid zone biota are still relatively poorly understood, especially among highly diverse invertebrate lineages, many of which are themselves poorly documented at the species level. Spiny trapdoor spiders (Idiopidae: Arbanitinae) are one such lineage, having mesic 'on-the-continent' Gondwanan origins, while also having experienced major arid zone radiations in select clades. In this study, we present new orthologous nuclear markers for the phylogenetic inference of mygalomorph spiders, and use them to infer the phylogeny of Australasian Idiopidae with a 12-gene parallel tagged amplicon next-generation sequencing approach. We use these data to test the mode and timing of diversification of arid-adapted idiopid lineages across mainland Australia, and employ a continent-wide sampling of the fauna's phylogenetic and geographic diversity to facilitate ancestral area inference. We further explore the evolution of phenotypic and behavioural characters associated with both arid and mesic environments, and test an 'out of south-western Australia' hypothesis for the origin of arid zone clades. Three lineages of Idiopidae are shown to have diversified in the arid zone during the Miocene, one (genus *Euoplos*) exclusively in Western Australia. Arid zone *Blakistonia* likely had their origins in South Australia, whereas in the most widespread genus *Aganippe*, a more complex scenario is evident, with likely range expansion from southern Western Australia to southern South Australia, from where the bulk of the arid zone fauna then originated. In *Aganippe*, remarkable adaptations to phragmotic burrow-plugging in transitional arid zone taxa have evolved twice independently in Western Australia, while in *Misgolas* and *Cataxia*, burrow door-building behaviours have likely been independently lost at least three times in the eastern Australian mesic zone. We also show that the presence of idiopids in New Zealand (*Cantuaria*) is likely to be the result of recent dispersal from Australia, rather than ancient continental vicariance. By providing the first comprehensive, continental synopsis of arid zone biogeography in an Australian arachnid lineage, we show that the diversification of arbanitine Idiopidae was intimately associated with climate shifts during the Neogene, resulting in multiple Mio-Pliocene radiations.

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1. Introduction

The aridification of Australia, and the concomitant contraction and fragmentation of the continent's inherited Gondwanan mesic zone, was the defining historical biogeographic process to affect Australia during the Cenozoic. Extremely widespread in its geographic scope and evolutionary influence, the "birth" of the arid zone biota (Byrne et al., 2008; see blue and green colour coding on maps in Fig. 6) in Australia's late Eocene signalled a profound shift in the overall nature and composition of the continent's fauna and flora. The arid zone is now the largest biome in Australia and includes one of the largest deserts in the world (Byrne et al., 2008). There is a good understanding of the geological and climatic mechanisms underlying this transition (e.g. see Hopper and Gioia, 2004; Byrne et al., 2008, 2011; Rix et al., 2015), namely the final separation of the Australasian Plate from East Antarctica by ca. 35 Ma, followed by the formation of the Antarctic Circum-Polar Current and the gradual northward movement of Australia towards Asia. The ultimate, most severe phase of aridification occurred during the glacial cycles of the Plio-Pleistocene. Dated phylogenies are consistent in evidencing the widespread diversification of major arid-adapted lineages during the Miocene and early Pliocene, with largely population-level genetic effects during the later Plio-Pleistocene (see Byrne et al., 2008; Rix et al., 2015, and references therein).

What is less well understood is where the arid zone biota originated from, in both geographic and evolutionary space. Byrne et al. (2008) highlighted that in evolutionary space, arid-adapted lineages have often evolved via multiple transitions from mesic ancestors (e.g. Rabosky et al., 2007). This is hardly surprising, given the enormous selective pressures that would have increasingly affected mesic organisms *in situ* over evolutionary time. Unfortunately, the question of geo-spatial origins and ancestral areas (i.e. from where in Australia did arid zone taxa evolve) is much harder to test, given the challenges of adequate geographic sampling, the potential extinction of key ancestral taxa, and the difficulty of detecting ancestral areas in taxa that have undergone rapid range expansions. However, one hypothesis that has gained some traction is the 'out of south-western Australia' hypothesis, which postulates that at least some elements of the modern arid zone biota may have had their origins in south-western Western Australia (SWWA) – a biodiversity hotspot (Rix et al., 2015). There is currently little empirical evidence for this hypothesis, beyond the occurrence of south-western sister lineages to arid zone taxa in select phylogenies (see Rix et al., 2015; Edwards et al., 2015), and the relatively high diversity of some major arid zone vertebrate groups in transitional south-western and adjacent inland or arid coastal areas (e.g. Edwards et al., 2012). For arid zone invertebrates, we know little about the evolution of those temperate mesic lineages that successfully colonised arid environments. In contrast, there is an increasingly good understanding of their mesic zone invertebrate relatives that failed to make an arid zone transition, and experienced severe range contraction, fragmentation and in many cases, allopatric speciation, as a result (e.g. Ponniah and Hughes, 2004; Cooper et al., 2011; Lucky, 2011; Rix and Harvey, 2012; Harvey et al., 2015).

Spiny trapdoor spiders (Idiopidae) are one of the few predominantly Austral invertebrate lineages with a distribution that includes all former Gondwanan landmasses, including New Zealand, the Asian Subcontinent, southern Africa, South America and the Middle-East (World Spider Catalog, 2016). The Australasian fauna is composed of the endemic subfamily Arbanitinae (Raven, 1985), found on mainland Australia, Tasmania and New Zealand (but absent from offshore Darwinian Islands, e.g. Lord Howe and Norfolk Islands). In Australia they are almost exclusively temperate or subtropical in their latitudinal distribution, occurring south of the Tropic of Capricorn across most of the continent except for the mesic zone of north-eastern Queensland, where they are also found in the Wet Tropics and rarely on Cape York Peninsula. They are typical of the Australian southern-temperate spider fauna (Platnick, 1991), with all available evidence suggesting mesic 'on-the-continent' origins that pre-date both the separation of Australia from Antarctica in the Eocene, and its subsequent aridification. Idiopid spiders in Australia are thus an inherited component of the country's Gondwanan biota and, along with Nemesiidae (open-holed trapdoor spiders), the dominant mygalomorph spiders of the Australian temperate mesic zone (see red colour coding in Fig. 6 and Byrne et al., 2011, Fig. 1, for mapped representations of the mesic zone). However, Idiopidae are also one of a number of mygalomorph spider taxa that have secondarily adapted to the arid zone, with varying degrees of success. Indeed, select idiopid genera are found in some of Australia's most arid environments, including all of the major deserts of the arid interior. As such, although largely undescribed at the species level, and with a confusing taxonomic history at the generic level (Main, 1985b), Idiopidae are a useful candidate lineage for understanding arid zone speciation in an endemic invertebrate lineage. Like other Mygalomorphae (Satler et al., 2013; Hedin et al., 2015), they are long-lived and dispersal-limited organisms, usually with strong population genetic structuring (see Main, 1987; Castalanelli et al., 2014). These characteristics make them even better suited to testing the mode, timing and evolutionary consequences of diversification, at broad geographic scales.

This study therefore has multiple aims. Firstly, we test the phylogeny and generic classification of the arbanitine Idiopidae of Australasia using a multi-locus next-generation sequencing approach. Secondly, we test the mode and timing of speciation in arid-adapted lineages across mainland Australia: when did arid-adapted lineages evolve, where did they evolve, and where (in evolutionary and geographic space) did they most likely originate? Our final aim was to explore the phenotypic consequences of post-Eocene climate change, including both convergent morphological adaptations in arid zone taxa, and convergent behavioural adaptations in niche-conserved taxa restricted to the mesic zone. By rigorously sampling the phylogenetic and geographic diversity of Idiopidae from across continental Australia, this study aims to provide a stable phylogenetic framework for understanding the evolution of the region's idiopid spider fauna, and for documenting the diversity of that fauna at the generic and species levels.

2. Materials and methods

The methodological pipeline for this study was completed in two parts (Fig. 1). Part I (seven phases) involved *de novo* locus development, and the optimisation of a next generation sequencing protocol for downstream bulk sequencing of target loci. Part II (two phases) involved the parallel tagged amplicon sequencing (TAS) of a 12-gene dataset for 113 taxa on the Illumina MiSeq platform, and subsequent phylogenetic analysis of those data. Fig. 1 summarises this approach graphically.

2.1. Phase 1: taxon sampling for transcriptomics

Transcriptomes were generated for eight arachnid taxa, including seven spider species (three of which were Idiopidae) and the scorpion *Urodacus planimanus* Pocock, 1893 (Urodacidae), the latter chosen as the most distant outgroup. Within the Araneae, our aim was to include species from both infraorders of Opisthothelae (i.e. Mygalomorphae and Araneomorphae; Platnick and Gertsch, 1976), from multiple morphologically diverse genera of Idiopidae

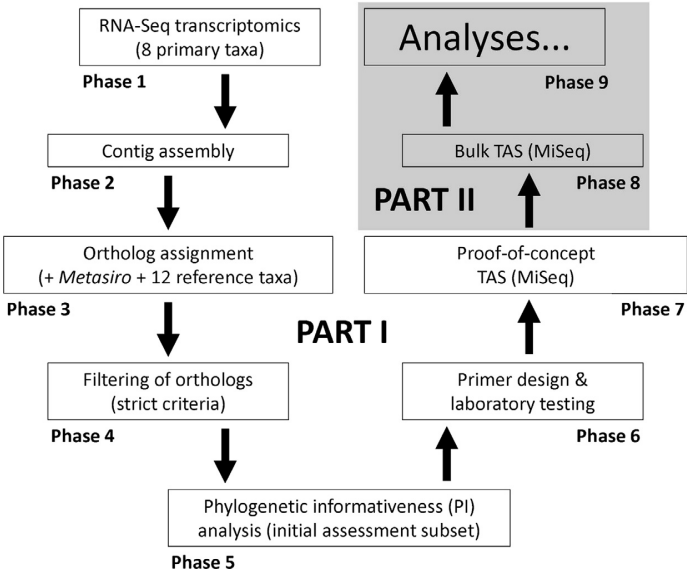

Fig. 1. Schematic diagram showing the methodological pipeline used for locus development (Part I) and bulk sequence generation (Part II). See text for details.

and from at least one other family of Mygalomorphae. *Latrodectus hasseltii* Thorell, 1870 (Theridiidae), *Nephila plumipes* (Latreille, 1804) and *N. edulis* (Labillardière, 1799) (Araneidae) were chosen as araneomorph exemplars, the latter two congeneric species because of their relatively recent (likely Miocene) speciation (Kuntner et al., 2013). Among the Mygalomorphae, *Cethegus fugax* (Simon, 1908) (Dipluridae) was chosen as an outgroup to the Idiopidae (Raven, 1985; Bond et al., 2012), along with the three idiopids *Aganippe* sp. 'T129362', *Euoplos* sp. 'T129363' and *Cataxia* sp. 'T129357'. With this core eight-taxon transcriptome (TR) dataset (Supplementary File 5) we expected to infer a backbone topology, with nodes at predictably different phylogenetic and temporal scales on an ultrametric tree (see Fig. 2).

2.2. Phases 1–2: transcriptome sequencing and contig assembly

Specimens for generating transcript libraries were collected and transported to the laboratory alive, where they were rapidly macerated and preserved in an RNase-free environment using sterile scalpels and RNA*later*® stabilization solution (Thermo Fisher Scientific, Inc.). For six of the eight TR taxa, single specimens were used for each sample; for both species of *Nephila*, two pooled individuals were used. Following dissection and stabilization, samples (which were mostly composed of cephalothoracic tissue) were quickly placed in snap-cap 1.5 ml tubes with Bullet Blender® beads, supplied as part of the Pink RNase-free bead lysis kit (Next Advance, Inc.). Tissues were then homogenized in a Bullet Blender® (Next Advance) with alternating spin-chill cycles, using Qiagen RLT lysis buffer (Qiagen, Inc.) with added β-mercaptoethanol. Total RNA was extracted from samples using the Qiagen RNeasy® mini-kit following the manufacturer's protocol, with subsequent RNA quantification and integrity analysis (see Gayral et al., 2011) performed using the standard sensitivity Experion™ Automated Electrophoresis System (Bio-Rad Laboratories, Inc.). Samples were then submitted to the Australian Genome Research Facility (AGRF; http://www.agrf.org.au/) for RNA-Seq poly(A+) mRNA enrichment and Illumina library preparation.

Next-generation transcriptome sequencing was performed on the Illumina HiSeq 2500 platform at the AGRF, with all eight samples pooled and run in a single flow-through cell. The resulting 150 bp paired-end (PE) reads were pre-trimmed and sanitized by AGRF, selecting for only the highest quality reads with Phred quality scores across all bases and sites >Q28 (as confirmed using FastQC; http://www.bioinformatics.babraham.ac.uk/projects/fastqc/). Transcriptomes were then *de novo* assembled in a two-step process, using the software packages Agalma (Dunn et al., 2013) and Trinity (Grabherr et al., 2013; Haas et al., 2013). Agalma was used to preassemble the data (command: [agalma preassemble]), by excluding reads that map to known ribosomal RNA, and creating 18S and 28S rRNA contigs. Assembly of the remaining reads was performed using Trinity, on an 8-core processor ([--CPU 8]) with 10 GB of jellyfish memory ([--JM 10G]) and a path reinforcement distance of 50 ([--path_reinforcement_distance 50]). Resulting fasta files and summary statistics were analysed using Geneious R6 (Biomatters Ltd.; http://www.geneious.com/). Raw paired-end sequence libraries are deposited in the NCBI Sequence Read Archive (SRA) under BioProject PRJNA356480, and assembled transcript libraries are linked in the NCBI Transcriptome Shotgun Assembly (TSA) Repository.

2.3. Phase 3: orthology assignment

Orthology assignment remains a vexing issue when selecting loci which are then used in downstream molecular phylogenetic studies. We adopted a conservative approach by targeting single-copy orthologs as identified by the Database of Orthologous Groups (OrthoDB; http://www.orthodb.org/) for a recently published set of 12 reference arthropod species (Misof et al., 2014, Table S3). This ortholog set, built on OrthoDB Version 5.0 (Waterhouse et al., 2011), comprised 1478 orthologous loci, and included the ixodid arachnid *Ixodes scapularis* Say, 1821, the cladoceran branchiopod *Daphnia pulex* Leydig, 1860, and 10 hexapod species for which full genomes and official gene sets were available (see Misof et al., 2014: Supplementary Material, Materials and Methods Section 2.6 and Supplementary Table S3). We refrained from generating a new ortholog set including the draft genome of the chelicerate *Tetranychus urticae* C.L. Koch, 1836 (then included in OrthoDB Version 6.0) as it would have decreased the

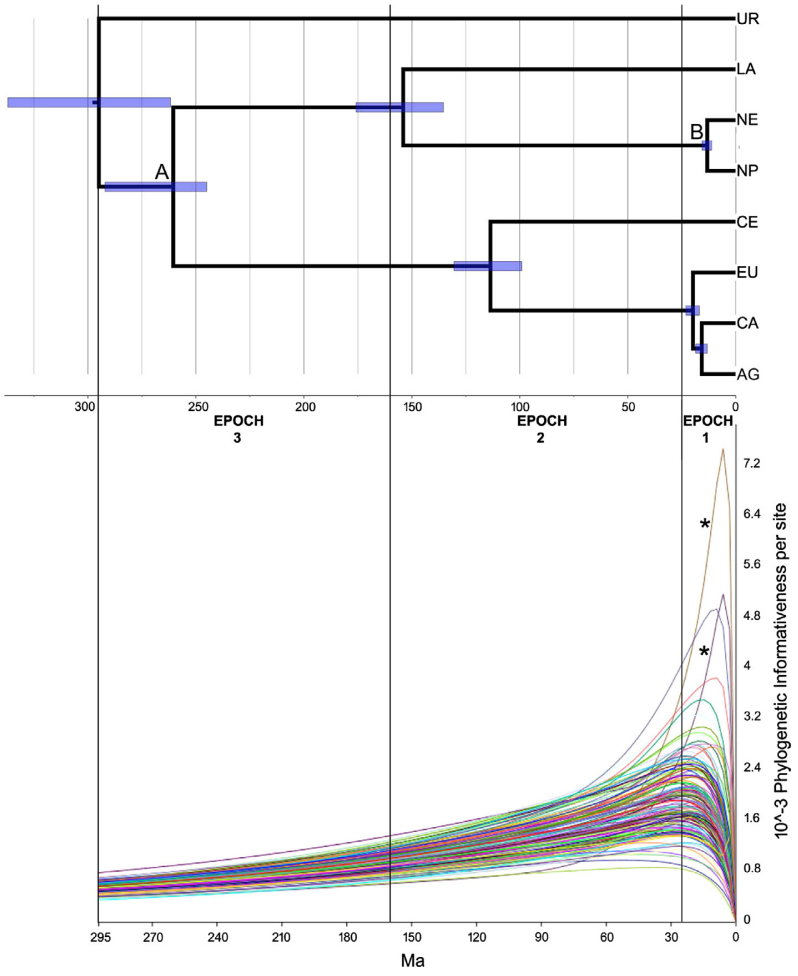

Fig. 2. Ultrametric chronogram for the eight newly-sequenced transcriptome species (upper panel), with a scaled nucleotide (per-site) phylogenetic informativeness profile for the 151 orthologous loci in the 'initial assessment subset' (lower panel) (see Table 1, Supplementary Files 1, 4). The upper chronogram was derived from a BEAST analysis of 11 loci in the 'initial assessment subset', and shows 95% highest posterior density estimates for node ages as horizontal bars. Note the three epochs (Epochs 1–3), used to rank the phylogenetic informativeness of loci at different temporal scales (Supplementary File 4), the two BEAST calibration points (A and B), and the rapid decay in information content for the two mitochondrial genes (*). See text for details and Supplementary File 5 for the identification of species codes used in the upper chronogram..

number of available orthologs (to 1057), and genomes of other chelicerates were not yet published at the time of the initial experimental design.

We assessed the orthology of transcripts for our eight newly sequenced transcriptome libraries and for the previously published library of the cyphophthalmid harvestman *Metasiro americanus* (Davis, 1933) (Neogoveidae; see Riesgo et al., 2012) (i.e. nine libraries in total). Ortholog assignments were made using HaMStRad (Github: https://github.com/mptrsen/HaMStRad), following the same procedure as described in Misof et al. (2014: Supplementary Material, Materials and Methods Section 2.6). We slightly modified settings considering the best reciprocity hit (BRH) criterion as being fulfilled if the candidate transcript was matched as best hit in the reference species *Ixodes scapularis* (option [-strict]) by a reciprocal BLAST search. In addition, we ran HaMStRad with the predicted transcript nucleotide sequences from the official gene set of *I. scapularis* (ISCAPW1.1) as an input, to receive a nucleotide output for this reference species. We subsequently removed multiply-assigned transcripts (one transcript each for *Metasiro* and *N. plumipes*, and two transcripts of *Urodacus*), and removed terminal stop codons and masked internal stop codons at the nucleotide level with 'NNN' and at the translational level with 'X' using custom-made PERL scripts. For ease of downstream comparison and filtering, we then removed all reference species except for *Ixodes*, and excluded all orthologous loci from further analyses that revealed a hit for only one out of the nine transcriptome species. We then separately aligned amino acids for the remaining orthologous genes using the LINS-i algorithm in MAFFT Version 7.123 (Katoh and Standley, 2013).

2.4. Phase 4: ortholog selection

Conservative minimum criteria for the inclusion of single-copy orthologous genes in a filtered 'initial assessment subset' (Table 1, Supplementary Files 1–2) were applied as per Hedin et al. (2012), with minor adjustments. In summary, transcripts on a translational level needed to: (i) be present in all eight of the transcriptome taxa, i.e. *Urodacus* and all seven spiders; (ii) have aligned open reading

Table 1
Summary of datasets analysed in this study.

Dataset (# taxa)	Number of genes	Conc. alignment length (nt/aa)	Mean aligned locus length (nt) ± StDev	Conc. alignment nexus file (nt/aa)	Locus Summary
Initial assessment subset (8)	151	223,309/74,323	1479 ± 717	Supplementary Files 1/2	–
FULL dataset (129)	12	9601	800 ± 623	Supplementary File 7	Supplementary File 6
MAJORITY dataset (120)	12	9601	800 ± 623	Supplementary File 8	Supplementary File 6
BEAST_9 dataset (101)	9	8565	952 ± 644		
BEAST_7 dataset (101)	7	7212	1030 ± 722		

frames of more than ~300 amino acid sites (minimum 278 aa; maximum 1675 aa); and (iii) span ⩾80% of the full alignment length for each orthologous locus (with shorter sequences permitted in two instances only for the outgroup *Urodacus*). Furthermore, we retained highly length-variable alignments only if all non-*Ixodes* sequences otherwise showed minimal length variation relative to each other (i.e. in instances where the *Ixodes* sequence was highly autapomorphic or poorly annotated). As a result of this strict filtration, the vast majority (90%) of all putative orthologs were removed, as the downstream focus was on a small selection of target loci for highly selective amplicon development, rather than maximum representation of orthologs *per se*. However, three additional putatively orthologous loci detected *ad hoc* in the transcripts (i.e. PGD, POLR2A, POLR2B) were added to the filtered (short-listed) orthologs, along with two mitochondrial genes used in downstream phylogenetic analyses of Idiopidae (i.e. CO1 and CYB), resulting in a set of 151 genes (Supplementary Files 1–2). These five additional genes were included to determine the relative performance of faster- versus slower-evolving nuclear orthologs in subsequent phylogenetic informativeness analyses (see below).

Following strict filtering, the 'initial assessment subset' (Table 1; Supplementary Files 1–2) was generated by creating clean alignments for each of the short-listed loci; this allowed for the inclusion in downstream analyses of only nucleotide sequences from original contigs. These nucleotide (and re-translated amino acid) sequences were aligned for all loci in the 'initial assessment subset' with the MAFFT v7.017 (Katoh et al., 2002) plugin in Geneious using default parameter settings (see Supplementary Files 1–2), with nucleotide alignments guided by the amino acids and minor manual adjustments made where required. For all such loci, alignment was largely trivial due to the small number of codon indels in each gene, but with minor 5′ or 3′ end-trimming required in some instances.

2.5. Phase 5: assessing phylogenetic informativeness

Several methods exist for predicting the utility of different genes for phylogenetic analysis, but there is currently no consensus on which criterion or measure performs best (e.g. Townsend, 2007; Klopfstein et al., 2010; Doyle et al., 2015). We thus conducted maximum likelihood (ML) analyses with 100 bootstrap replicates for each gene of the 'initial assessment subset' separately in RAxML (Stamatakis, 2014). In addition, we calculated Townsend's phylogenetic informativeness (PI; Townsend, 2007) as implemented in PhyDesign (López-Giráldez and Townsend, 2011; http://phydesign.townsend.yale.edu/) and performed likelihood quartet mapping (Strimmer and von Haeseler, 1997). These two measures of phylogenetic informativeness were then compared with the ML bootstrap support achieved by the single genes (for details see Supplementary File 3). The correlation coefficient between the two measures and ML bootstrap support differed substantially between the epochs considered, with quartet mapping showing stronger correlation with the recovery of the deep nodes, and PI performing better on lower taxonomic levels (Supplementary File 3). Given that the focus of our study was on the subfamily Arbanitinae, we decided to focus on PI as a measure of informativeness. PhyDesign was used to rank all 151 genes in the 'initial assessment subset', so that more highly-ranked orthologous loci could be further targeted for manual primer design and amplicon development using polymerase chain reaction (PCR). Rankings were calculated across three separate epochs: a recent epoch spanning 0–25 Ma; an intermediate epoch spanning 25–160 Ma; and a 'deep-phylogeny' epoch spanning 160–295 Ma (Fig. 2, Table 2, Supplementary File 4). This approach allowed for faster-evolving genes potentially informative at the genus-, species- or population-levels to be distinguished from more conservative loci.

To generate the ultrametric guide tree required for PI analysis, a chronogram was inferred using a relaxed Bayesian molecular clock (Drummond et al., 2006) in BEAST Version 1.8.0 (Drummond and Rambaut, 2007; Suchard and Rambaut, 2009; Drummond et al., 2012). Analysis was performed using a random selection of 11 loci from the 'initial assessment subset' (CDK5, CDKAL1, COPS5, CYOP, ELP3, HEM, CYB, NDUFS1, NLE1, PIGA, RIOK2; see Supplementary File 1 for locus details), which together formed a concatenated dataset of 17,970 bp. The BEAST input (.xml) file was created using BEAUti Version 1.8 (part of the BEAST software package), applying a relaxed uncorrelated lognormal molecular clock, a Yule speciation process for the tree prior, and the general time-reversible substitution model with gamma-distributed site heterogeneity and a proportion of invariant sites. Substitution and clock models were unlinked for all genes, base frequencies were estimated and codon partitioning was not applied. Priors on the estimated means for the lognormal relaxed clock for each gene were specified as uniform, with a starting value of 0.00115 and maximum and minimum bounds of 0.0115 and 0.0001, respectively. These values correspond to a general arthropod mitochondrial rate (upper bound; see Brower, 1994), and a starting rate one order of magnitude slower for nuclear genes (after Opatova and Arnedo, 2014). Two calibrations were applied as follows: the age of the ancestor of the two included *Nephila* species (calibration node B in Fig. 2) was defined using a normal prior (mean = 17 Ma; StDev = 2), in accordance with a previously inferred age for this clade (see Kuntner et al., 2013). The crown group age of Opisthothelae (i.e. Mygalomorphae plus Araneomorphae; calibration node A in Fig. 2) was defined using a lognormal prior (log[mean] = 3; log [StDev] = 0.7), with an offset of 242 Ma, based on the earliest mygalomorph spider known from the fossil record (*Rosamygale grauvogely* Selden and Gall, 1992) (Selden and Penney, 2010; Opatova and Arnedo, 2014). This crown group prior for Opisthothelae is consistent with a recent extended cross-bracing analysis (Shih and Matzke, 2013), which inferred the age of the older node separating Opisthothelae and Mesothelae at 260 Ma (Sharma and Wheeler, 2014). Bayesian MCMC inference (BI) was run in BEAST for 10 million generations, with the first 1 million generations discarded as 'burnin'. Trace files and summary statistics of estimated parameters were visualised using Tracer Version 1.6, ensuring ESS values >200 for at least the likelihood, root height and yule.birthrate. TreeAnnotator Version 1.8.0 (part of the BEAST package)

Table 2
Nucleotide (per-site) phylogenetic informativeness rankings and quantitation outputs from PhyDesign (López-Giráldez and Townsend, 2011; see Supplementary File 4) for single exon transcriptome loci successfully targeted for sequencing and included in the 'FULL dataset' (see Table 1, Fig. 5, Supplementary Files 5–6). Loci are arranged according to their epoch of relevance, and rankings are out of 151; those ranked within the top 10% for a particular epoch are marked in bold. Note that nuclear loci are generally informative across multiple epochs.

Locus	#_rates	Mean_rate	StDev	0–25 Ma	25–160 Ma	160–295 Ma
EPOCH 1						
CYB	1110	0.288863246	1.018578263	**1**	79	126
CO1	658	0.160510272	0.767923309	**3**	140	151
MRPL45	930	0.038952465	0.341535159	**2**	**1**	53
EPOCH 2						
RPF2	951	0.036225273	0.346475223	**6**	**2**	33
XPNPEP3	1443	0.016101414	0.235768567	16	**4**	**2**
EPOCH 3						
HAT1	1236	0.012255977	0.19344061	**13**	16	**8**

and FigTree Version 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) were used to visualise the final chronogram and highest posterior density estimates.

Per-site PI values were calculated in PhyDesign for both nucleotide (Supplementary File 1) and amino acid (Supplementary File 2) sequences in the 'initial assessment subset' data using HyPhy (Pond et al., 2005) and rate4site (Mayrose et al., 2004) site rate distributions, respectively. Net PI values were not calculated due to the confounding effects of sequence length on net calculations, and the inability to downstream PCR-amplify target genes in their entirety. Genes were ranked according to the integrals below PI profile curves for each locus across each epoch, and genes were ranked accordingly (Supplementary File 4). The top-10 ranked genes for each epoch were then targeted for downstream PCR amplification and optimisation (see Table 2, Supplementary File 4).

2.6. Phase 6: laboratory techniques and primer design

After the top-10 ranked loci for each epoch were identified using PI quantitation analysis, PCR optimisation was required to successfully amplify a select number of nuclear loci for downstream parallel tagged amplicon sequencing (TAS). Using the selected alignments for the eight transcriptome (TR) taxa plus *Metasiro*, suites of primers were manually designed to screen potential (conserved) primer sites across a range of non-TR test taxa. For this purpose we tested primers on a further 12 mygalomorph spider species (see Supplementary Files 5–6), eight of which were idiopid test taxa that spanned the phylogenetic diversity of the Arbanitinae, and included generic type species for four of the nine valid Australian genera. DNA extractions for the 12 test taxa were performed using the Qiagen DNeasy® blood and tissue kit, and bulk screening employed standard PCR amplification, nested PCR and touchdown methods across a range of annealing temperatures. Between 10 and 20 primers were tested for each locus using variable primer combinations. MyTaq DNA Polymerase (Bioline, Taunton, MA) chemistry was used for PCR reactions, in a Bio-Rad T100 Thermal Cycler. For each 25 μl PCR reaction, 2–5 μl of template DNA, 5 μl of 5× MyTaq buffer, 0.5 μl of each primer (at 10 μM concentration) and 0.2 μl of MyTaq DNA polymerase were used. For all loci, 1.5% agarose gel screening was employed to identify single band orthologs, especially single exon fragments that would be further Sanger-sequenceable (i.e. <1000 bp in length).

In addition to the screening of selected top-ranked nuclear orthologs, eight other 'standard' genes were PCR amplified, to supplement the dataset and for comparison to previous published studies on Mygalomorphae. These included two mitochondrial genes (the barcoding fragment of cytochrome *c* oxidase subunit 1 and a fragment of cytochrome *b*) and six nuclear genes (5.8S, 18S and 28S ribosomal RNA, internal transcribed spacers 1 and 2, and histone H3) (see Supplementary File 6). PCR conditions and primers for the amplification of all target genes in all test species are summarised in Supplementary Files 5–6.

2.7. Phase 7: proof-of-concept parallel tagged amplicon sequencing

For the eight TR taxa and the other eight idiopid test species used for optimising PCR protocols (16 samples in total), a tagged amplicon sequencing approach (Bybee et al., 2011) was used to sequence amplicons in parallel on the Illumina MiSeq platform (Fig. 3). This method, largely developed on the Roche 454 sequencing platform (e.g. Bybee et al., 2011; O'Neill et al., 2013), requires PCR products to be pooled for each specimen prior to library preparation and next-generation sequencing (Fig. 3). Following PCR amplification of up to18 genes in up to 16 separate PCRs (i.e. ITS1, 5.8S rRNA and ITS2 were amplified together), amplicons were pooled for each specimen in equal fractions ('relative fractionation') to make up 16 pooled samples, each 33–35 μl in volume. For the eight TR species, this involved pooling only three 11 μl amplicon aliquots for the ribosomal RNA polycistron (i.e. 18S, ITS1-5.8S-ITS2, 28S), which was not necessarily recovered in full in each transcriptome assembly (due to Agalma preassembly). For the other eight idiopid test species, between 9 and 16 amplicons were pooled using 2–4.13 μl aliquots (with aliquot volumes dependent upon the number of amplicons pooled in each instance). This pooling strategy using approximate relative fractionation (i.e. PCR products varied slightly in DNA concentration between loci and samples) was employed to reduce potential representation biases that can occur during downstream Illumina library preparation. Pooled samples were then purified using the UltraClean® PCR Clean-Up Kit (MoBio Laboratories, Inc.), and submitted to AGRF for Illumina library preparation using the Nextera sample preparation kit (Illumina, Inc.).

Next-generation sequencing was performed on the Illumina MiSeq platform using 250 bp PE read lengths, with all 16 samples pooled and run in a single flow-through cell. As for transcriptome HiSeq sequencing, the resulting 250 bp PE reads were pre-trimmed and sanitized by AGRF, selecting for only high quality Phred-score reads. Resulting raw reads were mapped using the 'Map to Reference' function in Geneious R6, and assembled to reference transcriptome sequences for each amplified locus. Haplotype phasing was not conducted on this short-read and very high coverage dataset, and consensus sequences were derived from nucleotides occurring in at least 25% of the assembled sequences. Resulting consensus sequences were aligned and end-trimmed in Geneious. It should be noted that while phasing is unnecessary for most analyses above the population or closely inter-specific levels (Lemmon and Lemmon, 2013), or for analyses without intra-specific sampling rigorous enough to detect recombination (Brito and

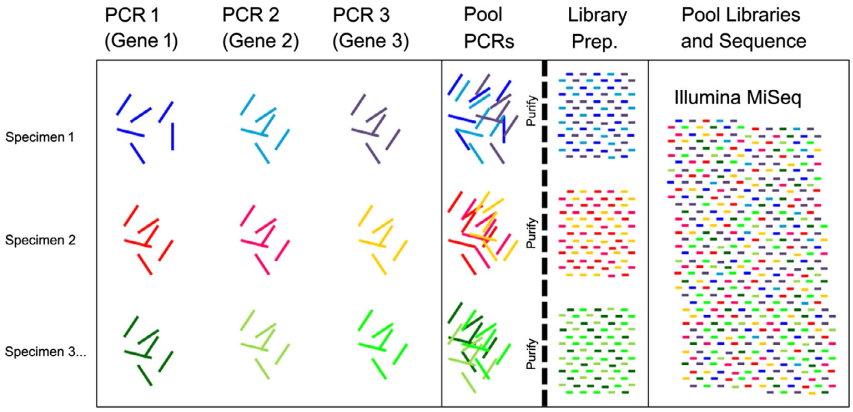

Fig. 3. Schematic diagram showing the protocol used to sequence tagged amplicons in parallel on the Illumina MiSeq platform. See text for details.

Edwards, 2009), the inability to easily phase heterozygotes is an obvious downside to this reduced-representation short-read MiSeq approach (O'Neill et al., 2013).

2.8. Phase 8: taxon sampling for phylogenetics

Following the optimisation of primer design for parallel tagged amplicon sequencing, we then applied these methods in bulk for the sequencing of taxa used in the phylogenetic analyses (Part II; see Fig. 1). To test the underlying phylogeny of Australasian Idiopidae, and to explore their diversification at a continental scale, we sampled 113 additional specimens from across Australasia (Fig. 4; Supplementary File 5). These taxa, combined with the 11 idiopid species sequenced as part of Phases 1 and 7, were carefully selected to provide a representative sample of the taxonomic and geographic diversity of Arbanitinae, and included members of all known genera and all of the type species of currently valid genera (as well as most of their junior generic synonyms). The Wet Tropics

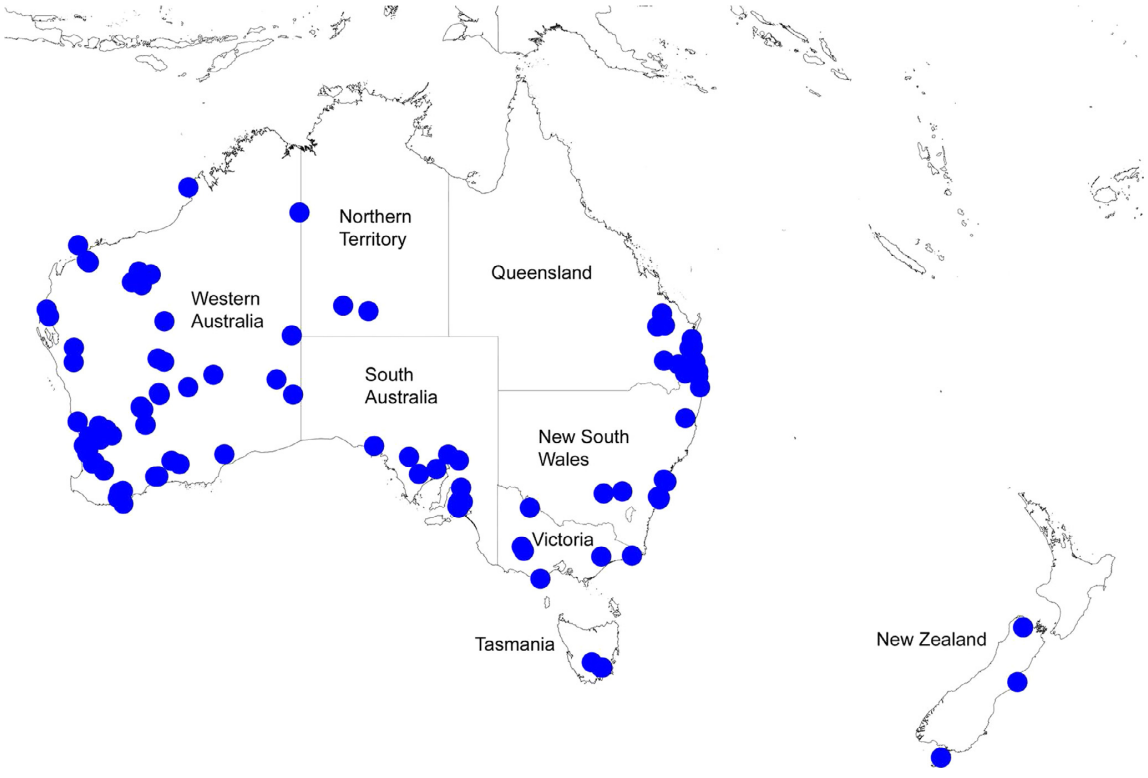

Fig. 4. Map of Australia and New Zealand showing localities of idiopid taxa sampled as part of this study ('FULL' dataset). See Supplementary File 5 for details. Map generated by the Atlas of Living Australia (ALA) mapping interface (http://www.ala.org.au/), reproduced under a Creative Commons Attribution 3.0 Australia Licence.

of Queensland and the inland arid zones of Queensland and New South Wales were not sampled for this study (Fig. 4), but only a select few lineages are known to occur in these regions, and all of these were thoroughly sampled elsewhere (i.e. from further south in the case of the Wet Tropics, and from east, west and south of inland areas in the case of Queensland and New South Wales). This sampling regime was further qualified by the subsequent taxonomic appraisal of idiopids stored in the Western Australian, South Australian and Queensland Museums, which together contain excellent representative collections from across Australia.

2.9. Phase 8: amplicon generation and parallel tagged amplicon sequencing

Primers developed and optimised during Part I for four new orthologous nuclear loci (i.e. 39S ribosomal protein L45, mitochondrial [MRPL45], ribosome production factor 2 homolog [RPF2], probable Xaa-Pro aminopeptidase 3 [XPNPEP3] and histone acetyltransferase type B catalytic subunit [HAT1]), for mitochondrial cytochrome *b* (CYB), and for the seven other 'standard' genes (i.e. cytochrome *c* oxidase subunit 1 [CO1], 5.8S, 18S and 28S ribosomal RNA [5.8S/18S/28S], internal transcribed spacers 1 and 2 (ITS1/ITS2), and histone H3 [H3]) (Supplementary File 6) were used to generate a 10-amplicon (12-gene) dataset for the newly sequenced idiopid taxa. DNA extractions were performed using QIAsymphony magnetic bead technology (Qiagen, Inc.) on 96-well plates. Diluted template DNA aliquots were then PCR-amplified using 96-well plates and 25 μl reactions (as for Phase 6), with one plate for each primer combination (see Supplementary File 5 for primer combinations and PCR conditions used for each sample). PCR products were visualised on E-Gel® pre-cast agarose gels (Invitrogen Inc.), and for faint bands or negative products, samples were individually re-amplified using undiluted template DNA.

Methods for bulk parallel tagged amplicon sequencing on the Illumina MiSeq platform were similar to those tested during Phase 7, with up to 10 amplicons pooled for each sample (to 50 μl) using approximate relative fractionation. Pooled samples were then purified and submitted to AGRF for Nextera library preparation. Next-generation sequencing was performed at the AGRF, with 48 samples run per flow-through cell (additional samples were run in parallel with the 113 analysed as part of this study). The resulting 250 bp PE reads were pre-trimmed, sanitized, assembled and aligned as described for Phase 7.

2.10. Phase 9: phylogenetic analyses

Phylogenetic analyses for Part II focussed on inferring a robust phylogeny for Australasian Idiopidae, and on using divergence dating to test the mode and timing of speciation across continental Australia. Four datasets were analysed: a 'FULL' concatenated dataset including all 12 genes and all 129 sequenced taxa (Supplementary File 7); a 'MAJORITY' reduced-representation dataset including all 12 genes but only those 120 taxa with ⩾90% of amplicons successfully sequenced (Supplementary File 8); a 'BEAST_9' reduced-representation dataset of 101 taxa and nine genes (ITS1, 5.8S and ITS2 removed), including only 'MAJORITY'-dataset taxa with complete amplicon representation (Supplementary File 9); and a 'BEAST_7' dataset, which was similar to 'BEAST_9' but with the mitochondrial genes (CO1, CYB) also removed (Supplementary File 10). The ITS amplicon was removed from the BEAST datasets due to it not being successfully sequenced in outgroup taxa, and mitochondrial genes were removed from the 'BEAST_7' dataset for comparative divergence dating approaches.

For the 'MAJORITY' dataset (Supplementary File 8), PartitionFinder Version 1.1.1 (Lanfear et al., 2012) was used to choose appropriate models of nucleotide substitution under an optimal partitioning strategy (of 13 partitions; see Supplementary Files 7–8). This partitioning strategy was employed in subsequent BI and ML analyses of both the 'FULL' and 'MAJORITY' datasets. BI non-clock analyses were conducted using MrBayes Version 3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) via the CIPRES Science Gateway (Miller et al., 2010). For both the 'FULL' and 'MAJORITY' datasets (Supplementary Files 7–8), substitution model parameters were estimated independently for each partition ([Unlink tratio = (all) pinvar = (all) shape = (all) statefreq = (all) revmat = (all)]) and rates were allowed to vary across partitions ([Prset applyto = (all) ratepr = variable]). Four Markov Chain Monte Carlo (MCMC) chains were run for 20 million generations, sampling every 1000 generations, with the first 10% of sampled trees discarded as 'burnin' ([burnin = 2000]). Burnin times, ESS values and summary statistics of estimated parameters were assessed using Tracer Version 1.6, and FigTree Version 1.4.2 was used to visualise a 50% majority-rule consensus tree of the post-burnin sample. ML analysis of the 'MAJORITY' dataset was also conducted using RAxML Blackbox (Stamatakis, 2014), via the CIPRES Science Gateway, using a gamma rate heterogeneity model with invariant sites for each partition. We sampled bootstrap replicates using an automatic halt function for bootstrapping, which automatically checks for convergence of bootstrap replicates and stops sampling replicates upon bootstrap convergence (see Pattengale et al., 2010).

Divergence dating using BEAST Version 1.8.0 on the BEAST datasets was conducted via the CIPRES Science Gateway. BEAST input (.xml) files were created using BEAUti Version 1.8.0, by applying different combinations of priors for the nucleotide substitution rate matrix, clock model and tree prior. Firstly, for the 'BEAST_9' dataset (Supplementary File 9), the nine genes were partitioned with unlinked site and clock models. BEAST analyses on these data were initially run for 10–40 million generations (sampling every 1000 generations) to explore the effects of different priors, including HKY (parameter-poor) versus GTR (parameter-rich) nucleotide substitution models, and strict versus relaxed (uncorrelated lognormal and uncorrelated exponential) clock models. A Yule speciation tree prior was used for all 'BEAST_9' analyses, and priors on the means of the uncorrelated lognormal, uncorrelated exponential and strict clock distributions were specified as uniform, usually with a starting value of 0.00115 and maximum and minimum bounds of 0.0115 and 0.0001, respectively (after Opatova and Arnedo, 2014; see Phase 5 Methods, above). However, for strict clock analyses, a generous maximum bound of 0.03 was also tested for the CYB partition. Clock rates were estimated for all partitions except CO1, for which a rate of 0.02 was specified based on the estimation of 4% CO1 divergence between lineages per million years for mygalomorph spiders (Bond et al., 2001). A strict clock could not be rejected based on ucld.stdev values (<1.0) for all protein coding genes in an exploratory relaxed clock analysis run for 40 million generations, and application of a strict clock further resulted in superior sampling of the posterior distribution for the vast majority of parameters, relative to relaxed clock analyses using the same mitochondrial rate. This strict clock rate-calibrated approach using the 'BEAST_9' dataset was then compared to a fossil-calibrated analysis for which one calibration point was available (of 242 Ma, equivalent to Node A in Fig. 2; see Phase 5 Methods, above; Selden and Penney, 2010; Opatova and Arnedo, 2014). This comparative analysis used the 'BEAST_7' dataset (Supplementary File 10), and applied a relaxed uncorrelated lognormal molecular clock. A GTR + Γ + I nucleotide substitution model was used for each gene partition in both of the final 'BEAST' analyses (each of 40 million generations with 50% burnin; see Supplementary Files 9–10). Output log files were visualised and assessed in Tracer Version 1.6, ensuring the majority of ESS values were >200. TreeAnnotator Version 1.8.0 and FigTree Version 1.4.2 were

used to visualise the final chronograms and highest posterior density estimates.

Ancestral state and ancestral area reconstructions were performed using parsimony in Mesquite Version 3.10 (Maddison and Maddison, 2016), using the 'FULL' taxon set (Supplementary File 12). Ancestral states were inferred to assess the evolution of two independent traits associated with adaptations in arid versus mesic zone taxa, respectively, while ancestral area reconstruction was performed for the tribe Aganippini to assess, at a broad scale, the origin/s of the arid zone fauna. For the latter, the Australian distributions of aganippine taxa were divided into four broad distributional categories: (1) temperate south-western Australia; (2) temperate south-eastern Australia; (3) eastern Australia; and (4) the arid zone (Fig. 7). This simple generic division was intended to test arid zone incursions under a null hypothesis of multiple directional shifts from temperate (mesic) habitats to arid habitats. As such, other more complex or finer-scale geographic scenarios requiring likelihood-based approaches were not tested (see Lamm and Redelings, 2009 for a discussion on the suitability or otherwise of parsimony-based approaches for ancestral area inference).

3. Results

3.1. Transcriptome sequencing and orthology assignment

Transcriptome sequencing of the eight target arachnids resulted in nearly 137 million 150 bp PE reads for a total of 41.37 Gb of data. *De novo* assembly using Agalma and Trinity resulted in an average of 77,646 contigs per sample (minimum 61,107; maximum 104,219), with a maximum recovered contig length of 27,303 bp. Orthology assignment using HaMSTRad given a set of 1478 orthologous loci resulted in 1396 orthologous loci with assigned transcript sequences for one or more transcriptome assemblies. We kept 146 orthologous loci after filtering against strict and highly conservative criteria for taxon and site coverage (see above). Dataset characteristics for this 'initial assessment subset' are summarised in Table 1, and full concatenated nucleotide and amino acid alignments are provided in Supplementary Files 1–2.

3.2. Assessing phylogenetic informativeness

The per-site phylogenetic informativeness (PI) of all orthologous loci in the 'initial assessment subset' was quantified separately for three epochs, for both nucleotide and amino acid sequence data in the 'initial assessment subset'. The input chronogram from the BEAST analysis of 11 loci was unsurprising in its topology (Fig. 2), and included a recent (calibrated) species-level cladogenic event (i.e. between the two *Nephila* species) plus two relatively recent inter-generic divergences among idiopid taxa, along with much older inter-familial and inter-infraordinal splits. These temporally divergent cladogenic events provided the necessary framework for defining the PI epoch windows: Epoch 1 capturing the three most recent (i.e. phylogenetically-relevant) post-Oligocene nodes; Epoch 2 capturing the next two much deeper (Mesozoic) nodes; and Epoch 3 capturing the most ancient (Palaeozoic) node (Fig. 2). Per-site PI values for the nucleotide data showed less variance between genes for Epochs 2 and 3 compared with the amino acid data, but were usually higher for the top-ranked genes across Epoch 1 (Supplementary File 4). This variation in the breadth of informativeness is unsurprising given the greater informativeness of amino acid data for deeper phylogenetic nodes, and the increased frequency of synonymous substitutions in genes with the fastest rates (see also Hedin et al., 2012). However, relative rankings at the highest levels were highly correlated irrespective of the type of sequence data, with 70% of loci ranked in the top-10 for nucleotide data also ranking in the top-10 for amino acid data (for all three epochs), and 90% of loci ranked in the top-10 for nucleotide data ranking in at least the top-15 for amino acid data in corresponding epochs (Supplementary File 4).

As an *a priori* proof of concept, the PI rankings of genes made biological sense when genes with known relative rates were considered, e.g. the mitochondrial genes CO1 and CYB genes were within the top-three ranked genes for Epoch 1 (using nucleotide data), and were likewise poorly ranked for Epoch 3 (151 and 126 of 151, respectively). Similarly, highly conserved and largely invariable genes such as POLR2B were very poorly ranked for all epochs (114, 139 and 150 of 151, respectively). Interestingly, nuclear loci highly ranked for one epoch were usually highly ranked across multiple epochs, with the greatest correlation across Epochs 1 and 2 (Table 2, Supplementary File 4). Some loci, for example HAT1, XPNPEP3 and MRPL45, were highly ranked across all epochs (Table 2).

3.3. Optimised loci for PCR

The top-10 loci for each epoch were subjected to PCR screening to identify genes useful for PCR amplification and downstream next-generation sequencing, with a focus on successful amplification of loci in idiopid spiders. Spider and other arachnid genomes appear to be large for Metazoa, with short exons and long introns (Cao et al., 2013; Sanggaard et al., 2014), presenting a challenge when designing and testing PCR primer combinations *de novo* in novel taxa. Indeed, over 1000 individual PCRs were tested during the optimisation phase of this study. Our aim was to target single exon fragments in top-ranked genes, and this was successfully realised for four highly-ranked nuclear loci (Table 2), in addition to the two default mitochondrial genes. All genes produced single bands useful for Sanger or next-generation sequencing in (at least) idiopid spiders, with high levels of informativeness spread across all three epochs (Table 2). These data, combined with six other 'standard' nuclear loci, resulted in bulk amplification methods for a combined 12-gene dataset, useful for phylogeny reconstruction at different temporal and taxonomic scales.

3.4. Parallel tagged amplicon sequencing

Phase 7 (proof-of-concept) sequencing of the 16 test spiders on the Illumina MiSeq platform resulted in nearly 13.23 million 250 bp PE reads for 6.61 Gb of data. Pooled amplicon sizes varied from ~350 bp (H3) to marginally >2 kbp (28S rRNA), and between 3 and 10 amplicons (for up to 12 genes) were successfully sequenced in parallel per specimen. Subsequent bulk sequencing for Phase 8, using 48 libraries per lane, resulted in equivalent amplicon recovery, and reference assemblies usually had much greater than 100× coverage. Resulting sequences were further checked *post hoc* using taxonomic positive controls already accessioned on GenBank (e.g. for *Nephila* spp. and *L. hasseltii*).

3.5. Phylogenetic analyses

Bayesian phylogenetic reconstruction of assembled sequences in the 'FULL dataset' (Table 1, Fig. 5, Supplementary Files 5, 11) resulted in a tree with high posterior probability support across most clades (Fig. 5, Supplementary File 11). BI and ML analyses of the 'MAJORITY' dataset recovered an almost identical topology, with the exception of five clades within the genera *Cantuaria* Hogg, *Euoplos* Rainbow and *Misgolas* Karsch (see Supplementary File 11). The core topology recovered all of the expected deeper clades (i.e. a monophyletic Araneae, Mygalomorphae, Idiopidae and Arbanitinae). Most previously-hypothesised genera were recovered as

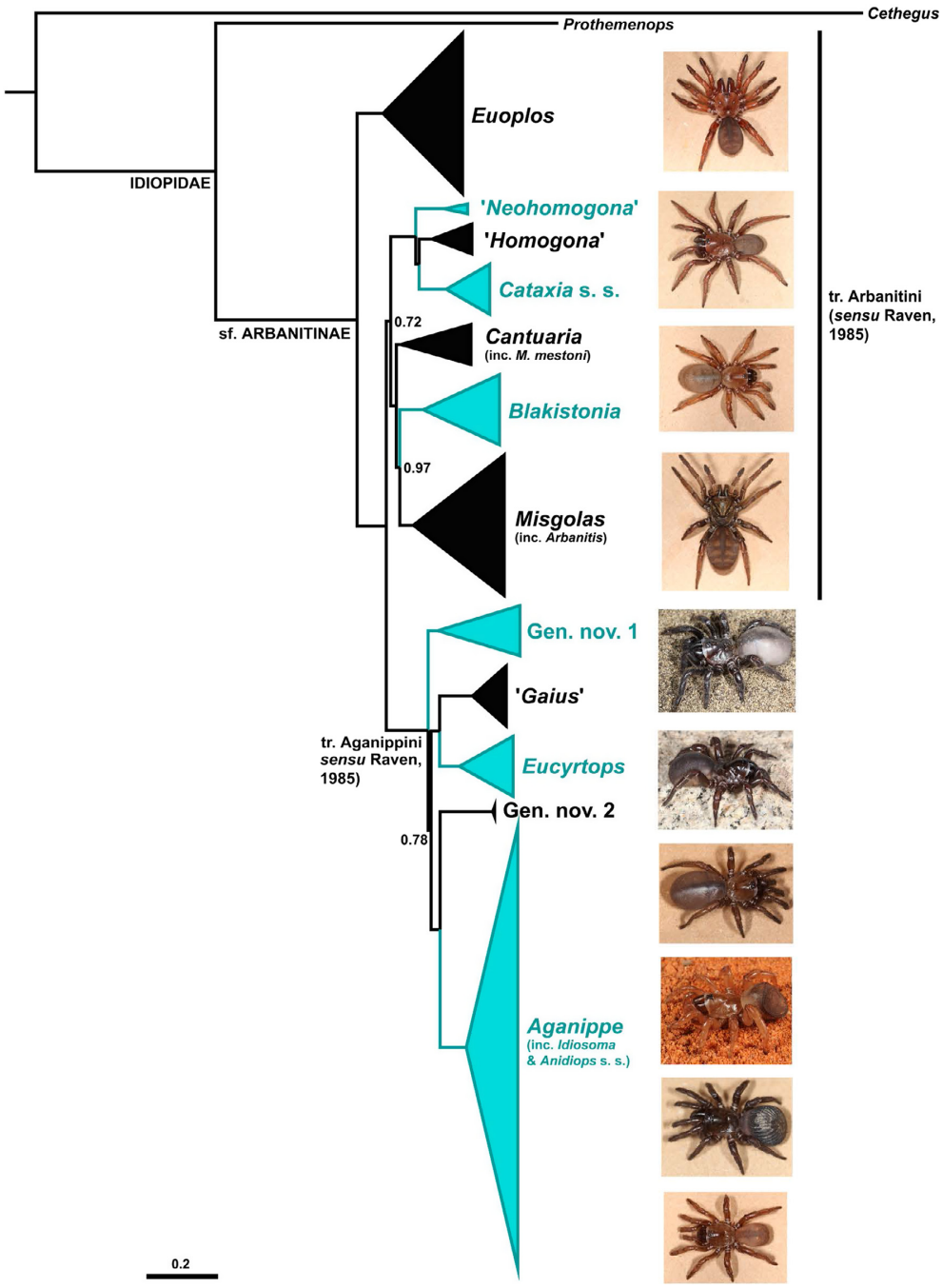

Fig. 5. Summary Bayesian (BI) majority-rule consensus tree resulting from a partitioned phylogenetic analysis of the 'FULL' (12-gene) dataset (129 taxa; 9601 bp; 20 million generations), showing collapsed nodes for the major genus-group lineages. Non-mygalomorph outgroups have been omitted for ease of presentation, and posterior probability values are >0.98 unless otherwise stated. Junior generic synonyms of currently valid genera are shown in inverted commas. See Supplementary File 11 for detail of the full topology.

monophyletic, with the following exceptions (by larger paraphyletic clade): *Cantuaria* included *Misgolas mestoni* (Hickman, 1928); *Misgolas* included *Arbanitis* L. Koch (*sensu* Raven and Wishart, 2006); and *Aganippe* O. P.-Cambridge included both *Idiosoma* Ausserer and *Anidiops* Pocock *sensu stricto*. *Anidiops* also currently includes '*Gaius*' Rainbow, which in our trees formed a separate clade. The phylogeny further provided evidence for two potentially new Western Australian genera in the Aganippini,

while Arbanitini (*sensu* Raven, 1985) was paraphyletic with respect to Aganippini.

Divergence dating using the 'BEAST' datasets, for both the rate-calibrated analysis (RCBA; with 'BEAST_9') and fossil-calibrated analysis (FCBA; with 'BEAST_7'), recovered the same monophyletic genera and largely the same backbone topology as the other phylogenetic analyses using the 'FULL' and 'MAJORITY' datasets (Fig. 6). However, the 'BEAST_7' analysis placed the *Cataxia* lineage sister to Aganippini, and placed the Gen. nov. 1 lineage sister to Gen. nov. 2 plus *Aganippe*. Despite their differing approaches, and the use of just a single deep calibration point for the FCBA, both BEAST analyses were concordant in evidencing species-level divergences that were mostly Miocene in age, with the highest posterior density (HPD) estimate for the primary divergence between *Euoplos* and all other Arbanitinae between 50 and 35 Ma for the RCBA, and between 34 and 22 Ma for the FCBA. However, strict-clock analysis of the 'BEAST_9' dataset inferred ancient, non-sensical divergence dates for non-mygalomorph outgroup taxa (>600 Ma); these erroneous deep-phylogeny HPD estimates were likely the result of a rapid decay in phylogenetic signal with increasing time before present (Fig. 2), a gene selection optimised for Cenozoic signal (Table 2), and the inflationary effects of disparate outgroups on a rate-calibrated analysis using a mitochondrial rate. As such, we favour the FCBA, for which the HPD estimates are slightly younger (despite the old age of the single calibration point).

Phylogenetic analyses were consistent in inferring three clades of arid-adapted idiopid taxa: one clade of *Euoplos*, one clade of *Blakistonia*, and the entire tribe Aganippini (Fig. 6). Divergence dating using the 'BEAST_7' dataset inferred HPD estimates for the crown-group ages of these lineages in the mid-late Miocene for *Euoplos* and *Blakistonia*, and the mid-Miocene for Aganippini. Ancestral area reconstruction revealed that all five genus-group lineages of Aganippini likely evolved in south-western Western Australia (SWWA), with early-branching taxa found in temperate SWWA, and all but one genus still entirely restricted to Western Australia (Figs. 6 and 7). As previously suggested (Main, 1985b), and as confirmed in the current study, *Aganippe* occurs across the entire Australian mainland (mostly south of the Tropic of Capricorn), in transitional and arid habitats from the Indian ocean coastline to just west of the Great Dividing Range along the east coast (Figs. 6 and 7). One of two major clades of *Agannipe* is south-western Australian in distribution (with a few extralimital derived taxa in the closely adjacent arid zone of southern Western Australia). The other clade includes south-eastern Australian species plus a lineage that contains the bulk of the arid zone fauna (Fig. 7). All early-branching lineages in this second eastern Australian/arid zone clade are from temperate South Australia, which we inferred as the ancestral area for the largest radiation of arid zone *Aganippe*. Surprisingly, the bulk of the arid zone fauna in Western Australia and central Australia were unrelated to species from SWWA.

Ancestral state reconstruction of phragmotic abdominal morphologies for burrow plugging (in arid adapted taxa) (Fig. 8) and open burrow-building behaviours (in mesic taxa) (Fig. 9), respectively, implies that phragmosis evolved in two independent lineages of *Aganippe* in SWWA (Fig. 8), and open burrows probably in at least three genus-group lineages from the mesic zone, with a fourth characterised by an additional 'semi-open' burrow morphology (Fig. 9). Reversals to door-building may have also occurred twice independently in *Cantuaria* and *Misgolas*.

4. Discussion

Resolving the arachnid 'Tree of Life' (Coddington et al., 2004), at both its deepest nodes and more distal branches, has proven extremely difficult, and is among the last of the major challenges for arthropod phylogenetics (Sharma et al., 2014). Numerous morphological (e.g. Weygoldt and Paulus, 1979; Shultz, 2007), smaller molecular (e.g. Murienne et al., 2008), combined (e.g. Wheeler and Hayashi, 1998; Giribet et al., 2002) and phylogenomic studies (e.g. Sharma et al., 2015) have attempted to test the phylogeny of major arachnid clades, often with limited success, especially at the ordinal level. Indeed, the backbone topology of the Arachnida is yet to be confidently resolved, despite recent applications of phylogenomic methods and in stark contrast to parallel developments in our understanding of other major arthropod taxa, in particular for the Hexapoda (Trautwein et al., 2012; Misof et al., 2014) and Myriapoda (Brewer and Bond, 2013; Fernández et al., 2016). Megadiverse groups such as the Araneae remain poorly understood at the family-group level, as recent phylogenetic work continues to demonstrate (Fernández et al., 2014). Detailed molecular analyses at other taxonomic levels are further hampered by a relatively modest selection of genetic markers (e.g. CO1, 18S, 28S, H3, etc.) – the 'usual suspects' of modern molecular studies (Dimitrov et al., in press). Only in recent years have more powerful phylogenomic and other NGS methods been applied to arachnid systematics, with mixed results (Sharma et al., 2015; Garrison et al., 2016).

In this study we used a combination of standard amplicon and NGS methods to develop a panel of new orthologous markers for the phylogenetic interrogation of Idiopidae. This approach was designed to complement markers previously optimised for spider phylogenetics, while providing stronger phylogenetic resolution at the relevant genus-group level. The resulting 12-, 9- and 7-gene datasets were unambiguous in resolving a common backbone topology in all phylogenetic analyses, thus providing evidence of the utility of this gene combination for resolving arbanitine idiopid phylogeny. Furthermore, by ranking transcriptome-generated orthologs according to their phylogenetic information content, and targeting only highly-ranked genes within specific temporal windows, four additional Sanger- or TAS-sequenceable exons are now available for arachnid phylogenetic reconstruction in any PCR-rated laboratory, along with a formidable panel of other nuclear loci available for hybrid enrichment studies at different taxonomic scales.

4.1. New informative markers for spider systematics

The four novel nuclear markers developed as part of this study for amplicon-based analyses – MRPL45, RPF2, HAT1 and XPNPEP3 – while optimally informative at different temporal scales, were also generally informative across at least two of the three epochs tested (Table 2). This result emphasizes their general utility for phylogenetic inference, especially compared with mitochondrial genes, which exhibit a characteristic (and unsurprisingly) rapid decay in information content with increasing time before present (Fig. 2). The analytical benefits of incorporating into systematic datasets a higher proportion of loci of greater phylogenetic informativeness are considerable, and include less homoplasy and more stable parameter convergence (O'Neill et al., 2013), among others. Clearly, the previous dearth of available markers for arachnid systematics has resulted in a majority of studies utilising only a relatively small selection of the 'usual suspects', the end result being predictably poor topological resolution. For example, nuclear ribosomal RNA genes have been relied upon heavily for deeper phylogenetic inference, usually with limited success due to sequence conservatism and/or nucleotide autocorrelation (Rix et al., 2008). Non-concerted evolution has also been shown to be problematic for certain groups (Rix and Harvey, 2012). Mitochondrial markers (e.g. CO1) and nuclear internal transcribed spacer genes (ITS1, ITS2) have likewise featured prominently in analyses at the species

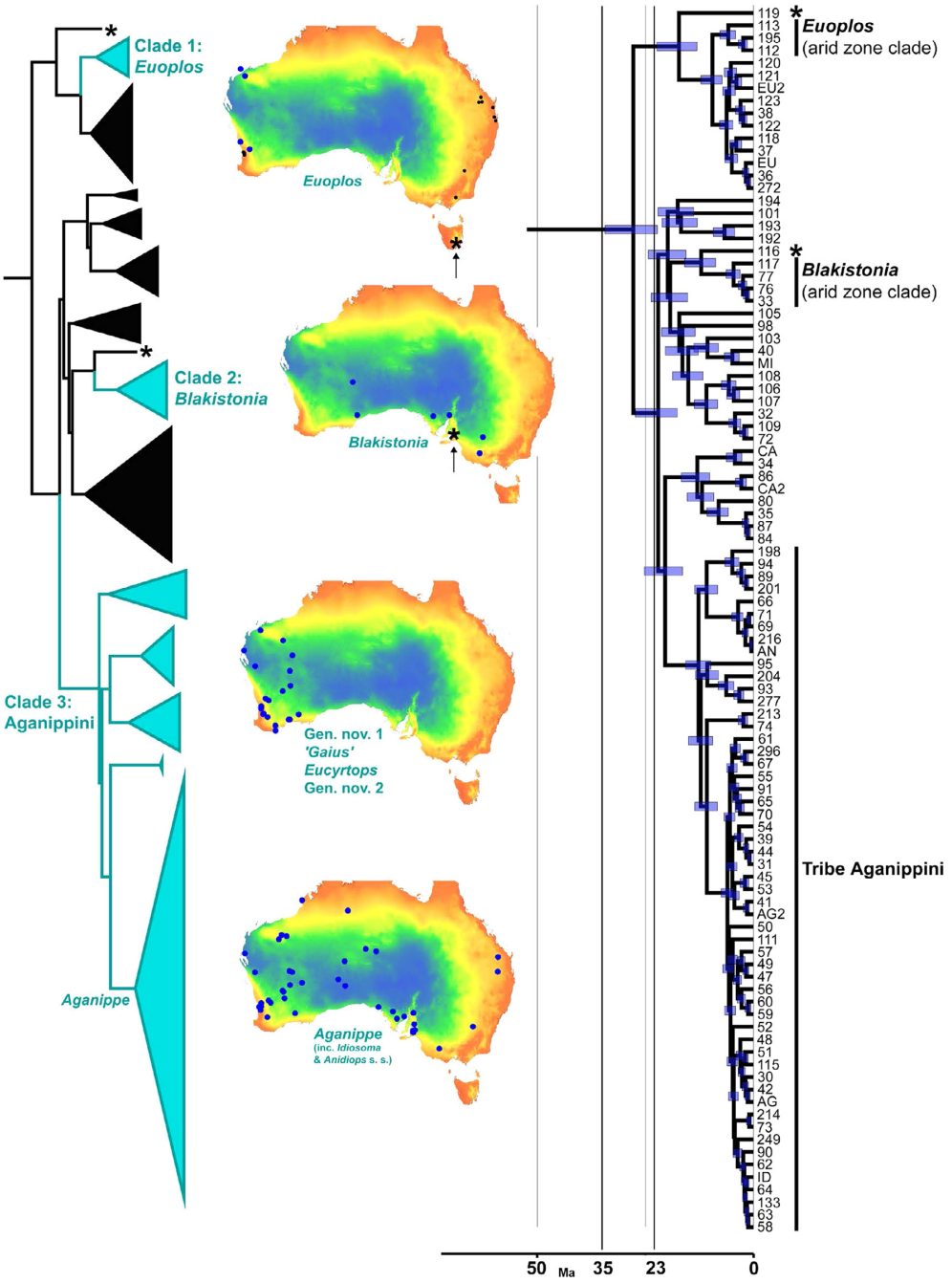

Fig. 6. Summary phylogeny resulting from BI analysis of the 'FULL' dataset (see Fig. 5) (left) and chronogram resulting from a fossil-calibrated BEAST analysis of the reduced-representation 'BEAST_7' dataset (right), showing arid incursions in Australian Idiopidae (highlighted in blue on left, and labelled on right). Maps show the sampled localities corresponding to each arid-adapted lineage, against mean annual rainfall (red–blue on map for highest to lowest rainfall, respectively). The time-scale at right highlights 35 Ma and the beginning of the Miocene at 23 Ma. Arid incursions have occurred three times independently, in a clade of Western Australian *Euoplos* (Clade 1), in a clade of *Blakistonia* (Clade 2), and in the Aganippini (Clade 3; see Figs. 7 and 8 for further details). Note the highlighted (*) mesic sister-groups of Clades 1 and 2. Maps generated by the Atlas of Living Australia (ALA) mapping interface (http://www.ala.org.au/), reproduced under a Creative Commons Attribution 3.0 Australia Licence. Note that non-idiopid outgroups have been omitted from chronogram for ease of presentation; see Supplementary File 5 for the identification of numbered taxa. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

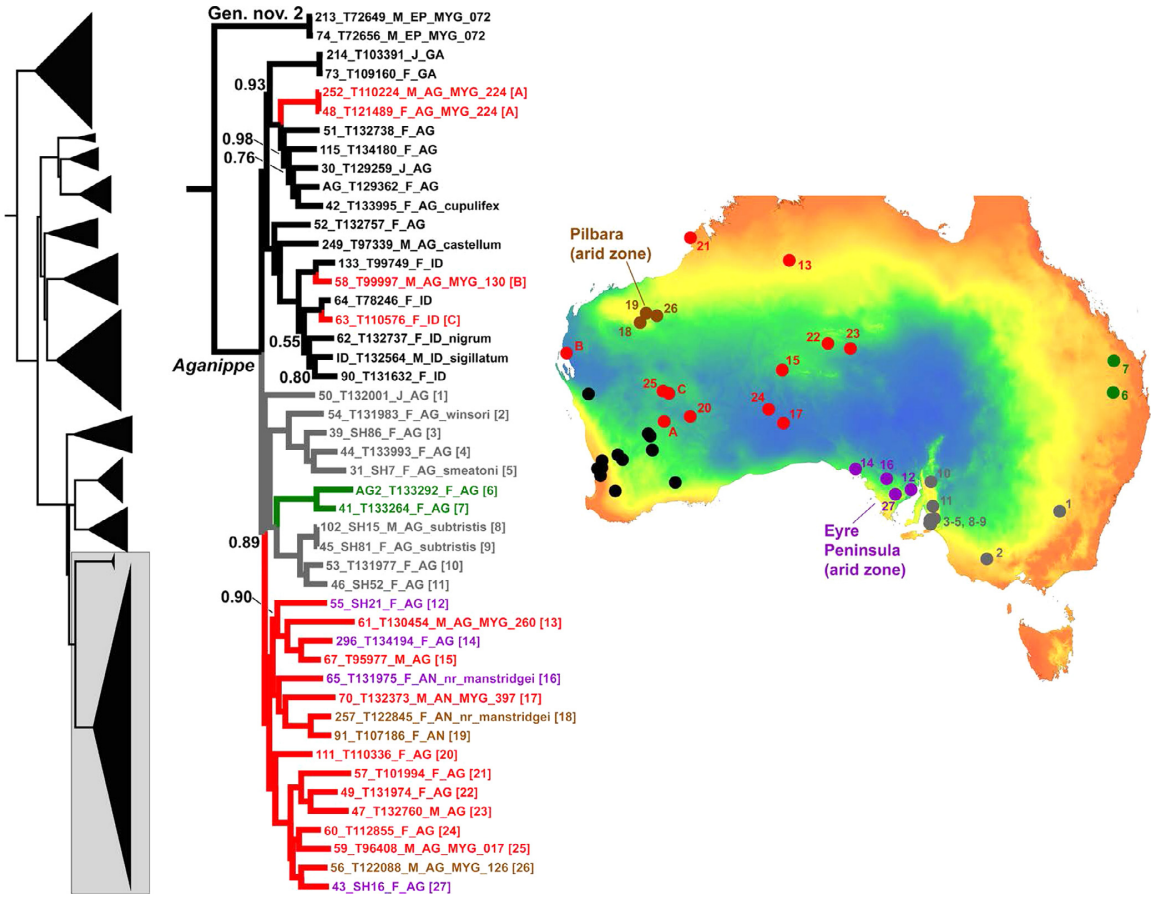

Fig. 7. Phylogeny resulting from BI analysis of the 'FULL' dataset (see Fig. 5), showing the distributions and inferred maximum parsimony ancestral areas (as coloured branches) of sampled *Aganippe* as an area phylogram against mean annual rainfall (red–blue on map for highest to lowest rainfall, respectively). The schematic summary phylogeny of Fig. 5 is shown at left for comparison. Black branches denote taxa from temperate south-western Australia; red branches denote taxa from the arid zone (including the Pilbara and Eyre Peninsula, denoted by brown and purple dots/tip labels, respectively); grey branches denote taxa from temperate south-eastern Australia; and green dots denote taxa from eastern Australia. South-western Australian-derived arid zone taxa are designated (A-C) in square brackets, and non-south-western Australian (i.e. south-eastern, eastern and arid inland) taxa are numbered (1–27) in square brackets, for ease of distributional interpretation on map. Note the monophyly of the temperate South Australian taxa plus the bulk of the arid zone fauna, and the polyphyly of the Pilbara and Eyre Peninsula sub-regions (the latter identified with brown and purple dots/tip labels, respectively). Map generated by the Atlas of Living Australia (ALA) mapping interface (http://www.ala.org.au/), reproduced under a Creative Commons Attribution 3.0 Australia Licence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

or population levels, as few other nuclear markers useful for species delimitation have been available. However, in one of the more rigorous amplicon-based studies conducted on a group of spiders, Satler et al. (2013) analysed one mitochondrial and five nuclear genes, including two novel nuclear markers (i.e. Mid1 nDNA, Anonymous nDNA). Similarly, Hedin et al. (2015) explored the phylogeography of montane mygalomorph spiders using one mitochondrial and seven nuclear gene regions. Their results highlight the value of larger multi-locus nuclear approaches to phylogenetic reconstruction and species delimitation, and of using matrices that are not saturated with mitochondrial data (the latter of which may inflate divergences in organisms with sex-biased dispersal; see also Brito and Edwards, 2009).

Multiple, sufficiently-informative genes are clearly important for confidently reconciling gene trees and species trees, and for undertaking molecular systematic synopses of large or otherwise highly diverse faunas. Townsend's PI is only one of a number of methods that can be used to optimise locus choice as a function of phylogenetic experimental design. Others include weighted geometric quartet mapping (Nieselt-Struwe and von Haeseler, 2001; Misof et al., 2013), the Fisher information matrix (Edwards, 1972; Goldman, 1998) and the Susko and Roger approach (Susko and Roger, 2012). For example, geometric quartet mapping has often been used to 'reduce' supermatrices for phylogenomic analyses using an implemented algorithm (Meusemann et al., 2010; von Reumont et al., 2012), or for selecting an optimal subset of partitions (e.g. Misof et al., 2014). Townsend's PI has been criticized to be biased towards overrating fast-evolving sites based on an empirical example (Klopfstein et al., 2010), but the extent of this bias and its effect on experimental design at the phylogenomic scale is unclear. Given the focus of the current study on a closely related group of organisms, this bias is unlikely to hamper our results. To our knowledge, none of the other approaches has been studied in any systematic way in relation to their performance in predicting the utility of different genes for phylogenetic inference. Given the increased need for tools to facilitate experimental design in the phylogenomic era, this would be a valuable avenue for future research.

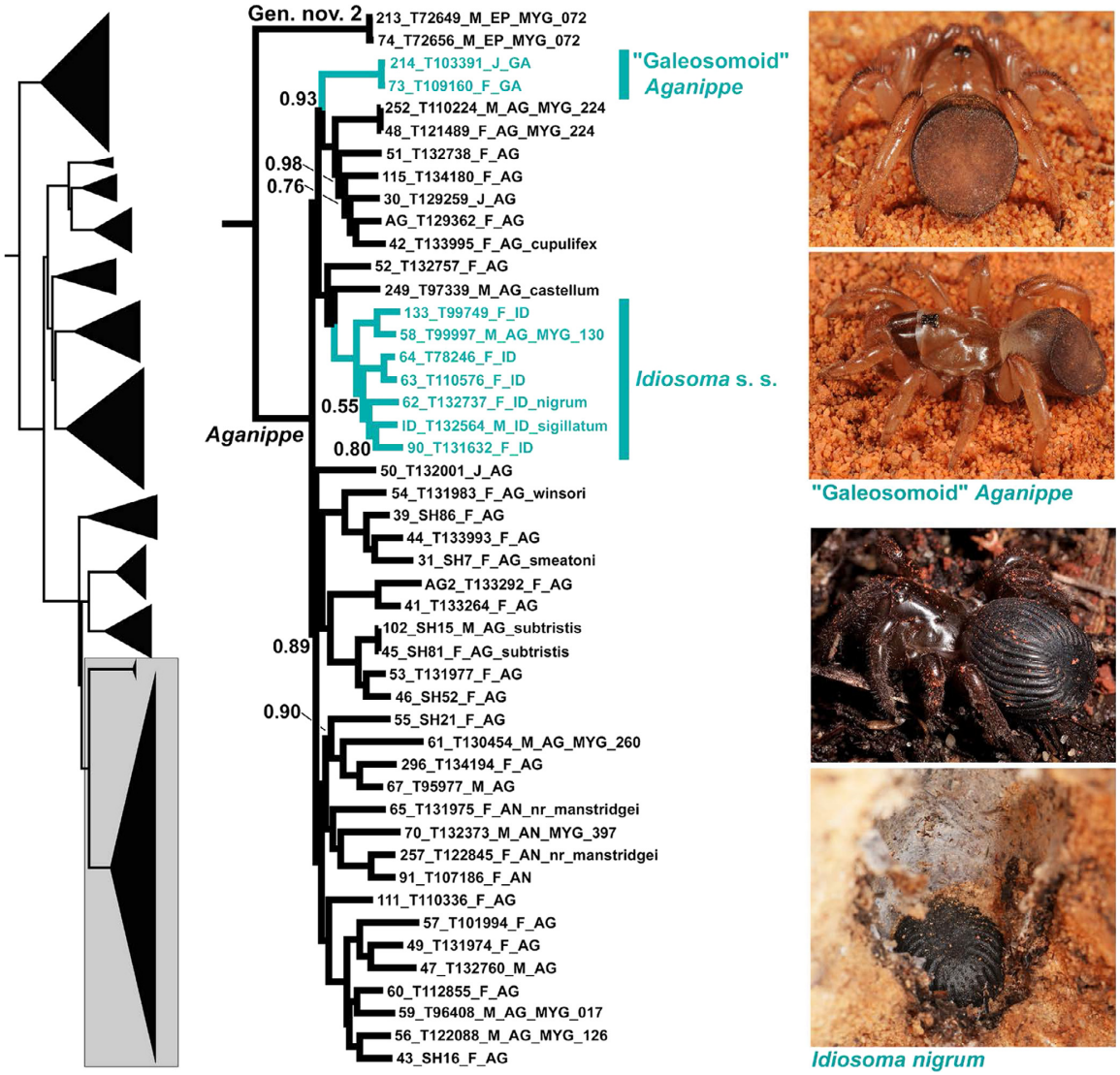

Fig. 8. Phylogeny resulting from BI analysis of the 'FULL' dataset (see Fig. 5), showing the independent evolution and maximum parsimony ancestral state optimisation (as coloured branches) of phragmotic burrow-plugging abdominal morphologies in Australian *Aganippe* (in blue). Black branches denote taxa with unmodified abdomens. Posterior probability values are >0.98 unless otherwise stated, and the schematic summary phylogeny of Fig. 5 is shown at left for comparison. Images of "Galeosomoid" *Aganippe* by Z. Hamilton, used with permission; top image of *Idiosoma nigrum* by V. Framenau, used with permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. The phylogeny and classification of Australasian Idiopidae

Our study resolves the arbanitine idiopid phylogeny with negligible incongruence between analyses, thus providing a solid and rigorously-tested foundation for future systematic studies on the family in Australasia. At least 10 monophyletic genus-group lineages were resolved (Fig. 5), many confirming current generic hypotheses and others clarifying previously ambiguous groups. The Aganippini was recovered as a monophyletic assemblage of five genera, with all but one genus restricted to Western Australia, and evidence for two new genera without existing genus-group names. The largest aganippine genus, *Aganippe*, included both *Idiosoma* and *Anidiops sensu stricto*, to the exclusion of '*Gaius*'. The Arbanitini (*sensu* Raven, 1985) was recovered as paraphyletic with respect to Aganippini, and included three major reciprocally-monophyletic lineages, each of which could be considered tribes in their own right. The generic composition of one of these, the *Cataxia* assemblage, has vacillated in different taxonomic treatments, with '*Neohomogona*' Main and '*Homogona*' Rainbow being variously considered junior synonyms of *Cataxia* Rainbow, or valid genera in their own right (e.g. Raven, 1985; Main, 1985b, 1993; Raven and Wishart, 2006). Our analyses resolved all three genus-group lineages as reciprocally monophyletic, and thus the treatment of each as a valid genus (or otherwise) is academic.

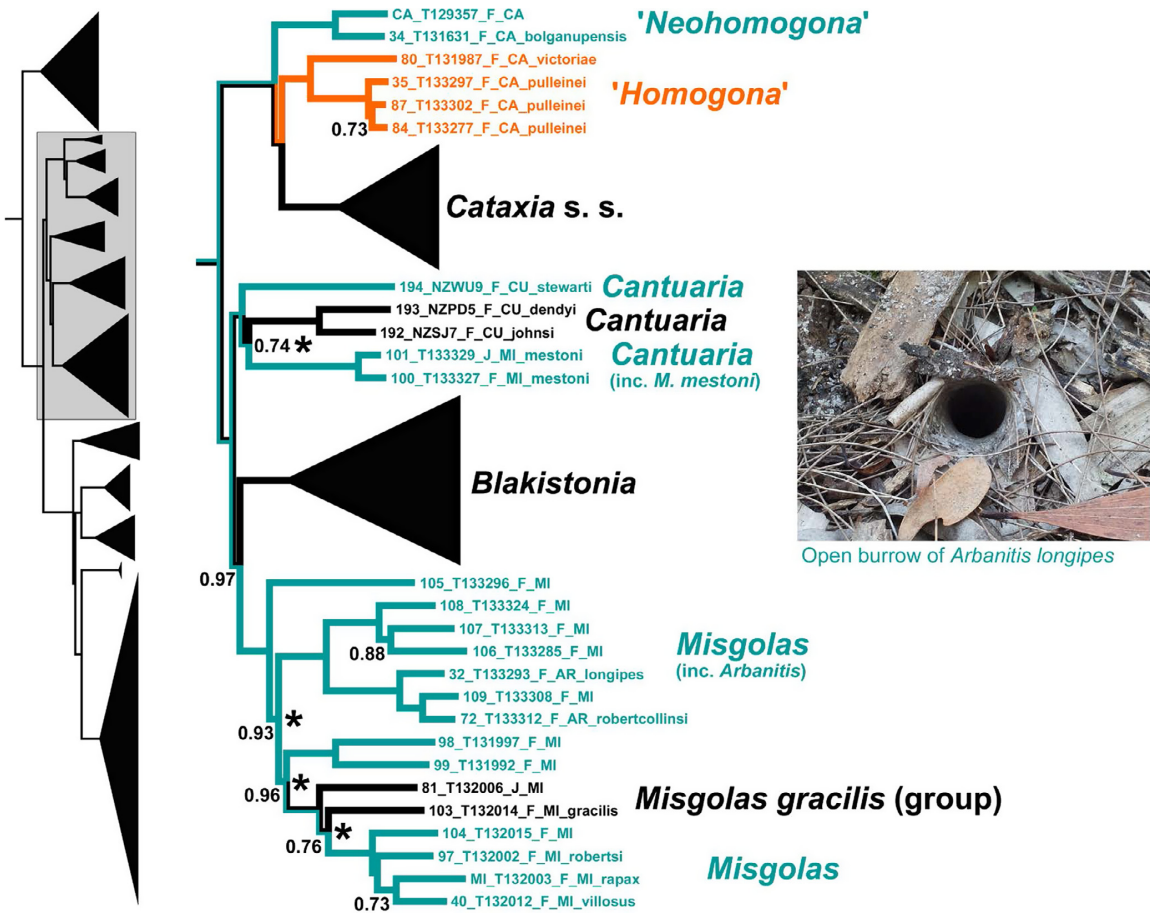

Fig. 9. Phylogeny resulting from Bayesian analysis of the 'FULL' dataset (see Fig. 5), showing the evolution and maximum parsimony ancestral state optimisation (as coloured branches) of open-holed burrow-building behaviours in mesic Australasian Idiopidae. Blue lineages denote taxa that build open burrows; the orange '*Homogona*' lineage is characterised by an intermediate 'semi-open' burrow morphology; black lineages are door-building. Highlighted clades (*) were ambiguous, in that they were not recovered as presented in Bayesian and/or likelihood analyses of the 'MAJORITY' dataset. Posterior probability values are >0.98 unless otherwise stated, and the schematic summary phylogeny of Fig. 5 is shown at left for comparison. Note the reversal to door-building in the *Misgolas gracilis* group and possibly also *Cantuaria*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. The evolution of arid-adapted Arbanitinae

The arid-adapted Idiopidae of Australia were recovered in three monophyletic lineages (Fig. 6). The first, a clade of *Euoplos*, is endemic to western Western Australia, occurring from the Avon Wheatbelt bioregion in the south, north to the Pilbara (Fig. 6). This clade diverged from a sister clade of otherwise mesic mainland taxa in the mid-Miocene and, given its restricted distribution, an 'out of SWWA' hypothesis for its geographic origin cannot be rejected. However, our sampling is insufficient to determine where the earliest-branching species occur, and the extinction of related taxa in eastern Australia remains a possibility. Currently, no mesic members of this Western Australia *Euoplos* lineage have ever been discovered, further obscuring the possible origins of this group.

A second clade in the genus *Blakistonia* has speciated throughout the central arid zone (Fig. 6; SEH, unpubl. data), with available evidence suggesting that this lineage may have originated in temperate South Australia. The closest relative to all arid-adapted *Blakistonia* species is a rare spider endemic to shaded mossy banks in the Mount Lofty region, which is the wettest closed forest habitat in South Australia. However, our sampling is otherwise sparse for the arid *Blakistonia* clade, and further analyses, including a wider selection of taxa, are required to test this 'out-of-South-Australia' hypothesis in more detail.

The third, most diverse clade of arid-adapted Idiopidae in Australia is the tribe Aganippini, members of which are absent from all but the transitional fringes of the mainland mesic zone (Fig. 6). Five genus-group lineages were recovered, all but one of which are endemic to Western Australia. The Aganippini provide compelling support for the 'out-of-SWWA' hypothesis, and indeed SWWA optimises as an ancestral area for all five aganippine genera; highly un-parsimonious levels of extinction across the rest of mainland Australia would need to be invoked to reject this hypothesis. This is true even of *Aganippe*, where the monophyly of the eastern Australian plus the derived arid zone species suggests an initial range expansion to temperate South Australia, prior to arid zone speciation. This more complex scenario highlights that, while SWWA may have been an important ancestral area for some arid zone lineages of *Aganippe*, temperate South Australia – and potentially the Eyre Peninsula specifically (Fig. 7) – also played a critical interme-

diate role. Indeed, *Aganippe* originating in temperate South Australia underwent a remarkable radiation in the Australian central arid zone, having colonised the major Australian desert systems from one side of the country to the other, with some species' ranges extending all the way to the arid margins of SWWA. This radiation was likely complex in its phylogenetic trajectory, as key subregions within the arid zone (e.g. the Pilbara and Eyre Peninsula) show evidence of multiple (polyphyletic) colonisations (Fig. 7). Unsurprisingly, like so many arid zone lineages (summarised in Byrne et al., 2008), the *Aganippe* radiation was inferred to be late Miocene and Pliocene in age.

The evolutionary and geographic origins of arid zone Idiopidae in Australia are therefore taxon-dependent, with three independent arid incursions during the Miocene, each resulting in subsequent speciation and range expansion in different areas. An initial 'out-of-SWWA' hypothesis cannot be rejected for two of the three lineages, however another 'out-of-temperate-South-Australia' scenario can also be invoked for *Blakistonia*, and for a lineage within *Aganippe* (the latter albeit with origins in SWWA in the first instance). That three groups of Australian Idiopidae even managed to make the transition from mesic to arid habitats at all is notable, given the temperate Gondwanan ancestry of the family, and the niche-conservatism characteristic of other taxa. Yet how these transitions occurred, and what (if anything) pre-adapted them to make the transition, remain unknown. However, analogous arid incursions and subsequent radiations have also occurred in other southern-temperate mygalomorph families in Australia, namely Nemesiidae, which also has a number of endemic Western Australian genera, and one genus, *Aname* L. Koch, that like *Aganippe*, has undergone a spectacular arid radiation (Castalanelli et al., 2014). Nemesiidae would make an excellent candidate lineage for testing the results of this study in another major sympatric spider group.

4.4. The evolution of phenotypic traits in the arid and mesic zones

There are few obvious morphological traits among Australian Idiopidae that seem correlated with arid- versus mesic-adaptation. Indeed, the somatic morphology of Arbanitinae is generally very conserved and, in the absence of males or molecular data, juveniles and females are often impossible to identify to genus. As such, it is currently unknown if taxa in the arid zone possess subtle morphological or physiological traits that facilitate persistence in some of Australia's driest terrestrial habitats. However, in the transitional arid zone of SWWA, two lineages of *Aganippe* have independently evolved phragmotic abdominal morphologies, which may also play a role in physiological resistance to desiccation (Main, 1982, 2003). Phragmosis, by which an organism uses its own body armour to defend itself in its burrow (Wheeler, 1927; Main, 1976), has evolved multiple times in Mygalomorphae, most notably in African species of *Galeosoma* Purcell (Idiopidae) and Northern Hemisphere *Cyclocosmia* Ausserer (Ctenizidae) (e.g. Schwendinger, 2005). In Western Australia, species of *Idiosoma s. str.* (an autapomorphic lineage of *Aganippe*) have long been recognised as having a phragmotic morphology (Main, 1976), in the form of a highly sclerotised, rugose abdomen bearing a large posterior circular plate (Main, 1952), analogous to those in *Cyclocosmia*. When threatened, these spiders wedge themselves about half-way down their burrows, with the hard plate and circular profile of the posterior abdomen used to plug the burrow shaft (Fig. 8). Remarkably, in 2010, populations were discovered of another *Aganippe* species from the Western Australian Coolgardie bioregion, with a rather different phragmotic abdominal morphology. In this species, the abdomen is reinforced with a circular rim of cuticle surrounding a thick, sclerotised pad, not unlike species of *Galeosoma* (Fig. 8). It too is a member of the SWWA clade of *Aganippe*, but is unrelated to *Idiosoma s. str.* (Figs. 7 and 8).

Phragmosis is an unusual and very rare solution to burrow defence among arthropods, utilised primarily by eusocial insects (Schwendinger, 2005). Its parallel evolution in *Aganippe* underscores the remarkable adaptive radiation of this genus in the Australian arid zone, and further highlights the significance of a burrowing lifestyle to all aspects of the evolutionary biology of trapdoor spiders. Indeed, burrow morphology itself has been suggested as one of the most important adaptive traits for both arid- and mesic-adapted idiopid taxa (Main, 1982), and door-building by ctenizoid mygalomorph spiders (including Idiopidae) is undoubtedly symplesiomorphic. All arid-adapted Idiopidae in Australia build a strong hinged door to their burrows, and resulting burrow micro-climates have been shown to be critical for the maintenance of conditions conducive to physiological persistence in Aganippini (Mason et al., 2013). Yet one of the most striking characteristics of many niche-conserved idiopid lineages from the Australian mesic zone is the complete absence of a burrow door, with open-holed burrows analogous to those made by Nemesiidae built by species in at least three genus-group lineages (Fig. 9). A fourth lineage, congruent with '*Homogona*' (currently a junior synonym of *Cataxia*), is characterised by a 'semi-open' sock-like burrow morphology (see Main, 1985a). Although the ancestral optimisation of door-building (or otherwise) is ambiguous among mesic zone lineages (Fig. 9), it is probable that given the symplesiomorphic condition for the family, the complete loss of a burrow door has occurred three times independently in Australasian Idiopidae: once in '*Neohomogona*' (currently a junior synonymy of *Cataxia*), once in *Cantuaria*, and once in *Misgolas* (Fig. 9). Similarly, burrow door-building behaviours have likely re-evolved twice in these same lineages – once in *Misgolas* and possibly once in *Cantuaria*. Although door-building was optimised on the phylogeny resulting from the 'FULL' dataset as being potentially polyphyletic in *Misgolas* (Fig. 9), relevant clades were weakly supported, and door-building taxa were otherwise recovered as monophyletic in both 'MAJORITY' analyses (BI and ML). We favour the latter, more parsimonious result, in which a single New South Wales clade (including *M. gracilis* (Rainbow and Pulleine, 1918)) likely re-evolved burrow door-building behaviours just once. However, whether door-building re-evolved once or multiple times in *Cantuaria* requires additional, more detailed sampling of the New Zealand fauna. Why burrow door-building behaviours have been lost (and indeed regained) in mesic taxa remains unknown, although an adaptive explanation seems likely given the fundamental role of the burrow in trapdoor spider biology.

4.5. The New Zealand fauna: vicariance or dispersal?

The presence of a diverse idiopid fauna in New Zealand has long been known (Forster, 1968), and the genus *Cantuaria* is currently the subject of detailed systematic analysis at the species level (V. Smith and C. Vink, pers. comm.). The recent paradigm shift in our understanding of the origins of the New Zealand biota, from a predominantly 'Moa's Ark' perspective (hypothesising ancient, vicariant origins), to alternative 'Goodbye Gondwana' explanations (hypothesising more recent dispersal scenarios) (see Trewick et al., 2007; Giribet and Boyer, 2010; and references therein), has been driven by evidence suggesting that much of the now exposed New Zealand land surface was submerged during the Oligocene (the 'Oligocene drowning' hypothesis). That Idiopidae are putatively Gondwanan and occur on New Zealand provides an opportunity to test these competing hypotheses, in another flightless, dispersal-limited invertebrate group (e.g. Boyer and Giribet, 2009; Giribet and Boyer, 2010; Murienne et al., 2013).

Divergence dating with the 'BEAST_7' dataset inferred a HPD estimate of between 24 and 15 Ma for the divergence of New Zealand *Cantuaria* from other Australian Arbanitinae, and a crown-group age estimate for *Cantuaria* of between 22 and 14 Ma (Supplementary File 13). These results are essentially below the 22 Ma 'barrier' proposed for distinguishing taxa present on New Zealand before a possible Oligocene drowning event from those that potentially arrived afterwards via dispersal (Giribet and Boyer, 2010). Similarly, the Australian *Cantuaria* fauna is rendered paraphyletic by New Zealand species (as expected under a dispersal hypothesis; Giribet and Boyer, 2010), with Tasmanian taxa being closest relatives to New Zealand species in the ML tree of the 'MAJORITY' dataset. An alternative vicariant origin cannot be entirely rejected, in the event that analysis of the 'BEAST_7' dataset severely under-estimated the age of divergence (New Zealand was last connected to Gondwana between 80 and 60 Ma; Sanmartin and Ronquist, 2004; Giribet and Boyer, 2010). However, in the absence of more detailed sampling of both the Australian and New Zealand taxa, and dating evidence to the contrary, we favour a dispersal scenario for the occurrence of *Cantuaria* in New Zealand, with subsequent *in situ* radiation.

5. Conclusion

Post-Eocene climate change, and the development of the Australian arid zone, resulted in the severe contraction and fragmentation of idiopid populations within niche-conserved lineages, and the concomitant evolution and expansion of three highly arid-adapted clades. This study provides the first comprehensive continental synopsis of arid zone biogeography in an Australian arachnid lineage, and the first empirical test of the 'out of south-western Australia' ancestral area hypothesis. Our data highlight the primacy of the Miocene and early Pliocene in generating this arid zone diversity, and the importance of both temperate Western *and* South Australia as ancestral areas. Idiopidae represent an excellent lineage for understanding processes of arid-adaptation in southern-temperate Austral invertebrates, and provide insights into the evolution of the Australian arid zone biota more generally, in both space and time. From an empirical perspective, the baseline ortholog dataset (of 149 genes) underpinning this work offers enormous potential for application to future studies using developing NGS platforms like hybrid enrichment, and for the phylogenetic interrogation of other arachnid lineages at all taxonomic levels. For the poorly-documented Australian fauna, this study further contributes a stable phylogenetic framework, and a rigorous molecular foundation for describing the morphological diversity of that fauna at the generic and species levels.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.01.008. Supplementary data files are also lodged in the Dryad Digital Repository, at: http://datadryad.org/ (http://dx.doi.org/10.5061/dryad.s1v34).

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APPENDIX 6.2: The Australasian spiny trapdoor spiders of the family Idiopidae (Mygalomorphae: Arbanitinae): a relimitation and revision at the generic level (2017, Invertebrate Systematics. 31, 566–634).

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The Australasian spiny trapdoor spiders of the family Idiopidae (Mygalomorphae : Arbanitinae): a relimitation and revision at the generic level

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Abstract. The Australasian spiny trapdoor spiders of the family Idiopidae (subfamily Arbanitinae) are revised at the generic level, using a multi-locus molecular phylogenetic foundation and comprehensive sampling of all known lineages. We propose a new family- and genus-group classification for the monophyletic Australasian fauna, and recognise 10 genera in four tribes. The Arbanitini Simon includes *Arbanitis* L. Koch, 1874 (61 species), *Blakistonia* Hogg, 1902 (one species) and *Cantuaria* Hogg, 1902 (43 species). The Aganippini Simon includes *Bungulla* Rix, Main, Raven & Harvey, gen. nov. (two species), *Eucanippe* Rix, Main, Raven & Harvey, gen. nov. (one species), *Eucyrtops* Pocock, 1897 (two species), *Gaius* Rainbow, 1914 (one species) and *Idiosoma* Ausserer, 1871 (14 species). The Cataxiini Rainbow and Euoplini Rainbow include just *Cataxia* Rainbow, 1914 (11 species) and *Euoplos* Rainbow, 1914 (12 species), respectively. Two distinctive new genera of Aganippini are described from Western Australia, and several previously valid genera are recognised as junior synonyms of existing genus-group names, including *Misgolas* Karsch, 1878 (= *Arbanitis*; new synonymy), *Aganippe* O. P.-Cambridge, 1877 (= *Idiosoma*; new synonymy) and *Anidiops* Pocock, 1897 (= *Idiosoma*; new synonymy). *Gaius* stat. rev. is further removed from synonymy of *Anidiops*. Other previously hypothesised generic synonyms are supported by both morphology and molecular phylogenetic data from 12 genes, including the synonymy of *Neohomogona* Main, 1985 and *Homogona* Rainbow, 1914 with *Cataxia*, and the synonymy of *Albaniana* Rainbow & Pulleine, 1918, *Armadalia* Rainbow & Pulleine, 1918, *Bancroftiana* Rainbow & Pulleine, 1918 and *Tambouriniana* Rainbow & Pulleine, 1918 with *Euoplos*. At the species level, the identifications of *Eucy. latior* (O. P.-Cambridge, 1877) and *I. manstridgei* (Pocock, 1897) are clarified, and three new species are described: *Bungulla bertmaini* Rix, Main, Raven & Harvey, sp. nov., *Eucanippe bifida* Rix, Main, Raven & Harvey, sp. nov. and *Idiosoma galeosomoides* Rix, Main, Raven & Harvey, sp. nov., the latter remarkable for its phragmotic abdominal morphology. The Tasmanian species *Mygale annulipes* C. L. Koch, 1842 is here transferred to the genus *Stanwellia* Rainbow & Pulleine, 1918 (family Nemesiidae), comb. nov., *Arbanitis mestoni* Hickman, 1928 is transferred to *Cantuaria*, comb. nov. and *Idiosoma hirsutum* Main, 1952 is synonymised with *I. sigillatum* (O. P.-Cambridge, 1870), new synonymy. In addition to the morphological synopses and an illustrated key to genera, molecular diagnoses are presented for all nominal taxa, along with live habitus and burrow images to assist in field identification. The Australasian idiopid fauna is highly diverse, with numerous new species known from all genera. As a result, this study provides a taxonomic and nomenclatural foundation for future species-level analyses, and a single reference point for the monographic documentation of a remarkable fauna.

http://zoobank.org/?lsid=urn:lsid:zoobank.org:pub:BACE065D-1EF9-40C6-9134-AADC9235FAD8

Additional keywords: biogeography, Domiothelina, Euctenizoidina, molecular systematics.

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Introduction

The arbanitine spiny trapdoor spiders (Idiopidae) are an iconic and highly diverse component of the Australasian ground-dwelling spider fauna, renowned for their longevity (Main 1987), cryptic fossorial life history (Main 1957), biogeography (Rix *et al.* 2017*a*) and conservation significance (Rix *et al.* 2017*b*). The family has a putatively Gondwanan (largely Austral) distribution, and is one of the few southern-temperate arthropod families to occur on all former Gondwanan land masses, with the exception of Antarctica (World Spider Catalog 2016). In Australia, the family is most abundant in temperate and sub-tropical habitats south of the Tropic of Capricorn, with only a minority of species occurring in the tropical arid zone and the mesic rainforests of north-eastern Australia. Multiple lineages have radiated in the mainland Australian arid zone, and a single lineage has diversified in New Zealand (Rix *et al.* 2017*a*). Idiopids exhibit a remarkable array of morphological and behavioural adaptations to different climates and substrates, and have evolved various predator avoidance strategies and methods of prey acquisition, along with the largest array of burrow morphologies among Australasian Mygalomorphae (Main 1957, 1978, 1987). Female Arbanitinae are also among the longest-lived of arachnids, with lifespans of some taxa known to exceed 40 years in the wild (Main 1987; pers. obs.). They are the quintessential 'trapdoor spiders' of Australia, and have featured heavily in studies on ecology and natural history (Main 1986, 1993, 1995; Ellis 2015), demographics (Main 1978, 1987, 2003), systematics (Faulder 1985; Main 1985*b*; Raven 1985; Raven and Wishart 2006; Wishart 2006; Castalanelli *et al.* 2014; Rix *et al.* 2017*a*), faunistics (Main *et al.* 2000), biogeography (Rix *et al.* 2017*a*) and conservation biology (Main 1990; Rix *et al.* 2017*b*).

The Idiopidae were long considered members of the family Ctenizidae, until Raven (1985) radically relimited the latter, removing all Australian taxa with the exception of *Conothele* Thorell, 1878 to the Idiopidae. Raven (1985) further divided the idiopids into three subfamilies – the Idiopinae Simon, Genysinae Simon and Arbanitinae Simon – the latter endemic to Australasia. The family is currently represented by 322 species in 22 genera worldwide (World Spider Catalog 2016), and has remained a distinctive, monophyletic group in both morphological and molecular phylogenetic studies (e.g. Goloboff 1993; Hedin and Bond 2006; Bond *et al.* 2012). However, the Australian fauna has had a long and confusing history of taxonomic documentation, with 20 genus-group names proposed in the literature, over half of which are currently junior synonyms, with most of the latter made by Main (1985*b*). As a result, before the stabilising works by Main (1985*b*, 1985*c*) and Raven (1985), the Australian idiopid (then ctenizid) fauna was a difficult to negotiate jungle of nominal taxa, most extremely poorly described in the first instance. Main (1985*b*) addressed many of these issues, but arbanitine idiopid taxonomy has remained hampered by phylogenetically untested and poorly enunciated generic concepts, and a prevalence of species-group names based on difficult to identify female type specimens. These problems were exemplified by the genus *Arbanitis* L. Koch, 1874, the identity of which vacillated for well over a century until Raven and Wishart (2006) reported the rediscovery of the holotype of *A. longipes* (L. Koch, 1873), resulting in several nomenclatural changes (see Raven and Wishart 2006). These generic-level challenges have been further amplified by the discovery in recent decades of a large number of new idiopid species from across Australasia, most of which require male specimens, molecules or a combination of both for accurate identification. Indeed, we now know that many of the species concepts promulgated in earlier taxonomic treatments (e.g. Main 1957) greatly underestimated the true species-level diversity. As such, with the exception of *Arbanitis* (then *Misgolas* Karsch, 1878) in central eastern New South Wales (e.g. Wishart 1992, 2006, 2011; Wishart and Rowell 1997, 2008) and perhaps *Cantuaria* in New Zealand (e.g. Forster 1968), the species-level diversity of Arbanitinae remains essentially unevaluated overall.

This tenuous taxonomic foundation has undoubtedly affected our ability to delimit arbanitine monophyla and thus confidently diagnose genera. Idiopids are notoriously conservative in their somatic and genitalic morphology, with most higher taxa seemingly more symplesiomorphic than apomorphic for most character systems (Goloboff 1993). Diagnostic generic characters have been proposed by various workers in modern treatments of the Australian fauna (e.g. Main 1985*b*; Raven and Wishart 2006), but obvious synapomorphies have remained elusive in most instances. For such a major component of the mygalomorph fauna, these endemic taxonomic limitations demanded a fresh assessment at a continental scale. To do this, Rix *et al.* (2017*a*) reconstructed the phylogeny and tested the generic classification of the Australasian Idiopidae using a multi-locus (12-gene) molecular approach. Representatives of all major lineages from across Australia and New Zealand were included in the analyses, which were further contextualised by the addition of most generic and junior generic type species, from their individual type localities wherever possible. These data recovered 10 monophyletic genus-group lineages in all analyses (Fig. 1). Most previously valid generic concepts were supported or at least clarified by the molecular data, with evidence for several other taxa requiring synonymy or removal from synonymy. Remarkably, two lineages were unnamed, and Rix *et al.* (2017*a*) identified these unexpected monophyletic groups as undescribed genera.

This study is therefore a formal taxonomic treatment of the results of Rix *et al.* (2017*a*; Fig. 1), and a reanalysis of the generic concepts of Main (1985*b*), Raven (1985) and Raven and Wishart (2006). The subfamily Arbanitinae is relimited to include 10 monophyletic genera in four tribes, each explicitly diagnosed with molecular and morphological characters. Two new genera and three new species are described, and all nominal taxa at the family-, genus- and species-group levels are stabilised. In doing so, this study aims to provide a molecular phylogenetic, morphological taxonomic and nomenclatural foundation for future species-level analyses, and a single reference point for the monographic documentation of the highly diverse Australian idiopid fauna.

Materials and methods

Specimens and descriptions

Specimens were examined following preservation in 70% or 95% ethanol, usually under a Zeiss Stemi SV11

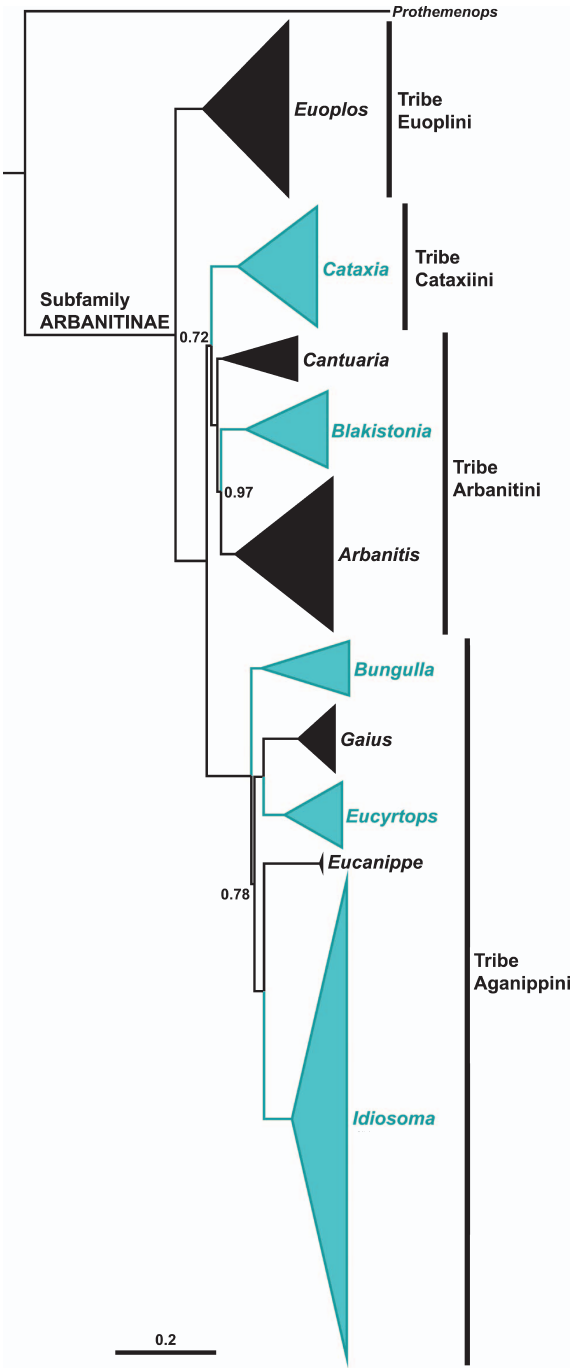


Fig. 1. Proposed classification and summary phylogeny of the Australasian idiopid genera from the analysis of Rix *et al.* (2017*a*), showing results from a partitioned Bayesian analysis of that study's 12-gene dataset (129 taxa, 9601 bp: *CO1*, *CYB*, *MRPL45*, *RPF2*, *XPNPEP3*, *HAT1*, *H3*, *ITS1*, *ITS2*, *5.8S* rDNA, *18S* rDNA, *28S* rRNA). Clade support values are shown for nodes with <99% posterior probability support.

stereomicroscope. Female genitalia were cleared in lactic acid. Measurements (in millimetres to one decimal place) and most digital automontage images were taken using a Leica M165C stereomicroscope with mounted DFC425 digital camera, and processed using Leica Application Suite Version 3.7 software. Leg segments were measured along the dorsal prolateral edge, in lateral view. Total length measurements include the chelicerae, in dorsal view.

This study is part of a major revision of the Idiopidae of Australia (see also Rix *et al.* 2017*a*), which will be supplemented by forthcoming species-level treatments of many genera. As such, descriptions of previously described genera have been omitted, as relevant higher-level arbanitine characters have been documented in previous works (e.g. Forster 1968; Main 1985*b*; Raven 1985). Descriptions of new taxa, and re-descriptions of previously described species (provided where relevant for stability), are here compressed and streamlined in an attempt to expedite taxonomy, and find a balance between brevity and morphological clarity. Relevant informative character systems are noted for each new genus and species, and are combined with detailed morphological and molecular diagnoses, molecular phylogenetics and digital imagery – these data, combined, provide the quantitative foundations for identification. Species concepts are unified (de Queiroz 2007) and integrative, combining morphological autapomorphy with molecular monophyly, the latter phylogenetic data derived from Rix *et al.* (2017*a*). All newly described genera and species therefore have representative nucleotide sequences lodged in GenBank (see Rix *et al.* 2017*a*: supplementary file 5; see also Dryad digital repository, http://dx.doi.org/10.5061/dryad.s1v34, accessed 6 April 2017). Molecular diagnoses for genera (using gene-specific numbered nucleotide positions) refer to the sequence alignments of stated loci in supplementary file 7 of Rix *et al.* (2017*a*) (see also Dryad digital repository, http://dx.doi.org/10.5061/dryad.s1v34); note that stated nucleotide positions for *28S* rRNA are therefore inclusive of the 38 bp 3′ end of the *ITS2* alignment, the latter of which is concatenated in supplementary file 7 of Rix *et al.* (2017*a*). These molecular diagnoses are the result of comprehensive sampling of the phylogenetic and geographic diversity for eight of the 10 genus-group lineages. When this molecular sampling was not so phylogenetically rigorous (e.g. for *Eucanippe* Rix, Main, Raven & Harvey, gen. nov. and *Cantuaria* Hogg, 1902), diagnoses are clarified accordingly. Illustrations for each genus focus on females in the live habitus plates, and on detailed male morphology in the representative morphological plates. Female genitalia of Australian Arbanitinae are simple and provide few (if any) characters useful at the genus-group level; these spermathecal morphologies were well summarised and comprehensively figured in Forster (1968) and Main (1985*b*: figs 187–208), and are not re-illustrated here.

For each genus, select species accounts are provided for nominal taxa sequenced, explicitly examined or otherwise formally treated as part of this study or as part of the molecular phylogenetic study of Rix *et al.* (2017*a*; Fig. 1); all other species are listed in Table 1. For exemplar specimens sequenced as part of the molecular phylogenetic analysis of Rix *et al.* (2017*a*; Fig. 1) or as part of ongoing (unpublished) molecular studies, DNA voucher codes are provided as

Table 1. Described species of Arbanitinae, listed according to their current classification

Type localities are summarised for all valid taxa; for Australian species each locality is annotated with its relevant State and Interim Biogeographic Regionalisation for Australia (IBRA) Version 7.0 bioregion; NP, national park; SF, state forest; SP, state park; generic type species are identified (*); new genera and new taxonomic actions at the species-group level are in bold (see text for details); newly designated *nomina dubia* are listed at the end of each genus in which they were previously placed, and synonymies are organised chronologically

Subfamily ARBANITINAE (*148 species in 10 genera*)	
Tribe ARBANITINI (*105 species in three genera*)	
Arbanitis L. Koch, 1874 (*61 species*)	
A. andrewsi (Hogg, 1902), comb. nov.	Type locality: Mount Compass (SA, KAN)
A. baehrae (Wishart & Rowell, 2008), comb. nov.	Type locality: Chichester SF (NSW, NNC)
A. beni (Wishart, 2006), comb. nov.	Type locality: Camden (NSW, SYB)
A. beaury Raven & Wishart, 2006	Type locality: Beaury SF (NSW, SEQ)
A. billsheari (Wishart & Rowell, 2008), comb. nov.	Type locality: Chichester SF (NSW, NNC)
A. biroi (Kulczyński, 1908), comb. nov.	Type locality: Mount Victoria (NSW, SYB)
A. bithongabel (Raven & Wishart, 2006), comb. nov.	Type locality: Mount Bithongabel (Qld, SEQ)
A. browningi (Wishart & Rowell, 2008), comb. nov.	Type locality: Kerewong SF (NSW, NNC)
A. campbelli (Wishart & Rowell, 2008), comb. nov.	Type locality: N. of Singleton (NSW, NNC)
A. cliffi (Wishart, 2006), comb. nov.	Type locality: Eastwood (NSW, SYB)
A. crawfordorum (Wishart & Rowell, 2008), comb. nov.	Type locality: Smiths Lake (NSW, NNC)
A. crispus (Karsch, 1878), comb. nov.	Type locality: 'Vandiemensland' (Tas.)
= *A. scaurus* Hickman, 1927 (by Main, 1985*b*; tentative synonymy)	
A. davidwilsoni (Wishart & Rowell, 2008), comb. nov.	Type locality: Lisarow (NSW, SYB)
A. dereki (Wishart, 1992), comb. nov.	Type locality: W. of Gerringong (NSW, SYB)
A. dougweiri (Wishart & Rowell, 2008), comb. nov.	Type locality: Killarney Vale (NSW, SYB)
A. echo (Raven & Wishart, 2006), comb. nov.	Type locality: Lamington NP (Qld, SEQ)
A. elegans Rainbow & Pulleine, 1918	Type locality: Kianga (NSW, SEC)
A. fredcoylei (Wishart & Rowell, 2008), comb. nov.	Type locality: Chichester SF (NSW, NNC)
A. gracilis Rainbow & Pulleine, 1918	Type locality: Sydney (NSW, SYB)
= *A. bradleyi* Rainbow, 1920 (by Wishart, 2006: 7)	
= *A. villosus* Rainbow, 1920 (by Wishart, 2006: 7)	
A. grayi (Wishart & Rowell, 2008), comb. nov.	Type locality: Gloucester Caves (NSW, NNC)
A. gwennethae (Wishart, 2011), comb. nov.	Type locality: Berry (NSW, SYB)
A. helensmithae (Wishart & Rowell, 2008), comb. nov.	Type locality: Bulga SF (NSW, NNC)
A. hirsutus Rainbow & Pulleine, 1918	Type locality: Kedron Brook (Qld, SEQ)
A. horsemanae (Wishart, 2011), comb. nov.	Type locality: Kioloa SF (NSW, SEC)
A. kampenae (Wishart, 2011), comb. nov.	Type locality: Benandarah SF (NSW, SEC)
A. kirstiae (Wishart, 1992), comb. nov.	Type locality: W. of Gerringong (NSW, SYB)
A. linklateri (Wishart & Rowell, 2008), comb. nov.	Type locality: Kerewong SF (NSW, NNC)
A. longipes (L. Koch, 1873)*	Type locality: Camira (Qld, SEQ)
= *A. pulchellus* Rainbow & Pulleine, 1918 (by Raven & Wishart, 2006)	
= *Aname pulchra* Rainbow & Pulleine, 1918 (by Main, 1972)	
A. lynabra (Wishart, 2006), comb. nov.	Type locality: Wahroonga (NSW, SYB)
A. macei (Wishart & Rowell, 2008), comb. nov.	Type locality: Bulga SF (NSW, NNC)
A. maculosus (Rainbow & Pulleine, 1918), comb. nov.	Type locality: La Perouse (NSW, SYB)
A. mascordi (Wishart, 1992), comb. nov.	Type locality: Dorrigo SP (NSW, NNC)
A. maxhicksi (Wishart & Rowell, 2008), comb. nov.	Type locality: Barrington Tops (NSW, NNC)
A. melancholicus (Rainbow & Pulleine, 1918), comb. nov.	Type locality: Clifton Gardens (NSW, SYB)
A. michaeli (Wishart, 2006), comb. nov.	Type locality: Douglas Park (NSW, SYB)
A. milledgei (Wishart & Rowell, 2008), comb. nov.	Type locality: Bondi (NSW, SYB)
A. montanus Rainbow & Pulleine, 1918	Type locality: Jenolan Caves (NSW, SEH)
A. monteithi (Raven & Wishart, 2006), comb. nov.	Type locality: Lamington NP (Qld, SEQ)
A. mudfordae (Wishart & Rowell, 2008), comb. nov.	Type locality: Bateau Bay (NSW, SYB)

(*continued next page*)

Table 1. (*continued*)

A. ornatus (Rainbow, 1914), comb. nov.	Type locality: Eidsvold (Qld, BBS)[A]
= *Aganippe ornata* Rainbow & Pulleine, 1918 (by Main, 1977)	
A. papillosus Rainbow & Pulleine, 1918	Type locality: Mount Tamborine (Qld, SEQ)
A. paulaskewi (Wishart, 2011), comb. nov.	Type locality: NW. of Quaama (NSW, SEC)
A. phippsi (Wishart, 2011), comb. nov.	Type locality: Mollymook (NSW, SYB)
A. rapax (Karsch, 1878), comb. nov.	Type locality: Gerringong (NSW, SYB)
= *Misgolas hubbardi* Wishart, 1992 (by Wishart & Rowell, 2008)	
A. raveni (Wishart & Rowell, 2008), comb. nov.	Type locality: Berkeley Vale (NSW, SYB)
A. robertcollinsi Raven & Wishart, 2006	Type locality: Springbrook (Qld, SEQ)
A. robertsi (Main & Mascord, 1974), comb. nov.	Type locality: Minnamurra Falls (NSW, SYB)
A. rodi (Wishart, 2006), comb. nov.	Type locality: Kurrajong (NSW, SYB)
A. rowelli (Wishart, 2011), comb. nov.	Type locality: Minnamurra (NSW, SYB)
A. shawi (Wishart, 2011), comb. nov.	Type locality: Bega (NSW, SEC)
A. sydjordanae (Wishart & Rowell, 2008), comb. nov.	Type locality: Kerewong SF (NSW, NNC)
A. taiti (Wishart & Rowell, 2008), comb. nov.	Type locality: Lochinvar (NSW, SYB)
A. tannerae (Wishart, 2011), comb. nov.	Type locality: Minnamurra Falls (NSW, SYB)
A. tarnawskiae (Wishart & Rowell, 2008), comb. nov.	Type locality: Cape Hawke (NSW, NNC)
A. thompsonae (Wishart & Rowell, 2008), comb. nov.	Type locality: Chichester SF (NSW, NNC)
A. trangae (Wishart, 2006), comb. nov.	Type locality: Narrabeen (NSW, SYB)
A. villosus (Rainbow, 1914), comb. nov.	Type locality: Enfield (NSW, SYB)
A. watsonorum (Wishart & Rowell, 2008), comb. nov.	Type locality: Cape Hawke (NSW, NNC)
A. wayorum (Wishart, 2006), comb. nov.	Type locality: Woolooware (NSW, SYB)
A. weigelorum (Wishart & Rowell, 2008), comb. nov.	Type locality: Gosford (NSW, SYB)
A. yorkmainae (Wishart & Rowell, 2008), comb. nov.	Type locality: Kerewong SF (NSW, NNC)
'*Arbanitis fuscipes* Rainbow, 1914' = ***nomen dubium*** ♀ from Willoughby (NSW)	
'*Dyarcyops ionthus* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from Burwood (NSW)	
'*Idioctis papuensis* Rainbow, 1920' = ***nomen dubium*** ♀ from 'Papua' (but probably NSW)	
'*Arbanitis chisholmii* Hickman, 1933' = ***nomen dubium*** ♀ from Comboyne (NSW)	
Blakistonia Hogg, 1902 (*one species*)[B]	
Bl. aurea Hogg, 1902*	Type locality: Adelaide, Blakiston (SA, FLB)
'*Cantuarides exsiccatus* Strand, 1907' = ***nomen dubium*** (syntypes lost) from 'Central Australia'	
Cantuaria Hogg, 1902 (*43 species*)	
Can. abdita Forster, 1968	Type locality: Hidden Island (NZ, Southland)
Can. allani Forster, 1968	Type locality: Halfmoon Bay (NZ, Stewart Is.)
Can. aperta Forster, 1968	Type locality: Waipiata (NZ, Otago)
Can. apica Forster, 1968	Type locality: Maungatua Summit (NZ, Otago)
Can. assimilis Forster, 1968	Type locality: Palmerston (NZ, Otago)
Can. borealis Forster, 1968	Type locality: Kaituna Valley (NZ, Canterbury)
Can. catlinsensis Forster, 1968	Type locality: Papatowai (NZ, Otago)
Can. cognata Forster, 1968	Type locality: Waimate (NZ, Canterbury)
Can. collensis (Todd, 1945)	Type locality: Bench Island (NZ, Southland)
Can. delli Forster, 1968	Type locality: Sealers Bay (NZ, Codfish Island)
Can. dendyi (Hogg, 1901)*	Type locality: Christchurch (NZ, Canterbury)
Can. depressa Forster, 1968	Type locality: E. of Clydevale (NZ, Otago)
Can. dunedinensis Forster, 1968	Type locality: Dunedin (NZ, Otago)
Can. gilliesi (O. P.-Cambridge, 1878)	Type locality: Oamaru (NZ, Otago)
Can. grandis Forster, 1968	Type locality: Duntroon (NZ, Otago)
Can. huttoni (O. P.-Cambridge, 1879)	Type locality: Dunedin (NZ, Otago)
Can. insulana Forster, 1968	Type locality: Mount Woore (NZ, D'Urville Is.)
Can. isolata Forster, 1968	Type locality: Whero Island (NZ, Southland)
Can. johnsi Forster, 1968	Type locality: Anatoki Beach (NZ, Nelson)
Can. kakahuensis Forster, 1968	Type locality: Kakahu (NZ, Canterbury)
Can. kakanuiensis Forster, 1968	Type locality: Kakanui (NZ, Otago)
Can. lomasi Forster, 1968	Type locality: Makarora (NZ, Otago)
Can. magna Forster, 1968	Type locality: Greymouth (NZ, West Coast)
Can. marplesi (Todd, 1945)	Type locality: Duntroon (NZ, Otago)

(*continued next page*)

Table 1. (*continued*)

Can. maxima Forster, 1968	Type locality: Hakataramea (NZ, Otago)
Can. mestoni (Hickman, 1928), comb. nov.	Type locality: Woodsdale (Tas., TSE)
Can. medialis Forster, 1968	Type locality: Mount Taraka (NZ, Marlborough)
Can. minor Forster, 1968	Type locality: Oban (NZ, Stewart Island)
Can. myersi Forster, 1968	Type locality: Keith Gorge (NZ, Wellington)
Can. napua Forster, 1968	Type locality: Oamaru (NZ, Otago)
Can. orepukiensis Forster, 1968	Type locality: S. of Orepuki (NZ, Southland)
Can. parrotti Forster, 1968	Type locality: Nelson (NZ, Nelson)
Can. pilama Forster, 1968	Type locality: Balclutha (NZ, Otago)
Can. prina Forster, 1968	Type locality: Westport (NZ, West Coast)
Can. reducta Forster, 1968	Type locality: Chalk Hill (NZ, Canterbury)
Can. secunda Forster, 1968	Type locality: Rockville (NZ, Tasman)
Can. sinclairi Forster, 1968	Type locality: Moana (NZ, West Coast)
Can. stephenensis Forster, 1968	Type locality: Stephens Is. (NZ, Marlborough)
Can. stewarti (Todd, 1945)	Type locality: Oban (NZ, Stewart Island)
Can. sylvatica Forster, 1968	Type locality: Thompson Sound (NZ, Southland)
Can. toddae Forster, 1968	Type locality: Cromwell (NZ, Otago)
Can. vellosa Forster, 1968	Type locality: Kakanui (NZ, Otago)
Can. wanganuiensis (Todd, 1945)	Type locality: Makirikiri (NZ, Wellington)
Tribe AGANIPPINI	
(*20 species in five genera*)	
Bungulla Rix, Main, Raven & Harvey, **gen. nov.** (*two species*)	
Bun. bertmaini Rix, Main, Raven & Harvey, **sp. nov.***	Type locality: Deception Hill (WA, MUR)
Bun. riparia (Main, 1957), comb. nov.	Type locality: W. of Mt Misery (WA, GES)
Eucanippe Rix, Main, Raven & Harvey, **gen. nov.** (*one species*)	
Eucan. bifida Rix, Main, Raven & Harvey, **sp. nov.***	Type locality: E. of Ravensthorpe (WA, ESP)
Eucyrtops Pocock, 1897 (*two species*)	
Eucy. eremaeus Main, 1957	Type locality: Cardinia Creek (WA, MUR)
Eucy. latior (O. P.-Cambridge, 1877)*	Type locality: Perth (WA, JAF)
Gaius Rainbow, 1914 (*one species*)	
G. villosus Rainbow, 1914*	Type locality: Minnivale (WA, AVW)
Idiosoma Ausserer, 1871 (*14 species*)	
I. berlandi (Rainbow, 1914), comb. nov.	Type locality: Narrabri (NSW, BBS)
I. castellum (Main, 1986), comb. nov.	Type locality: Minnivale (WA, AVW)
I. cupulifex (Main, 1957), comb. nov.	Type locality: Chittering Lakes (WA, JAF)
I. galeosomoides Rix, Main, Raven & Harvey, **sp. nov.**	Type locality: Deception Hill (WA, COO)
I. manstridgei (Pocock, 1897), comb. nov.	Type locality: Lawlers (WA, MUR)
I. montanum (Faulder, 1985), comb. nov.	Type locality: Young (NSW, NSS)
I. nigrum Main, 1952	Type locality: Wongan Hills (WA, AVW)
I. occidentale (Hogg, 1903), comb. nov.	Type locality: Roebourne (WA, PIL)
I. planites (Faulder, 1985), comb. nov.	Type locality: Hillston (NSW, RIV)
I. rhaphiduca (Rainbow & Pulleine, 1918), comb. nov.	Type locality: Kings Park (WA, SCP)
I. sigillatum (O. P.-Cambridge, 1870)*	Type locality: Swan River (WA, SCP)
= *I. hirsutum* Main, 1952 **new synonymy**	
I. smeatoni (Hogg, 1902), comb. nov.	Type locality: Blakiston (SA, FLB)
I. subtriste (O. P-Cambridge, 1877), comb. nov.	Type locality: Adelaide (SA, FLB)
= *Idiommata schomburgki* Karsch, 1878 (by Main, 1957)	
= *Aganippe pulleinei* Hogg, 1902 (by Main, 1957)	
I. winsori (Faulder, 1985), comb. nov.	Type locality: Grampians NP (Vic., VIM)
'*Aganippe whitei* Rainbow, 1915' = ***nomen dubium*** ♀ from Port Augusta (SA)	
'*Aganippe modesta* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from Mount Lofty (SA)	
'*Aganippe pelochroa* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from Mount Lofty (SA)	
'*Aganippe robusta* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from Adelaide (SA)	
'*Blakistonia bancrofti* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from Eidsvold (Qld)[1]	

(*continued next page*)

Table 1. (*continued*)

'*Gaius hirsutus* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from N. of Everard Ranges (SA)	
'*Aganippe simpsoni* Hickman, 1944' = ***nomen dubium*** ♀ from E. of Hale River (NT)	
Tribe CATAXIINI (*11 species in one genus*)	
Cataxia Rainbow, 1914 (*11 species*)	
Cat. babindaensis Main, 1969	Type locality: Babinda (Qld, WET)
Cat. bolganupensis (Main, 1985*b*)	Type locality: Porongurup NP (WA, JAF)
Cat. cunicularis (Main, 1983)	Type locality: North Cedar Creek (Qld, WET)
Cat. dietrichae Main, 1985*b*	Type locality: W. of Bowen (Qld, BBN)
Cat. eungellaensis Main, 1969	Type locality: Eungella NP (Qld, CMC)
Cat. maculata Rainbow, 1914*	Type locality: Eidsvold (Qld, BBS)[A]
= *Arbanitis inornatus* Rainbow & Pulleine, 1918 (by Main, 1969)	
= *Cat. tetrica* Rainbow & Pulleine, 1918 (by Main, 1969)	
Cat. pallida (Rainbow & Pulleine, 1918)	Type locality: Eidsvold (Qld, BBS)[A]
Cat. pulleinei (Rainbow, 1914)	Type locality: Lismore (NSW, SEQ)
Cat. spinipectoris Main, 1969	Type locality: Toowoomba (Qld, BBS)
Cat. stirlingi (Main, 1985*b*)	Type locality: Bluff Knoll (WA, ESP)
Cat. victoriae (Main, 1985*a*)	Type locality: Grampians NP (Vic., VIM)
Tribe EUOPLINI (*12 species in one genus*)	
Euoplos Rainbow, 1914 (*12 species*)	
Euo. bairnsdale (Main, 1995)	Type locality: Bairnsdale (Vic., SCP)
Euo. ballidu (Main, 2000)	Type locality: Ballidu (WA, AVW)
Euo. festivus (Rainbow & Pulleine, 1918)	Type locality: Nannup (WA, JAF)
Euo. hoggi (Simon, 1908)	Type locality: Eradu (WA, GES)
Euo. inornatus (Rainbow & Pulleine, 1918)	Type locality: Armadale (WA, JAF)
= *Albaniana flavomaculata* Rainbow & Pulleine, 1918 (by Main, 1985*b*)	
= *Armadalia setosa* Rainbow & Pulleine, 1918 (by Main, 1985*b*)	
Euo. mcmillani (Main, 2000)	Type locality: Eneabba (WA, GES)
Euo. ornatus (Rainbow & Pulleine, 1918)	Type locality: Eidsvold (Qld, BBS)[A]
= *Armadalia ornata* Rainbow & Pulleine, 1918 (by Main, 1985*b*)	
= *Bancroftiana speciosa* Rainbow & Pulleine, 1918 (by Main, 1985*b*)	
Euo. similaris (Rainbow & Pulleine, 1918)	Type locality: Kedron Brook (Qld, SEQ)
Euo. spinnipes Rainbow, 1914*	Type locality: Eidsvold (Qld, BBS)[A]
Euo. tasmanicus (Hickman, 1928)	Type locality: Prince of Wales Bay (Tas., TSE)
Euo. variabilis (Rainbow & Pulleine, 1918)	Type locality: Mount Tamborine (Qld, SEQ)
= *Tambouriniana variabilis flavomaculata* Rainbow & Pulleine, 1918 (by Bonnet, 1959)	
= *Albaniana villosa* Rainbow & Pulleine, 1918 (by Main, 1985*b*)	
Euo. victoriensis (Main, 1995)	Type locality: Buffalo River Dam (Vic., VIM)
'*Macrothele aculeata* Urquhart, 1893' = ***nomen dubium*** ♂ from 'Tasmania' (Tas.)	
'*Arbanitis maculipes* Hogg, 1903' = ***nomen dubium*** ♀ from 'Tasmania' (Tas.)	
'*Armadalia zorodes* Rainbow & Pulleine, 1918' = ***nomen dubium*** ♀ from Mount Lofty (SA)	

[A]Denotes both 'Eidsvold' and 'Upper Burnett River' (see Rainbow and Pulleine 1918).
[B]NB. *Aganippe rainbowi* Pulleine, 1919 = *Moggridgea rainbowi* (Pulleine) (family Migidae) (see Harrison *et al.* 2016).

superscripts to repository registration numbers. The type genera of tribes and generic type species are treated first under each inclusive taxon; other genera and species are arranged alphabetically thereafter. Detailed material examined data are provided for newly described species only.

Abbreviations and repositories

The following abbreviations are used throughout the text: *5.8S*/*18S*/*28S* rRNA, *5.8S*, *18S*, *28S* rRNA; ALE, anterior lateral eye/s; AME, anterior median eye/s; *CO1*, cytochrome *c* oxidase subunit 1; *CYB*, cytochrome *b*; *H3*, histone H3; *HAT1*, histone acetyltransferase type B catalytic subunit; IBRA, Interim Biogeographic Regionalisation of Australia Version 7 (see https://www.environment.gov.au/land/nrs/science/ibra, accessed 6 April 2017); *ITS1* and *ITS2*, internal transcribed spacers 1 and 2; *MRPL45*, 39S ribosomal protein L45, mitochondrial; PLE, posterior lateral eye/s; PME, posterior median eye/s; PMS, posterior median spinnerets; *RPF2*,

ribosome production factor 2 homologue; RTA, retrolateral tibial apophysis (of male pedipalp); *XPNPEP3*, probable Xaa-Pro aminopeptidase 3.

Specimens are deposited in the following repositories: AMS, Australian Museum (Sydney); BMNH, Natural History Museum (London); CMNZ, Canterbury Museum (Christchurch); NMV, Museum Victoria (Melbourne); OMD, Otago Museum (Dunedin); OUM, Oxford University Museum of Natural History (Oxford); QMB, Queensland Museum (Brisbane); QVM, Queen Victoria Museum and Art Gallery (Launceston); SAM, South Australian Museum (Adelaide); WAM, Western Australian Museum (Perth); ZMB, Museum für Naturkunde (Berlin); ZMH, Zoologisches Universität und Zoologisches Museum (Hamburg).

Systematics

Family **IDIOPIDAE** Simon, 1889

Subfamily **ARBANITINAE** Simon, 1903

Arbaniteae Simon, 1903: 885, 903. Type genus *Arbanitis* L. Koch, 1874.

Diagnosis

Species of Arbanitinae can be distinguished from other Idiopidae in the subfamilies Idiopinae and Genysinae by the combined presence of a straight (Figs 4, 35) or procurved (Figs 69, 83, 289) fovea and an eye group that is as wide as (Figs 39, 212) or wider than long (Figs 71, 87) (Raven 1985).

Distribution

Arbanitinae are known only from Australia (including Tasmania) and New Zealand. They have not been recorded from Australasian oceanic islands (e.g. Lord Howe Island, Norfolk Island), New Caledonia or other Austral land masses.

Included tribes

Aganippini Simon, 1903, Arbanitini Simon, 1903, Cataxiini Rainbow, 1914 and Euoplini Rainbow, 1914.

Included genera

Arbanitis L. Koch, 1874, *Blakistonia* Hogg, 1902, *Bungulla* Rix, Main, Raven & Harvey, gen. nov., *Cantuaria* Hogg, 1902, *Cataxia* Rainbow, 1914, *Eucanippe* Rix, Main, Raven & Harvey, gen. nov., *Eucyrtops* Pocock, 1897, *Euoplos* Rainbow, 1914, *Gaius* Rainbow, 1914 and *Idiosoma* Ausserer, 1871.

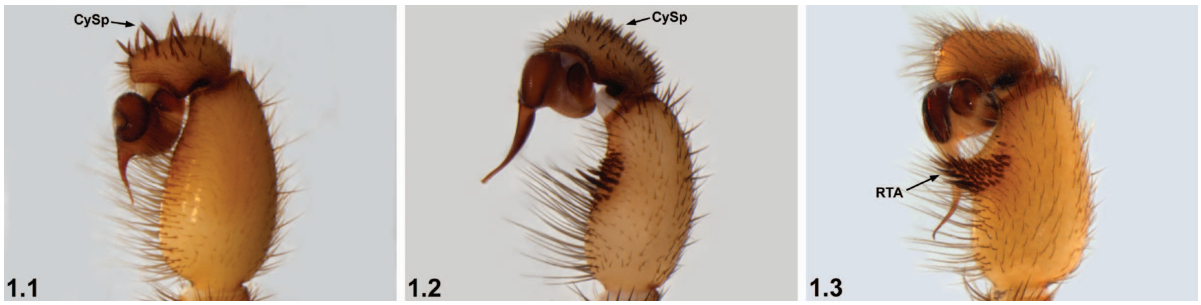
Phylogeny, biogeography and evolution

The arbanitine Idiopidae are endemic to Australasia, where they are the sole representatives of the family. The biodiversity hotspot of south-western Western Australia (Rix *et al*. 2015) is home to the largest concentration of genera, with up to eight of the 10 genus-group lineages represented in the Wheatbelt and/or South Coast region alone (e.g. in the Stirling Range National Park). Four major monophyletic lineages were recovered in the multi-locus molecular analyses of Rix *et al*. (2017*a*; Fig. 1), and these are concordant with the tribal names formalised in this study. In Australia, three genera –*Arbanitis*, *Cataxia* and *Euoplos* – are characteristic of the eastern Australian mesic zone, extending along and east of the Great Dividing Range from the Wet Tropics of north-eastern Queensland south to Tasmania (Figs 34, 288, 321). The ancestor of *Cantuaria* likely dispersed from Australia to New Zealand during the Cenozoic (Rix *et al*. 2017*a*). The remaining six genera, including the entire tribe Aganippini, are all arid zone specialists, having radiated extensively during the Miocene and Pliocene. Most idiopid genera in Australasia include numerous undescribed species, especially *Idiosoma* – the most derived, widespread and speciose lineage within the subfamily.

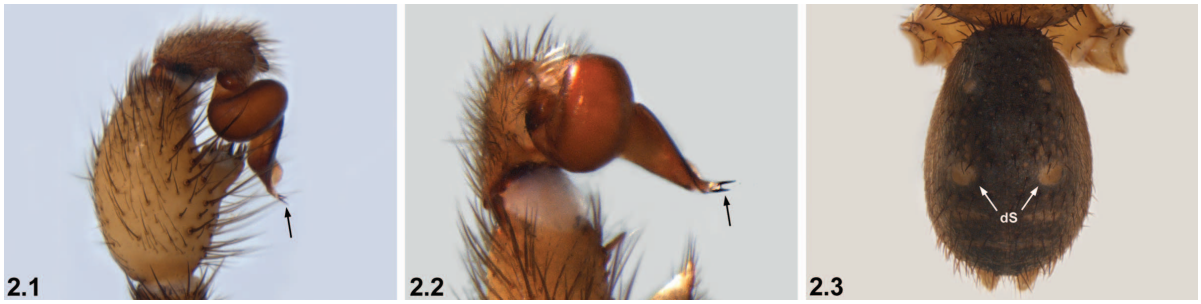
Key to the genera of Arbanitinae from Australia and New Zealand (males required)

NB. A key to females is not provided, as so few diagnostic characters are available at the genus-group level. See generic diagnoses for diagnostic nucleotide substitutions and other morphological characters relevant to females.

1. RTA absent (*1.1*, *1.2*); cymbium usually with field of strong dorsal spinules (CySp) (*1.1*, *1.2*).....*Bungulla* Rix, Main, Raven & Harvey, gen. nov.
   RTA present (*1.3*); cymbium with or without (*1.3*) spinules.....2



2. Embolus distally bifurcate (*2.1*, *2.2*); abdomen with pair of large, sclerotised dorsal sigilla (dS) (*2.3*)..... .....*Eucanippe* Rix, Main, Raven & Harvey, gen. nov.
Embolus not bifurcate distally; abdomen with or without sclerotised dorsal sigilla..... 3



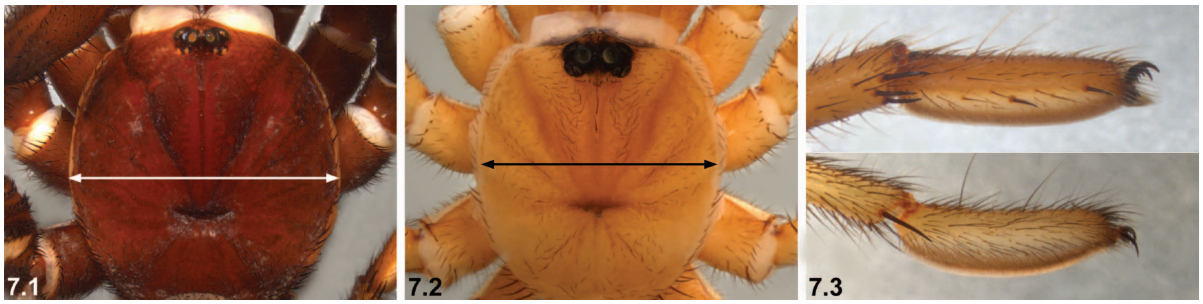
3. Male pedipalp with median retrolateral digital process (DP) (rarely reduced to a nubbin) (*3.1*); RTA short, burr-like (*3.1*); abdomen usually with pair of sclerotised dorsal sigilla (dS) (*3.2*) ..... *Idiosoma*
Male pedipalp without median retrolateral digital process (*3.3*); RTA conical, pointed or subtriangular (*3.3*); abdomen without sclerotised dorsal sigilla.. 4

4. Eye group trapezoidal, posterior eye row broader than anterior eye row and anterior eye row strongly procurved (*4.1*)..... 5
Eye group rectangular (*4.2*), square (*4.3*) or subquadrate, anterior eye row straight or nearly so (*4.2*) to strongly procurved (*4.3*)..... 7

5. Male pedipalp with strongly developed distal retrolateral tibial apophysis (dRTA) (*5.1*, *5.2*); RTA usually massive (*5.1*); body, legs and ventral pedipalpal tibia (*5.1*, *5.2*) densely setose ..... *Gaius*
Male pedipalp usually without strongly developed dRTA (*5.3*); RTA smaller (*5.3*); body and appendages setose but not densely so 6

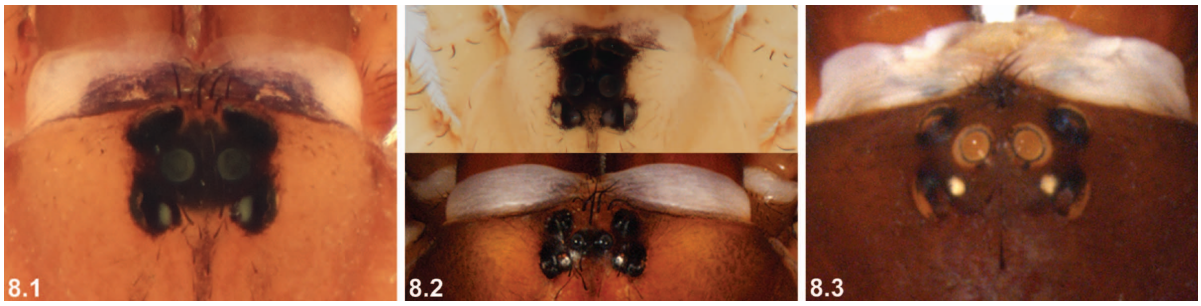
6. RTA with attenuate base (*6.1*, *6.2*) ..... *Eucyrtops* (in part, most species)
RTA without distinctly attenuate base (*6.3*) ..... *Blakistonia* (in part, rarely)[1]

7. Carapace with broad profile in dorsal view at level of coxa II (*7.1*, *7.2*); eye group small and rectangular (*7.1*, *7.2*); fovea usually strongly procurved (*7.1*); male anterior leg tarsi usually ventrally incrassate, with pallid scopulate pad (*7.3*) ..... *Euoplos*
Carapace narrower in dorsal view; male anterior leg tarsi rarely incrassate 8

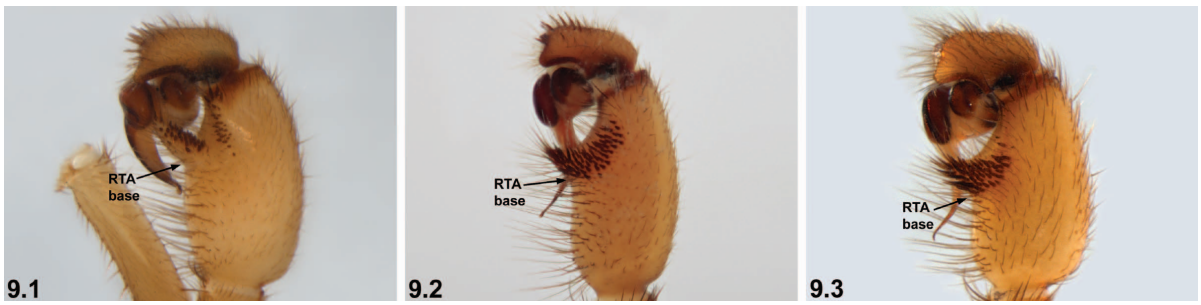


[1]A few species of *Blakistonia* have a trapezoidal eye group (Figs 42, 54).

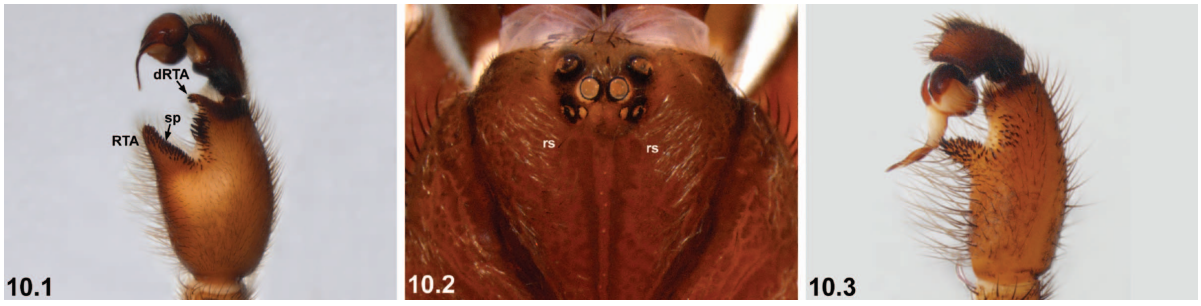
8. Eye group square (*8.1*) or subquadrate (*8.2*) and anterior eye row strongly procurved; anterior margin of carapace adjacent to eye group straight or rounded-convex in dorsal view (*8.1*, *8.2*) 9
Eye group rectangular (*8.3*), anterior eye row straight or procurved; anterior margin of carapace adjacent to eye group straight, rounded-convex or pointed (*8.3*) medially 10



9. RTA with attenuate base (*9.1*) ..... *Eucyrtops* (in part, rarely)[2]
RTA without distinctly attenuate base (*9.2*, *9.3*) ..... *Blakistonia* (in part, most species)



10. Male pedipalp usually with small to large distal retrolateral tibial apophysis (dRTA) (*10.1*); RTA usually strongly pointed and directed anteriorly, with field of spinules (sp) restricted to antero-dorsal surface (*10.1*); carapace usually strongly hirsute (*10.2*), rarely glabrous, with covering of fine downy reflective setae (rs); scopulae present on anterior leg tarsi and usually also metatarsi ..... *Arbanitis*
Male pedipalp with or without (*10.3*) dRTA; carapace glabrous or hirsute; RTA otherwise, with field of spinules usually also extending around retrolateral surface (*10.3*); scopulae present or absent on anterior leg metatarsi 11



[2]A few species of *Eucyrtops* (e.g. *E. eremaeus* Main, 1957) have a square eye group (Fig. 212).

11. Carapace glabrous, never strongly hirsute (*11.1*); scopulae (sc) present on anterior leg tarsi, but absent on metatarsi (*11.2*); chelicerae with or sometimes without rastellum; PMS present or sometimes absent ..... *Cataxia*
Carapace glabrous or hirsute; scopulae (sc) present on anterior leg tarsi and usually also metatarsi (*11.3*); rastellum and PMS present ..... *Cantuaria*

Tribe **ARBANITINI** Simon, 1903

Arbaniteae Simon, 1903: 885, 903. Type genus *Arbanitis* L. Koch, 1874.

Diagnosis

Species of Arbanitini can be distinguished from Euoplini by the narrower carapace in dorsal view (Figs 2, 35, 69) and absence (usually) of ventrally incrassate anterior leg tarsi in males; from Cataxiini by the presence of scopulae on the anterior leg tarsi and usually also metatarsi of males and females (Fig. 19); and from most Aganippini by the presence of a rectangular or square eye group that is not significantly broader behind than in front (Figs 6–9, 39–41, 71). Some species of *Eucyrtops* (Aganippini) have a similar subquadrate eye group to species of *Blakistonia* (e.g. *E. eremaeus* Main, 1957; Fig. 212), just as some *Blakistonia* can have a marginally trapezoidal eye group (Figs 42, 54); in both cases, species of Aganippini can be distinguished from similar Arbanitini by the presence of a more strongly attenuate base to the RTA (Fig. 216).

Males, females and juveniles of this tribe can also be identified (on the basis of 28 molecular exemplar specimens; see Figs 34, 68, 82) by the following four nuclear nucleotide substitutions: *MRPL45* A(442) and G(672; rarely homoplastic in *Idiosoma*); *RPF2* G(462; rarely homoplastic in *Bungulla*); and *28S* G(1024).

Distribution

Widely distributed in eastern and south-eastern Australia, from tropical eastern Queensland south to Tasmania, south-western Western Australia, the central arid zone and New Zealand (Figs 34, 68, 82).

Included genera

Arbanitis L. Koch, 1874, *Blakistonia* Hogg, 1902 and *Cantuaria* Hogg, 1902.

Remarks

The Arbanitini is a diverse clade of three genera, characteristic of the Australasian temperate and eastern mesic zone. Indeed, *Arbanitis* is by far the most abundant idiopid lineage along the Great Dividing Range, occurring widely in rainforest and sclerophyllous habitats, including in urban areas. Most species of *Arbanitis* and many species of *Cantuaria* build open-holed burrows (Figs 25, 26, 28–31, 80, 81), and in eastern Australia these are otherwise likely to be confused only with sympatric Nemesiidae. Open holes are unknown in *Blakistonia* (Figs 58–67). The Arbanitini appears to be sister to the tribe Cataxiini (Fig. 1), but with weak support. While the three genera together form a well-supported monophyletic clade with molecular data (Fig. 1), obvious morphological synapomorphies are lacking.

Genus ***Arbanitis*** L. Koch, 1874

(Figs 1–34)

Pholeuon L. Koch, 1873: 471 (junior homonym of the beetle *Pholeuon* Hampe, 1856). Type species *Pholeuon longipes* L. Koch, 1873, by monotypy.

Arbanitis L. Koch, 1874: 491 (replacement name for *Pholeuon* L. Koch, 1873, preoccupied in Coleoptera).

Misgolas Karsch, 1878: 821. Type species by original designation *M. rapax* Karsch, 1878. New synonymy.

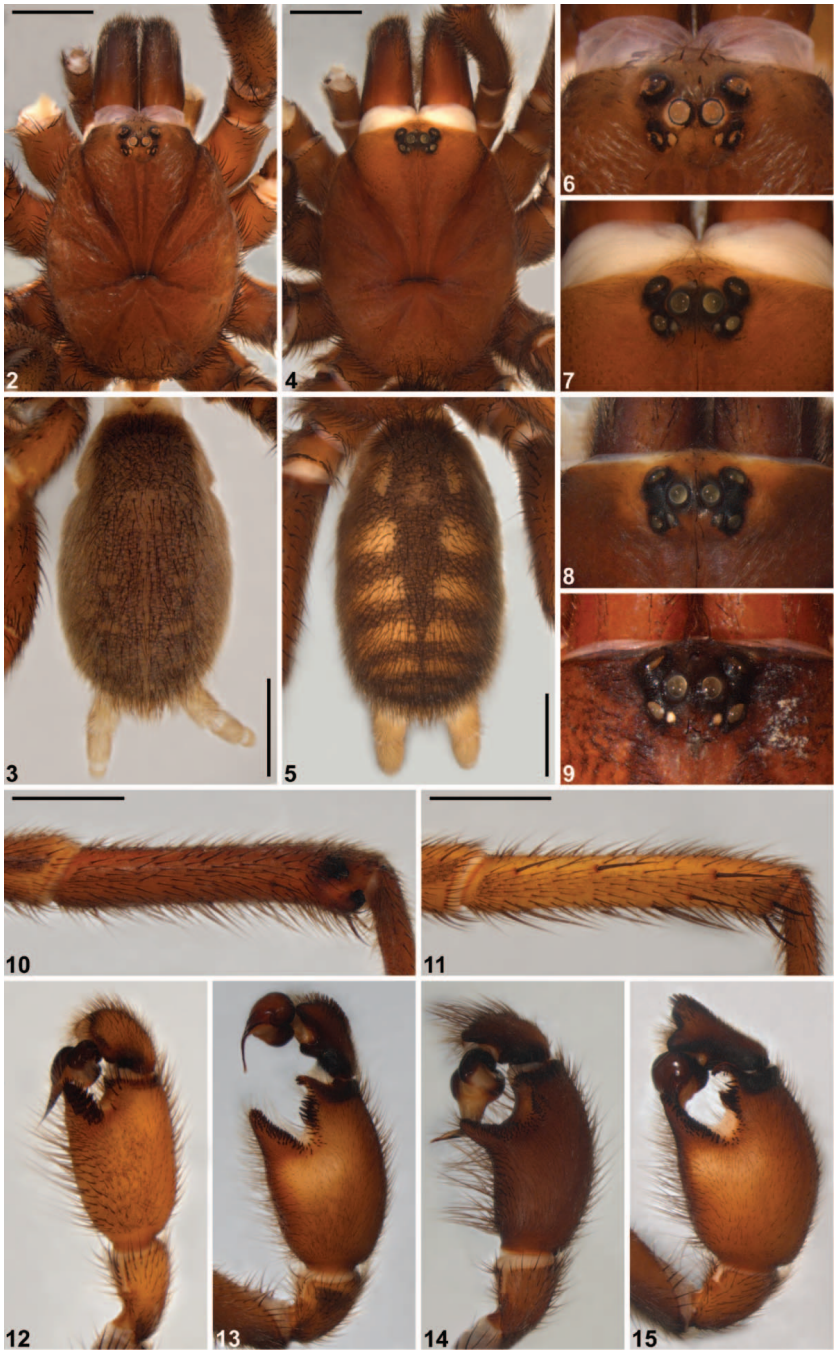
Hermeas Karsch, 1878: 823. Type species by original designation *H. crispus* Karsch, 1878 (synonymised with *Misgolas* Karsch, 1878 by Main, 1985*b*: 33). New synonymy.

Dyarcyops Hogg, 1902: 130. Type species by original designation *D. andrewsi* Hogg, 1902 (synonymised with *Misgolas* Karsch, 1878 by Main, 1985*b*: 33). New synonymy.

Megalosara Rainbow, 1914: 205. Type species by original designation *Meg. villosa* Rainbow, 1914 (synonymised with *Misgolas* Karsch, 1878 by Main, 1985*b*: 33). New synonymy.

Diagnosis

Most species of *Arbanitis* can be distinguished from all other Arbanitinae by the combined presence of a small to large distal retrolateral tibial apophysis (dRTA) on the male pedipalp (Figs 13–15), the presence of a rectangular eye group (with a straight or procurved anterior eye row) (Figs 6–9), the presence of scopulae on the anterior leg tarsi and metatarsi of males and females (Fig. 19), and a strongly hirsute carapace (Figs 16, 17, 19–24). When the dRTA is lacking (as in



Figs 2–15. Morphology of *Arbanitis* L. Koch. *2–5*, Male carapace and abdomen, dorsal view: *2*, *3*, *A. longipes* (L. Koch, 1873) (QMB S54310); *4*, *5*, *A. robertsi* (Main & Mascord, 1974) (QMB S15513). *6–9*, Eyes, dorsal view: *6*, male *A. longipes* (QMB S54310); *7*, male *A. robertsi* (QMB S15513); *8*, male *A. rapax* (Karsch, 1878) (QMB S20548); *9*, male *A.* sp. nr. *andrewsi* from Mosquito Hill, South Australia (SAM N20613). *10*, *11*, Male leg I tibia, prolateral view: *10*, *A. robertsi* (QMB S15513); *11*, *A. longipes* (QMB S54310). *12–15*, Male pedipalp, retrolateral view: *12*, *A. longipes* (QMB S54310); *13*, *A. robertsi* (QMB S15513); *14*, *A.* sp. from Boat Mountain Regional Park, Queensland (QMB S46439); *15*, *A. rapax* (QMB S20548). Scale bars = 2.0 mm.

Figs 16–24. Images of live *Arbanitis* L. Koch. *16*, Female *A. longipes* (L. Koch, 1873) from Camira, Queensland; *17*, female *A. rapax* (Karsch, 1878) from Gerringong, New South Wales; *18*, female *A.* sp. from Grampians National Park, Victoria; *19*, female *A. robertsi* (Main & Mascord, 1974) from Kiama, New South Wales; *20*, female *A.* sp. from Minnamurra Falls, Budderoo National Park, New South Wales; *21*, female *A. gracilis* (Rainbow & Pulleine, 1918) from Clifton Gardens, Sydney Harbour National Park, New South Wales; *22*, female *A. villosus* (Rainbow, 1914) from Lane Cove National Park, New South Wales; *23*, female *A.* sp. from Clifton Gardens, Sydney Harbour National Park, New South Wales; *24*, female *A.* sp. from Point Lookout, New England National Park, New South Wales. Note the golden pilosity of the carapace of many species. All images by M. Rix.

A. longipes and several other taxa; Fig. 12), species can usually be distinguished by the strongly hirsute carapace (Fig. 16), combined with the shape of the RTA, which is strongly pointed and directed anteriorly in most species (Figs 12, 13, 15), with the field of spinules usually restricted to the antero-dorsal surface (Figs 12–15).

Males, females and juveniles of this genus can also be identified (on the basis of 15 molecular exemplar specimens; see Fig. 34) by the unique 'TT' motif at positions 839–840 of nuclear *28S* rRNA, and by the following nuclear nucleotide substitution: *MRPL45* C(48).

Description

See Main (1977: 70), Main (1985*b*: 33) and Raven and Wishart (2006).

Distribution

Widely distributed in eastern and south-eastern Australia, from central eastern Queensland south to Tasmania and west into south-eastern South Australia (Fig. 34). Absent from Western Australia and the central arid zone.

Composition

Arbanitis includes 61 described species (Table 1). *Arbanitis mestoni* Hickman, 1928 is here transferred from *Misgolas* to *Cantuaria* on the basis of molecules and male pedipalp morphology (see 'Remarks' under *Cantuaria* and *Euoplos*, below). A further four species, all of which are represented by female holotypes that cannot be confidently identified or associated with a named species, are designated as *nomina dubia*: *A. fuscipes* Rainbow, 1914 from Willoughby

Figs 25–33. Burrows of *Arbanitis* L. Koch. *25*, *Arbanitis longipes* (L. Koch, 1873) from Camira, Queensland; *26*, *A. rapax* (Karsch, 1878) from Gerringong, New South Wales; *27*, *A. gracilis* (Rainbow & Pulleine, 1918) from Echo Point, Kanangra-Boyd National Park, New South Wales; *28*, *A. robertsi* (Main & Mascord, 1974) from Kiama, New South Wales; *29*, *A.* sp. from Clifton Gardens, Sydney Harbour National Park, New South Wales; *30*, *A.* sp. from Point Lookout, New England National Park, New South Wales; *31*, *A. villosus* (Rainbow, 1914) from Lane Cove National Park, New South Wales; *32*, *A.* sp. from Minnamurra Falls, Budderoo National Park, New South Wales; *33*, *A.* sp. from Tamborine National Park, Queensland. Note the tube or palisade burrows (*28*, *29*) and the wafer-like (*27*) or flappy (*32*) lids built by some species. A very few taxa camouflage their burrow entrances in friable soil with an inverted silken hymen incorporating soil granules (*33*). All images by M. Rix.

(New South Wales; see Wishart 2006: 2); *Dyarcyops ionthus* Rainbow & Pulleine, 1918 from Burwood (New South Wales; see Wishart 2006: 2); *Idioctis papuensis* Rainbow, 1920 from 'Papua' (but probably NSW) (here removed from synonymy of *A. gracilis* Rainbow & Pulleine, 1918 *contra* Wishart, 2006: 7 by extension of Main, 1985*b*: 54); and *A. chisholmii* Hickman, 1933 from Comboyne (New South Wales; see Wishart 2006: 2). The late Graham Wishart and colleagues have extensively revised the genus in central eastern New South Wales (see Wishart 1992, 2006, 2011; Wishart and Rowell 1997, 2008; Raven and Wishart 2006).

Remarks

Arbanitis is the dominant idiopid genus in mesic eastern and south-eastern Australia, and burrows are often found in large numbers in rainforests, sclerophyll forests, parks and gardens on and east of the Great Dividing Range. They are especially abundant in New South Wales including in and around Sydney, where species such as the 'Sydney brown trapdoor spider', *A. villosus* (Rainbow, 1914) (Fig. 22), and the more cryptic *A. gracilis* Rainbow & Pulleine, 1918 (Fig. 21) are familiar occupants of leafy suburban gardens. Most species build non-descript open burrows without trapdoors (Figs 25, 26, 30, 31), although a few taxa (e.g. *A. gracilis*) have apparently re-evolved hinged burrow doors independently (Figs 27, 32). Some species build supported tubes (e.g. *A. robertsi* (Main & Mascord, 1974); Fig. 28) or ornate palisade burrows (Fig. 29), while others conceal their burrow entrances with a fragile hymen of silk camouflaged with soil debris (Fig. 33).

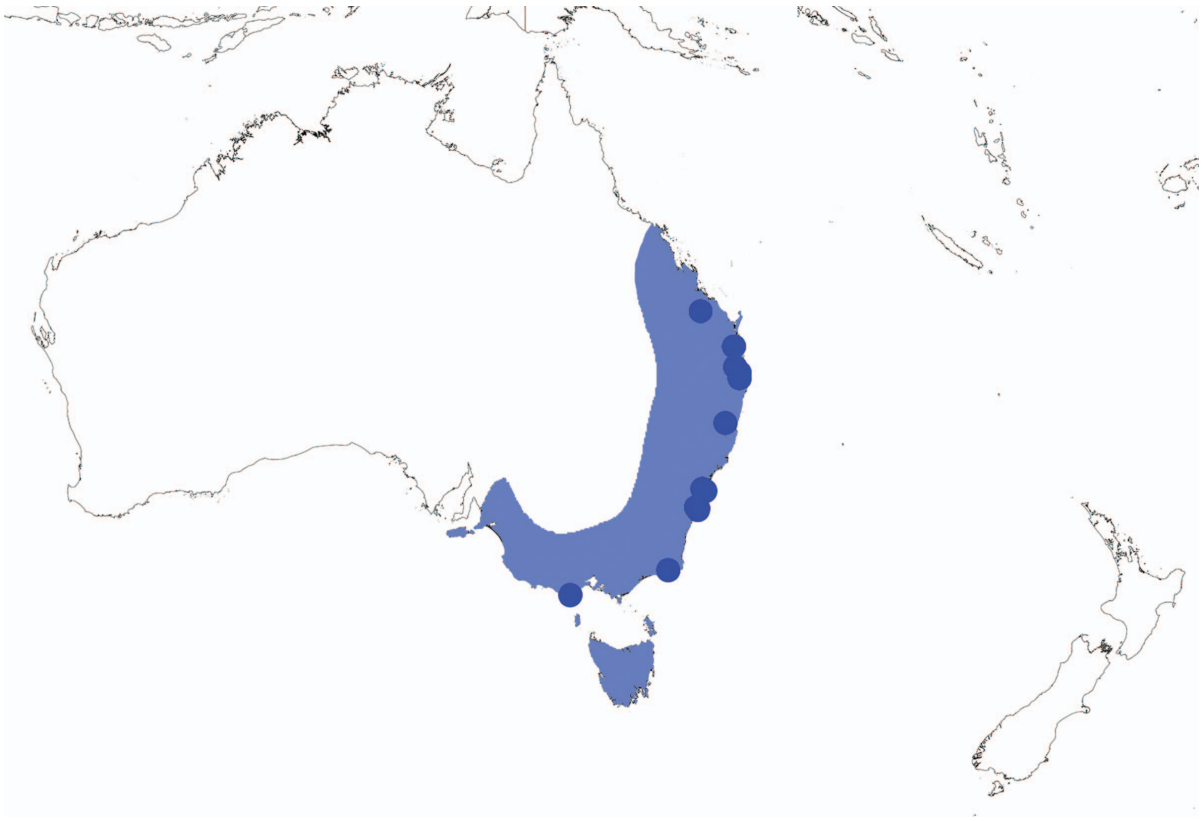


Fig. 34. Map showing the approximate extent of occurrence of the genus *Arbanitis* L. Koch in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al*. (2017*a*). Note the absence of this genus from the west and arid interior.

Arbanitis longipes (L. Koch, 1873)

(Figs 2, 3, 6, 11, 12, 16, 25)

Pholeuon longipes L. Koch, 1873: 472, pl. 36, fig. 3.
Arbanitis longipes (L. Koch): L. Koch, 1874: 491.
Arbanitis pulchellus Rainbow & Pulleine, 1918: 114, pl. 14, fig. 11, pl. 22, figs 61, 62 (presumed replacement name for *Arbanitis pulchra* Rainbow & Pulleine, 1918: 86 *nomen nudum*) (synonymised by Raven & Wishart, 2006: 534).
Aname pulchra Rainbow & Pulleine, 1918: 153, pl. 24, figs 107, 108 (synonymised with *Arbanitis pulchellus* Rainbow & Pulleine, 1918 by Main, 1972: 100).
Misgolas pulchellus (Rainbow & Pulleine): Main, 1985*c*: 24.

Material examined

Holotype (of *Phol. longipes*). Australia: Queensland: ♂, 'Bowen' (corrected to Camira, Brisbane by Raven and Wishart (2006)) (ZMH; examined [RJR]).

Holotype (of *A. pulchellus*). Australia: Queensland: ♀, Mount Tamborine (AMS KS6327; examined [RJR, BYM]).

Holotype (of *Ana. pulchra*). Australia: Queensland: ♂, Mount Tamborine (AMS KS8375; examined [RJR]).

Select material examined. **Australia:** Queensland: 1 ♀, Camira, reserve off Addison Road and Cobalt Street (WAM T133293^{DNA_Voucher_119}); 1 ♂, Camerons Scrub (QMB S54310).

Remarks

Arbanitis longipes, the type species of the genus, is a common spider around greater Brisbane (Raven and Wishart 2006), and is found in both sclerophyllous and rainforest habitats. It is a medium-sized species with a silvery-gold pilosity on the carapace (Fig. 16), and builds an open-holed burrow (Fig. 25).

Arbanitis gracilis Rainbow & Pulleine, 1918

(Figs 21, 27)

Arbanitis gracilis Rainbow & Pulleine, 1918: 110, pl. 22, figs 57, 58.
Arbanitis bradleyi Rainbow, 1920: 80, figs 4–6 (synonymised by Wishart, 2006: 7).
Arbanitis villosus Rainbow, 1920: 78, figs 1–3 (synonymised by Wishart, 2006: 7).
Dyarcyops gracilis (Rainbow & Pulleine): Main, 1977: 71.
Misgolas gracilis (Rainbow & Pulleine): Main, 1985*b*: 52.

Material examined

Holotype (of *A. gracilis*). Australia: New South Wales: ♀, The Domain, Sydney (AMS KS6262; examined [BYM]).

Syntypes (of *A. bradleyi*). **Australia:** New South Wales: 1 ♂, 1 juvenile, 'Papua' (but probably New South Wales, Australia) (AMS KS6472; examined [BYM]).

Syntypes (of *A. villosus*). **Australia:** New South Wales: 1 ♂, 'Papua' (but probably New South Wales, Australia) (AMS KS8620; not examined); 1 ♀, same data (AMS KS8621; not examined); 1 ♀, same data (AMS KS8622; examined [BYM]).

Select material examined. **Australia:** New South Wales: 1 ♀, Clifton Gardens, Sydney (WAM T132014[DNA_Voucher_103]).

Remarks

Arbanitis gracilis (Fig. 21) is very common in and around Sydney, and sometimes occurs in parks and gardens. It is one of the few species of *Arbanitis* to build a genuine hinged door to its burrow (Fig. 27), and this door-building behaviour seems to have evolved independently from ancestors that constructed open-holed burrows (Rix *et al.* 2017*a*). Its burrows can often be found in friable, sometimes sandy substrates, and occur in large numbers in some areas.

Arbanitis rapax (Karsch, 1878), comb. nov.

(Figs 8, 15, 17, 26)

Misgolas rapax Karsch, 1878: 821.

Misgolas hubbardi Wishart, 1992: 264, figs 1–6, 28, 29 (synonymised by Wishart & Rowell, 2008: 85).

Material examined

Holotype (of *M. rapax*). Australia: New South Wales: ♀, Gerringong (as per Wishart 2006) (ZMB; examined [BYM]).

Holotype (of *M. hubbardi*). Australia: New South Wales: ♂, 'Scalloway', near Gerringong (AMS KS 22301; not examined).

Select material examined. **Australia:** New South Wales: 1 ♀, Gerringong (WAM T132003[DNA_Voucher_MI]); 1 ♂, 'Scalloway', near Gerringong (QMB S20548).

Remarks

Arbanitis rapax, the type species of *Misgolas*, is a relatively large species from the Gerringong region of coastal New South Wales (see Wishart 2011). It builds an open-holed burrow (Fig. 26), and is rich brown in colour with a golden pilosity on the carapace (Fig. 17).

Arbanitis robertcollinsi Raven & Wishart, 2006

Arbanitis robertcollinsi Raven & Wishart, 2006: 542, figs 5E, 6, 7, 12, 13.

Material examined

Holotype. Australia: Queensland: ♂, Springbrook Repeater Station (QMB S28822; examined [RJR]).

Select material examined. **Australia:** Queensland: 1 ♀, Lamington National Park, Binna Burra, start of Coomera Circuit Track (WAM T133312[DNA_Voucher_72]).

Remarks

Arbanitis robertcollinsi is found on the Lamington Plateau, south of Brisbane (Raven and Wishart 2006), and is closely related to *A. longipes*. It builds a non-descript, open-holed burrow in montane rainforest habitats.

Arbanitis robertsi (Main & Mascord, 1974), comb. nov.

(Figs 4, 5, 7, 10, 13, 19, 28)

Dyarcyops robertsi Main & Mascord, 1974: 17, pl. 2, figs 1–12.

Dyarcyops roberti Main & Mascord: Brignoli, 1983: 114 (unjustified emendation).

Misgolas robertsi (Main & Mascord): Main, 1985*b*: 53.

Material examined

Holotype. Australia: New South Wales: ♀, Minnamurra Falls, near Kiama (AMS KS12; examined [BYM]).

Select material examined. **Australia:** New South Wales: 1 ♀, Kiama (WAM T132002[DNA_Voucher_97]); 1 ♂, 'Scalloway', near Gerringong (QMB S15513).

Remarks

Arbanitis robertsi is a distinctive species from the Illawarra region of New South Wales (Wishart 2011). Known as the 'tube spider', it builds long, parchment-like tube burrows that extend above the ground by attaching to logs, rocks or large tree roots (Fig. 28). The spiders are a rich brown colour, with pronounced dorsal abdominal chevrons and a golden pilosity on the carapace (Fig. 19).

Arbanitis villosus (Rainbow, 1914), comb. nov.

(Figs 22, 31)

Megalosara villosa Rainbow, 1914: 206, figs 16–22.

Misgolas villosus (Rainbow): Wishart, 2006: 3, fig. 1A–F (removed from synonymy of *Misgolas rapax* Karsch, 1878 *contra* Main, 1985*c*: 25).

Material examined

Holotype. Australia: New South Wales: ♂, Enfield, Sydney (AMS KS7178; examined [BYM]).

Select material examined. **Australia:** New South Wales: 1 ♀, Lane Cove National Park, Sydney (WAM T132012[DNA_Voucher_40]).

Remarks

Arbanitis villosus, the 'Sydney brown trapdoor spider' (Fig. 22), is common in the Sydney Basin. It is similar in appearance and behaviour to *A. rapax*, and is closely related. It builds an open-holed burrow in forested habitats, parks and well-watered gardens (Fig. 31).

Genus ***Blakistonia*** Hogg, 1902

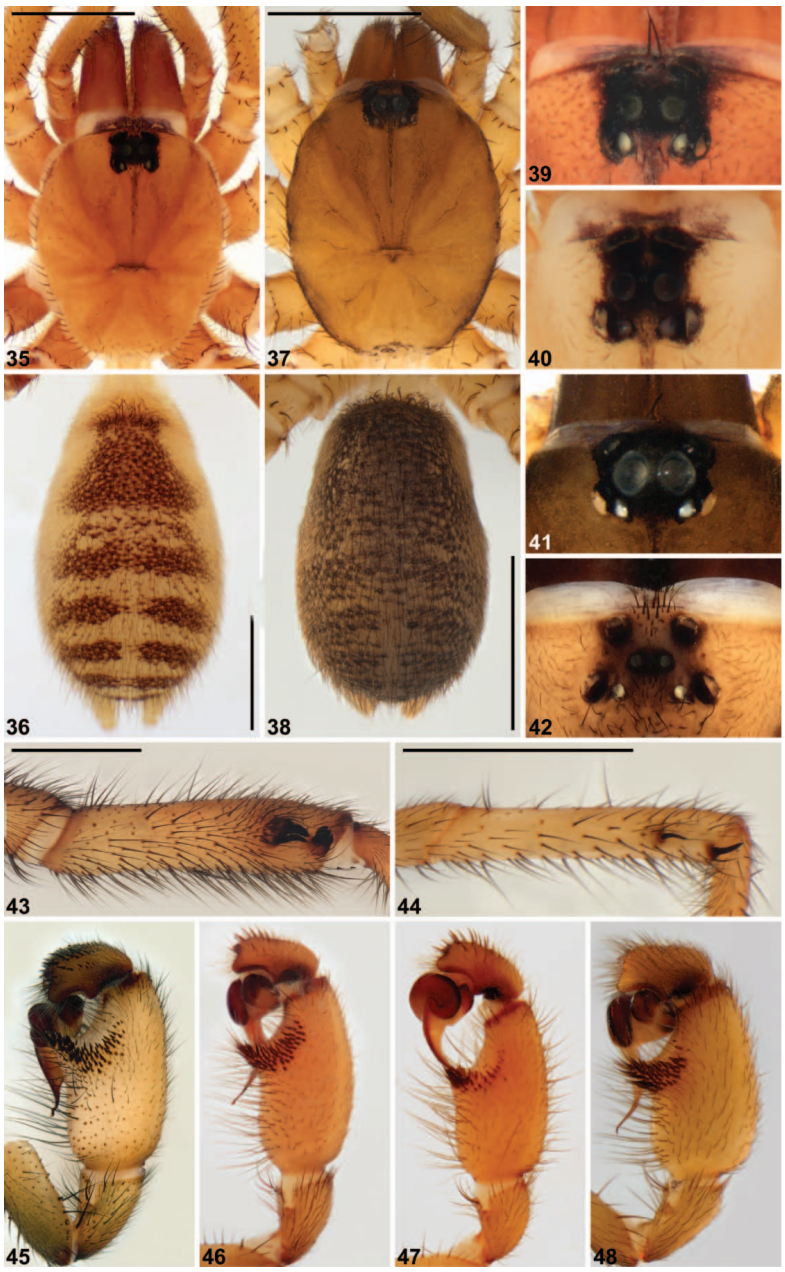
(Figs 1, 35–68)

Blakistonia Hogg, 1902: 131. Type species *Blakistonia aurea* Hogg, 1902, by original designation.

Cantuarides Strand, 1907: 8. Type species by original designation *Cantuarides exsiccatus* Strand, 1907 (synonymised by Main, 1985*b*: 39).

Diagnosis

Species of *Blakistonia* can be distinguished from *Euoplos* by the narrower carapace in dorsal view (Figs 35, 37) and presence of



Figs 35–48. Morphology of *Blakistonia* Hogg. *35–38*, Male carapace and abdomen, dorsal view: *35*, *36*, *Bl.* sp. from Weetootla Well, South Australia (SAM NN20097); *37*, *38*, *Bl.* sp. from Durokoppin Nature Reserve, Western Australia (WAM T139467). *39–42*, Eyes, dorsal view: *39*, male *Bl.* sp. from Mount Crawford, South Australia (SAM NN20090); *40*, male *Bl.* sp. from Beresford Railway Station, South Australia (SAM NN20066); *41*, male *Bl.* sp. from Peak Charles National Park, Western Australia (WAM T127864); *42*, female *Bl.* sp. from east of Madura, Western Australia (WAM T141142). *43*, *44*, Male leg I tibia, prolateral view: *43*, *Bl. aurea* Hogg, 1902 (SAM NN29564); *44*, *Bl.* sp. from Coolinup Nature Reserve, Western Australia (WAM T139466). *45–48*, Male pedipalp, retrolateral view: *45*, *Bl. aurea* (SAM NN29564); *46*, *Bl.* sp. from Mount Crawford, South Australia (SAM NN20090); *47*, *Bl.* sp. from Weetootla Well, South Australia (SAM NN20097); *48*, *Bl.* sp. from Durokoppin Nature Reserve, Western Australia (WAM T139467). Scale bars = 2.0 mm.

Figs 49–57. Images of live *Blakistonia* Hogg. *49*, Female *Bl. aurea* Hogg, 1902 from Orroroo, South Australia; *50*, female (left) and male *Bl. aurea* from Adelaide, South Australia; *51*, female *Bl. aurea* from north of Meringur, Victoria; *52*, female *Bl.* sp. from Cleland Conservation Park, Mount Lofty Range, South Australia; *53*, female *Bl.* sp. from Gawler Ranges National Park, South Australia; *54*, female *Bl.* sp. from east of Madura, Western Australia; *55*, female *Bl.* sp. from Mount Ragged, Cape Arid National Park, Western Australia; *56*, juvenile *Bl.* sp. from Grampians National Park, Victoria; *57*, female *Bl.* sp. from near Ashton, Mount Lofty Range, South Australia. Note the square or subquadrate eye group characteristic of this genus. All images by M. Rix except: (*50*, *52*) by N. Birks, used with permission; (*54*, *55*) by M. Harvey; (*57*) by S. Harrison.

a longer (more subquadrate) eye group (Figs 39–42); from *Cataxia* by the presence of scopulae on the anterior leg tarsi of females (Figs 49, 51) and presence of a longer (more subquadrate) eye group (Figs 39–42); from *Arbanitis* by the absence of a distal retrolateral tibial apophysis on the male pedipalp (Figs 45–48) and longer (more subquadrate) eye group (Figs 39–42); from *Cantuaria* by the presence of a longer (more subquadrate) eye group (Figs 39–42); and from most Aganippini by the presence of a square or subquadrate (i.e. not trapezoidal) eye group (Figs 39–41). Some anomalous *Eucyrtops* (Aganippini) have a similar subquadrate eye group to species of *Blakistonia* (e.g. *E. eremaeus* Main, 1957; Fig. 212), just as some *Blakistonia* can have a marginally trapezoidal eye group (Figs 42, 54); in both cases, species of Aganippini can be distinguished from similar *Blakistonia* by the presence of a more strongly attenuate base to the RTA (Fig. 216).

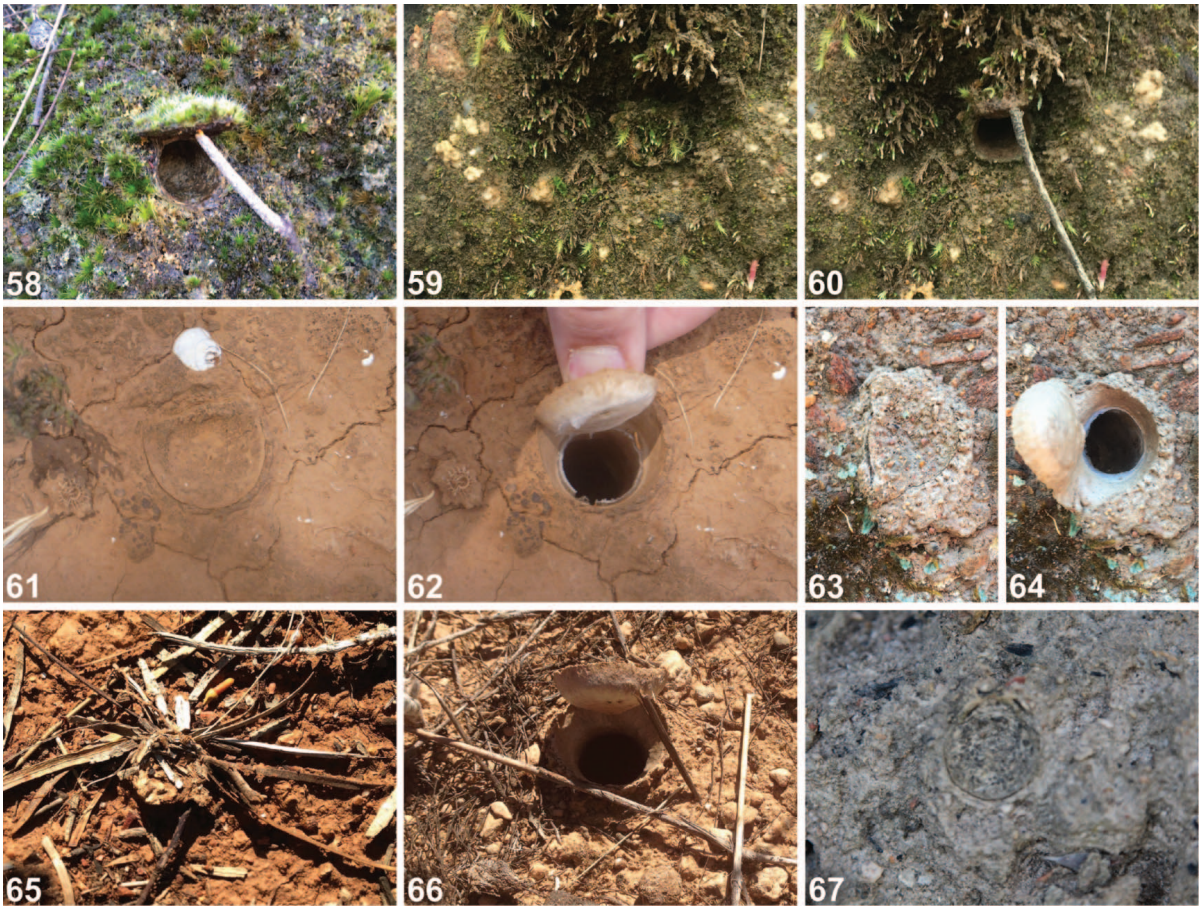
Males, females and juveniles of this genus can also be identified (on the basis of eight molecular exemplar specimens; see Fig. 68) by the following eight nuclear nucleotide substitutions: *MRPL45* C(129), A(186), G(300; homoplastic in *Cantuaria mestoni*), T(498), G(501); *RPF2* C(657; homoplastic in *Cataxia bolganupensis*); *HAT1* G(467); and *28S* T(278).

Description

See Main (1985*b*: 39).

Distribution

South Australia and surrounding areas, including the central arid zone (north to the MacDonnell Ranges), inland Queensland, western inland New South Wales, western Victoria, eastern inland Western Australia and south-western



Figs 58–67. Burrows of *Blakistonia* Hogg. *58*, *Blakistonia* sp. from near Ashton, Mount Lofty Range, South Australia; *59*, *60*, *Bl.* sp. from Cleland Conservation Park, Mount Lofty Range, South Australia; *61*, *62*, *Bl. aurea* Hogg, 1902 from Orroroo, South Australia; *63*, *64*, *Bl. aurea* from the Mount Lofty Range, South Australia; *65*, *Bl.* sp. from Tumby Bay, South Australia; *66*, *Bl.* sp. from east of Madura, Western Australia; *67*, *Bl.* sp. from Mount Ragged, Cape Arid National Park, Western Australia. Note the thick, plug-like doors and bevelled burrow entrances characteristic of most species (*60*, *62*, *64*, *66*), the much thinner, wafer-like doors found in some taxa (*58*) and the radiating twig-lines built by a very few species (*65*). Note also the D-shaped doors characteristic of *Bl. aurea* (*61*, *63*), and the unusual 'scalloped' burrow morphology of some *Bl. aurea* specimens from the Mount Lofty Range (*63*, *64*). All images by S. Harrison except: (*61*, *62*) by M. Rix.

Western Australia (Fig. 68). Absent from mesic eastern and south-eastern Australia (east of the Grampians Range) and the west coast of Western Australia.

Composition

Blakistonia includes one described species (Table 1). *Cantuarides exsiccatus* Strand, 1907, for which the female syntypes are lost and the type locality ('Central Australia') is unknown, is designated as a *nomen dubium*.

Remarks

Blakistonia is a distinctive idiopid genus from southern Australia, with a distribution centred on South Australia. The type species, *Bl. aurea* (Figs 49–51), is extremely common around Adelaide and the Adelaide Hills, and numerous other undescribed species are known from more xeric habitats in the temperate and central arid zone (SEH, unpubl. data). The undescribed sister species to all other *Blakistonia* is a rare spider from mesic habitats in the Mount Lofty Ranges, east of Adelaide (Fig. 57). Little is known of its biology or the extent of its distribution, but it will be named in a forthcoming treatment of the genus (SEH, unpubl. data). Species of *Blakistonia*, like *Euoplos* in Western Australia, have independently adapted to the Australian arid zone, occurring at least as far north as Uluru-Kata Tjuta National Park in the Northern Territory, Wingellina in central Western Australia and Noonbah Station in central Queensland (Fig. 68). Most (but not all) species build a thick, plug-like door to their burrow (Figs 60, 62, 64, 66), which is characteristically D-shaped in *Bl. aurea* (Figs 61, 63). At least one

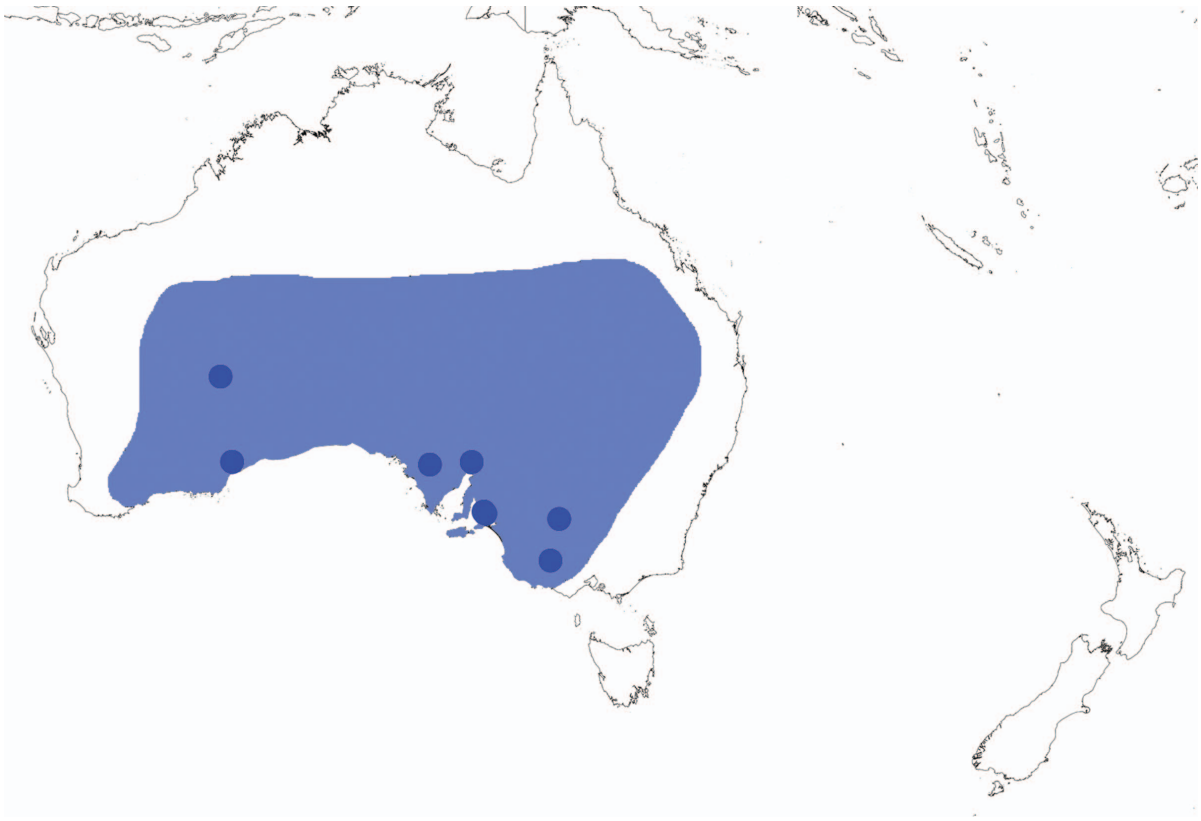


Fig. 68. Map showing the approximate extent of occurrence of the genus *Blakistonia* Hogg in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al.* (2017*a*). Note the absence of this genus from the mesic east, south-east and the far west.

species from the Eyre Peninsula incorporates radiating twig-lines, similar to species of *Gaius* and *Idiosoma* (Fig. 65).

Blakistonia aurea Hogg, 1902

(Figs 43, 45, 49–51, 61–64)

Blakistonia aurea Hogg, 1902: 132, figs 25B–E, pl. 13, figs 1, 2.
Aganippe villosa Rainbow & Pulleine, 1918: 96, pl. 21, fig. 44 (synonymised by Main, 1985*b*: 40).

Material examined

Syntypes (of *Bl. aurea*). **Australia:** South Australia: 1 ♂, 4 ♀, Adelaide, Blakiston and Mount Lofty Ranges (presumed lost; putatively deposited in BMNH, SAM).

Holotype (of *Ag. villosa*). Australia: South Australia: ♀, Bridgewater (AMS KS6156; examined [BYM]).

Select material examined. **Australia:** South Australia: 1 ♂, Valley View, Adelaide (SAM NN29564^{DNA_Voucher_33}); 1 ♀, Pichi Richi, Flinders Ranges (SAM (NN29570^{DNA_Voucher_77}). Victoria: 1 ♀, Chinkapook (SAM NN29606^{DNA_Voucher_76}).

Remarks

Blakistonia aurea (Figs 49–51), the type species of the genus, is an abundant spider in south-eastern South Australia, and is the dominant species of *Blakistonia* around Adelaide. It builds a thick, plug-like and D-shaped door (Figs 61, 62), sometimes with an ornate 'scalloped' rim (Figs 63, 64).

Genus ***Cantuaria*** Hogg, 1902

(Figs 1, 69–82)

Maoriana Hogg, 1901: 236 (junior homonym of the marine snail *Maoriana* Suter, 1891). Type species *Maoriana dendyi* Hogg, 1901, by original designation.
Cantuaria Hogg, 1902: 123 (replacement name for *Maoriana* Hogg, 1901, preoccupied in Gastropoda). Removed from synonymy of *Arbanitis* L. Koch, 1874 (*contra* Todd, 1945: 387) by Forster, 1968: 15. Removed from synonymy of *Hermeas* Karsch, 1878 = *Arbanitis* L. Koch, 1874 (*contra* Raven, 1985: 150) by Raven & Wishart, 2006: 545.
Korua Todd, 1945: 389. Type species by original designation *K. wanganuiensis* Todd, 1945 (synonymised with *Arbanitis* L. Koch, 1874 by Main, 1985*b*: 23).

Diagnosis

Most species of *Cantuaria* (as currently delimited; see 'Remarks', below) can be distinguished from all other Arbanitinae by the combined presence of scopulae on the

Figs 69–75. Morphology of *Cantuaria* Hogg. *69–71*, Male *Can. dendyi* (Hogg, 1901) (WAM T139533): *69*, *70*, carapace and abdomen, dorsal view; *71*, eyes, dorsal view; *72*, leg I tibia, prolateral view; *73*, pedipalp, retrolateral view. *74*, *75*, Male pedipalp, retrolateral view: *74*, *Can. mestoni* (Hickman, 1928) (QMB S56882); *75*, possible *Can.* sp. from Mount Crawford Forest Reserve, South Australia (SAM N1994458). Scale bars = 2.0 mm.

anterior leg tarsi and usually also metatarsi of males and females, the presence of a rectangular eye group (with a straight or procurved anterior eye row; Fig. 71), the absence of a distal retrolateral tibial apophysis (dRTA) on the male pedipalp (Figs 73–75), and the absence of ventrally incrassate anterior leg tarsi on males. With their rectangular eye group and symplesiomorphic male palpal tibia bearing a largely unmodified RTA, species of *Cantuaria* are superficially most similar to species of *Euoplos* and *Blakistonia*, from which they can be distinguished by the narrower carapace in dorsal view (Fig. 69) combined with the absence of ventrally incrassate anterior leg tarsi on males (*Euoplos*), and the presence of a shorter (more rectangular) eye group (*Blakistonia*) (Fig. 71). Most species of *Arbanitis*, in comparison, possess a dRTA on the male pedipalp (Figs 13–15).

Males, females and juveniles of this genus can also be tentatively identified (on the basis of a relatively limited molecular taxon sample of five specimens; see Fig. 82) by the

Figs 76–81. Burrows and images of live *Cantuaria* Hogg. *76*, *77*, Female and male *Can. dendyi* (Hogg, 1901) from Canterbury, New Zealand; *78*, *81*, female and burrow of *Can. mestoni* (C. L. Koch, 1842) from Fern Tree, Tasmania; *79*, burrow of *Can.* sp. from central Otago, New Zealand; *80*, burrow of *Can. stewarti* from Stewart Island, New Zealand. Images (*76*, *77*) by B. McQuillan, used with permission; (*78*, *81*) by M. Rix; (*79*, *80*) by V. Smith, used with permission.

unique 'TC' motif at positions 615–616 of nuclear *ITS1*, and by the following nuclear nucleotide substitution: *RPF2* A(517).

Description

See Forster (1968: 15). See also 'Remarks', below.

Distribution

New Zealand and Tasmania (Fig. 82). Possibly more widespread in south-eastern mainland Australia (see 'Remarks', below).

Composition and remarks

Cantuaria includes 43 described species (Table 1). Molecular phylogenetic data reveal that *Cantuaria* also occurs in Tasmania, and includes *Arbanitis mestoni* Hickman, 1928 (Figs 74, 78), the latter formerly included within *Misgolas* (= *Arbanitis*). Numerous undescribed New Zealand species are known from collections (V. Smith and C. Vink, unpubl. data), and based on morphology this genus may also occur on the Australian mainland (Fig. 75; although this requires testing with molecular data). As the genus is currently the subject of a detailed systematic revision by colleagues in New Zealand, we refrain from providing a detailed account here.

Cantuaria dendyi (Hogg, 1901)

(Figs 69–73, 76, 77)

Maoriana dendyi Hogg, 1901: 237, fig. 25.
Cantuaria dendyi (Hogg): Hogg, 1902: 123.
Arbanitis dendyi (Hogg): Todd, 1945: 387, figs 3, 7, 27, 41, 57.
Cantuaria dendyi (Hogg): Forster, 1968: 16, figs 17–24.
Hermeas dendyi (Hogg): Raven, 1985: 150.
Cantuaria dendyi (Hogg): Raven & Wishart, 2006: 545.

Material examined

Holotype. New Zealand: Canterbury: ♀, Christchurch (BMNH; examined [RJR]).

Select material examined. **New Zealand:** Canterbury: 1 ♂, Springfield (WAM T139533); 1 ♀, Christchurch (CMNZ^{DNA_Voucher_193}).

Remarks

Cantuaria dendyi (Figs 76, 77), the type species of the genus, is known from the Christchurch region of New Zealand. It builds a door to its burrow.

Cantuaria johnsi Forster, 1968

Cantuaria johnsi Forster, 1968: 47, figs 126–133.
Hermeas johnsi (Forster): Raven, 1985: 150.
Cantuaria johnsi Forster: Raven & Wishart, 2006: 545.

Material examined

Holotype. New Zealand: Nelson: ♂, Anatoki Beach (CMNZ; not examined).

Select material examined. **New Zealand:** Nelson: 1 ♀, Takaka Hill (CMNZ^{DNA_Voucher_192}).

Remarks

Cantuaria johnsi is known from Nelson, New Zealand. It builds a door to its burrow.

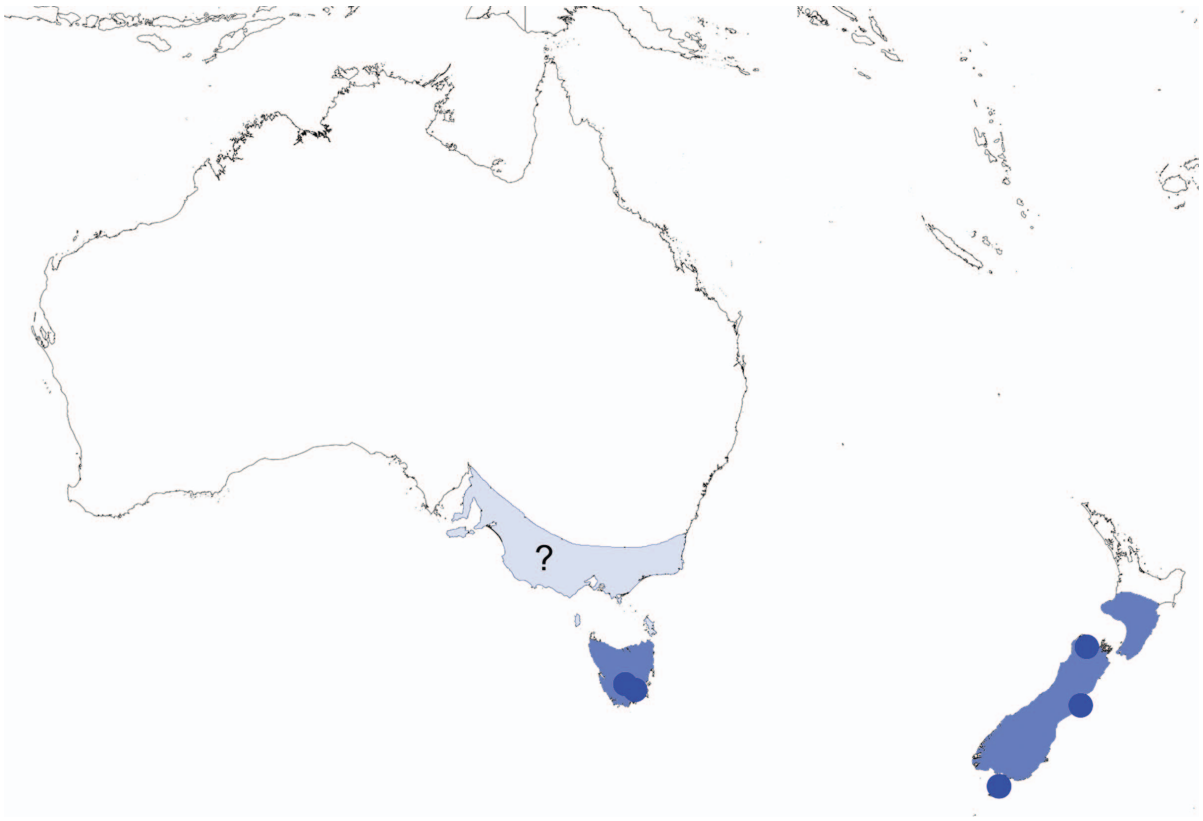


Fig. 82. Map showing the approximate extent of occurrence of the genus *Cantuaria* Hogg in Australia and New Zealand, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al.* (2017*a*). Note the unconfirmed (but likely) occurrence of this genus on the south-eastern Australian mainland.

Cantuaria mestoni (Hickman, 1928), comb. nov.

(Figs 74, 78, 81)

Arbanitis mestoni Hickman, 1928: 162, figs 2–5, pl. 23.
Arbanitis annulipes (C. L. Koch): Hickman, 1967: 16, figs 20, 21, pl. 2, figs 1, 2 (misidentification).
Misgolas mestoni (Hickman): Main, 1977: 72.

Material examined

Syntypes. **Australia:** Tasmania: 1 ♂, 1 ♀, Woodsdale (QVM; examined [RJR]).

Select material examined. **Australia:** Tasmania: 1 ♀, Fern Tree, Hobart, off Huon Road (WAM T133327^{DNA_Voucher_100}); 1 ♂, Warra Forest, near Geeveston (QMB S56882); 1 juvenile, Mount Field National Park, near entrance to Russell Falls track (WAM T133329^{DNA_Voucher_101}).

Remarks

Cantuaria mestoni (Fig. 78) is a medium-sized species from Tasmania common around Hobart (Hickman 1967). This species was for a long time erroneously associated with the name *Mygale annulipes* (C. L. Koch, 1842); however, the recently discovered female holotype of the latter (ZMB 2095) is clearly a species of *Stanwellia* Rainbow & Pulleine, 1918 (Nemesiidae) (Figs 322–324) (see 'Remarks' under *Euoplos*, below). We therefore attribute references to '*Arbanitis annulipes*' in Hickman (1967) to *Can. mestoni*. This species has distinctive annulate and heavily spined legs, a low caput and glabrous carapace (Fig. 78), and builds an open-holed burrow in mesic forested habitats throughout Tasmania (e.g. around Mount Wellington and at Mount Field National Park) (Fig. 81). Molecular phylogenetic data convincingly show that this species is not congeneric with *Arbanitis* or *Euoplos*, and indeed Main (1985*b*: 32) was the first to recognise its unusual morphology relative to other Australian taxa. The pedipalp morphology (Fig. 74; see also Hickman 1928: fig. 4 and Hickman 1967: fig. 21) is consistent with its molecular placement in the genus *Cantuaria*, and it is hereby transferred to that genus.

Cantuaria stewarti (Todd, 1945)

(Fig. 80)

Arbanitis huttoni stewarti Todd, 1945: 382.
Cantuaria stewarti (Todd): Forster, 1968: 64, figs 180–186.
Hermeas stewarti (Todd): Raven, 1985: 150.
Cantuaria stewarti (Todd): Raven & Wishart, 2006: 545.

Material examined

Holotype. New Zealand: Southland: ♂, Oban, Stewart Island (OMD; examined [RJR]).

Select material examined. **New Zealand:** Southland: 1♀, Oban, Stewart Island (CMNZ^{DNA_Voucher_192}).

Remarks

Cantuaria stewarti is known only from Stewart Island, New Zealand. It builds an open-holed burrow (Fig. 80).

Tribe **AGANIPPINI** Simon, 1903

Aganippeae Simon, 1903: 884, 901 (published June 1903). Here removed from synonymy of Aganippae Pocock, 1903 (*contra* Main, 1985*b*: 10). Type genus *Aganippe* O. P.-Cambridge, 1877 (= *Idiosoma* Ausserer, 1871).

Aganippae Pocock, 1903: 349 (published August 1903 *contra* Main, 1985*b*: 10). Type genus *Aganippe* O. P.-Cambridge, 1877 (= *Idiosoma* Ausserer, 1871). New synonymy.

Diagnosis

Species of Aganippini can be distinguished from all other Arbanitinae by the presence of a trapezoidal eye group in which the posterior eye row is broader than the anterior eye row, the latter of which is also strongly procurved (Figs 87, 120, 152, 194, 227, 245). Some anomalous *Eucyrtops* (Aganippini) have a similar subquadrate eye group to species of *Blakistonia* (e.g. *E. eremaeus* Main, 1957; Fig. 212), just as some *Blakistonia* can have a trapezoidal eye group (Figs 42, 54); in both cases, species of Aganippini can be distinguished from similar Arbanitini by the presence of a more strongly attenuate base to the RTA (Fig. 216).

Males, females and juveniles of this tribe can also be identified (on the basis of 67 molecular exemplar specimens; see Figs 115, 162, 190, 223, 256) by the unique 'TACCC' motif at positions 527–531 of nuclear *18S* rRNA, by the unique 'CT' motif at positions 489–490 of nuclear *28S* rRNA and by the following 11 nuclear nucleotide substitutions: *MRPL45* T(297); *RPF2* A(159; homoplastic in *Homogona pulleinei*), C(512; homoplastic in *Cantuaria mestoni*), G(633; rarely homoplastic in *Misgolas*); *XPNPEP3* G(325); *HAT1* T(154; homoplastic in *Can. mestoni*), G(377), G(441; homoplastic in *Homogona victoriae*), T(573; homoplastic in *Can. stewarti*); *ITS1* T(479); and *28S* T(701).

Distribution

Mainland Australia (all states and territories), mostly south of the Tropic of Capricorn and west of the Great Dividing Range (Figs 115, 131, 145, 162, 175, 190, 204, 223, 237, 256). Absent from Tasmania.

Included genera

Idiosoma Ausserer, 1871, *Bungulla* Rix, Main, Raven & Harvey, gen. nov., *Eucanippe* Rix, Main, Raven & Harvey, gen. nov., *Eucyrtops* Pocock, 1897 and *Gaius* Rainbow, 1914.

Remarks

The Aganippini is the most derived, diverse and the most widespread tribe of Arbanitinae, found across most of continental mainland Australia. The five genera form an extremely well-supported monophyletic clade (Fig. 1), which has radiated throughout the arid zone since the Miocene (Rix *et al*. 2017*a*). Most genera are endemic to Western Australia (Figs 162, 190, 223, 256), although one genus (*Idiosoma*) also occurs across the rest of the Australian mainland (Fig. 115). In southern Western Australia, the diversity of aganippine spiders, at both the generic and species levels, is remarkable, and all five genera often occur in sympatry. Between 100 and 200 new species remain to be described, and all known species build a door to their burrows (Figs 106–114, 129, 130, 160, 161, 221, 222, 254, 255).

Genus ***Idiosoma*** Ausserer, 1871

(Figs 1, 83–145)

Idiosoma Ausserer, 1871: 150. Type species *Idiops sigillatus* O. P.-Cambridge, 1870, by monotypy.

Aganippe O. P.-Cambridge, 1877. Type species by subsequent designation (of Simon, 1892: 106) *Aganippe subtristis* O. P.-Cambridge, 1877. New synonymy.

Anidiops Pocock, 1897: 114. Type species by monotypy *Anidiops manstridgei* Pocock, 1897. New synonymy.

Diagnosis

Species of *Idiosoma* can be distinguished from all other Arbanitinae by the presence of a median retrolateral digital process on the male pedipalp, distal to the burr-like RTA (this digital process secondarily reduced to a nubbin in a very few species) (Figs 93–96, 142). Males and females of most (but not all) *Idiosoma* species possess prominent paired sigilla on the dorsal abdomen (also present in *Eucanippe* Rix, Main, Raven & Harvey, gen. nov.) (Figs 84, 97, 98, 100, 101, 103–105, 118).

Males, females and juveniles of this genus can also be identified (on the basis of 45 molecular exemplar specimens; see Fig. 115) by the unique 'AA' (rarely 'AG' or 'GA') motif at positions 643–644 of nuclear *MRPL45*, by the unique 'GCGC' motif at positions 156–159 of nuclear *HAT1*, and by the following six nuclear nucleotide substitutions: *MRPL45* G (654; rarely homoplastic in *Arbanitis*); *RPF2* G(483); *XPNPEP3* T(194); *HAT1* C(330); *ITS2* C(85); and *28S* G (1917; rarely homoplastic in *Bungulla*).

Description

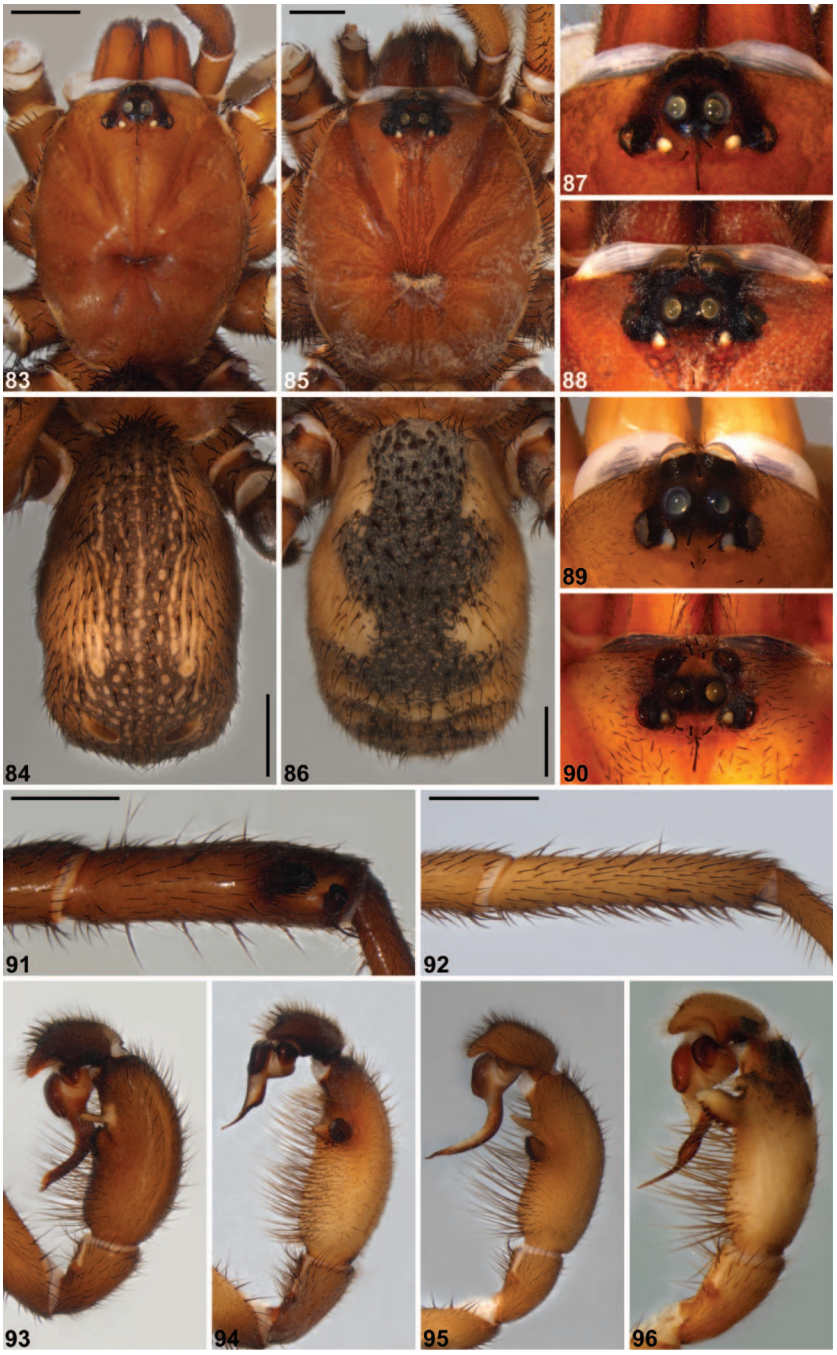
See Main (1985*b*: 11–13).

Distribution

Mainland Australia (all states and territories), mostly south of the Tropic of Capricorn and west of the Great Dividing Range (Fig. 115). Absent from Tasmania.

Composition

Idiosoma includes 14 described species (Table 1). A further seven species, all of which are represented by female holotypes that cannot be confidently identified or associated with a named species, are designated as *nomina dubia*: *Aganippe whitei*



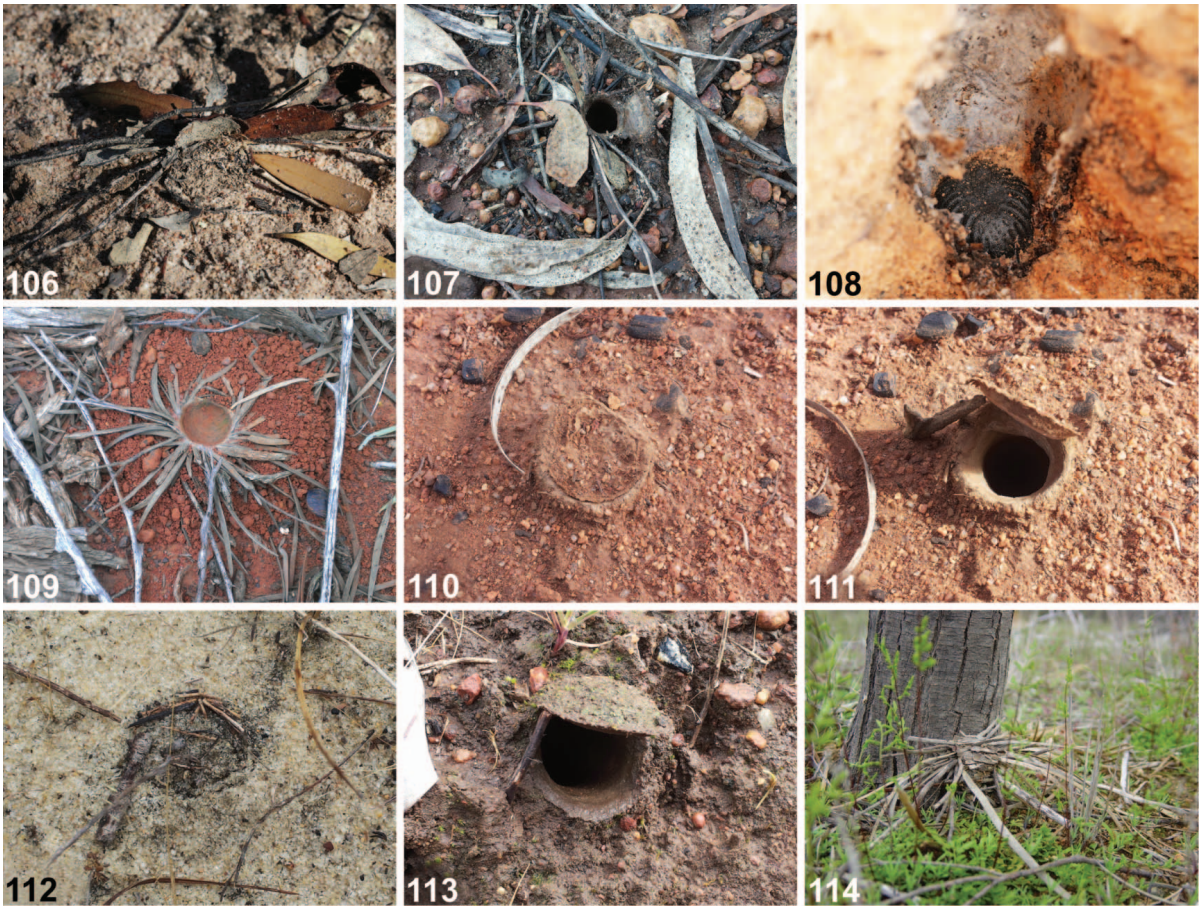
Figs 83–96. Morphology of *Idiosoma* Ausserer. *83–86*, Male carapace and abdomen, dorsal view: *83*, *84*, *I. sigillatum* (O. P.-Cambridge, 1870) (WAM T139480); *85*, *86*, *I.* sp. from Woomera, South Australia (SAM NN20641). *87–90*, Eyes, dorsal view: *87*, male *I. sigillatum* (WAM T139480); *88*, male *I.* sp. from Woomera, South Australia (SAM NN20641); *89*, male *I. castellum* (Main, 1986) (holotype); *90*, male *I. montanum* (Faulder, 1985) (holotype). *91*, *92*, Male leg I tibia, prolateral view: *91*, *I. sigillatum* (WAM T139480); *92*, *I. castellum* (holotype). *93–96*, Male pedipalp, retrolateral view: *93*, *I. sigillatum* (WAM T139480); *94*, *I.* sp. from Woomera, South Australia (SAM NN20641); *95*, *I. castellum* (holotype); *96*, *I. berlandi* (Rainbow, 1914) (holotype). Scale bars = 2.0 mm.

Figs 97–105. Images of live *Idiosoma* Ausserer. *97*, Female *I. sigillatum* (O. P.-Cambridge, 1870) from Shenton Park, Perth, Western Australia; *98*, female *I.* sp. nr. *nigrum* from Meenaar Nature Reserve, Western Australia; *99*, female *I. galeosomoides* Rix, Main, Raven & Harvey, sp. nov. from Deception Hill, Western Australia; *100*, female *I. winsori* (Faulder, 1985) from Grampians National Park, Victoria; *101*, female *I.* sp. from Watarrka National Park, Northern Territory; *102*, female *I.* sp. from Gawler Ranges National Park, South Australia; *103*, female *I.* sp. from Lake Broadwater Conservation Park, Queensland; *104*, female *I.* sp. from Eidsvold, Queensland; *105*, female *I.* sp. from near Laverton, Western Australia. Note the sclerotised abdominal sigilla present on most species, and the phragmotic abdominal modifications of *I. sigillatum*, *I.* sp. nr. *nigrum* and *I. galeosomoides* (*97–99*). All images by M. Rix except: (*99*) by Z. Hamilton, used with permission.

Rainbow, 1915 from Port Augusta (South Australia) (here removed from synonymy of *An. manstridgei* Pocock, 1897 *contra* Main 1957: 426); *Ag. modesta* Rainbow & Pulleine, 1918 from Mount Lofty (South Australia); *Ag. pelochroa* Rainbow & Pulleine, 1918 from Mount Lofty (South Australia); *Ag. robusta* Rainbow & Pulleine, 1918 from Adelaide (South Australia); *Ag. simpsoni* Hickman, 1944 from east of Hale River (Northern Territory); *Blakistonia bancrofti* Rainbow & Pulleine, 1918 from Eidsvold (Queensland); and *Gaius hirsutus* Rainbow & Pulleine, 1918 from north of the Everard Ranges (South Australia) (here removed from synonymy of *An. manstridgei* Pocock, 1897 *contra* Main 1957: 426). Associating females with males is especially difficult in *Idiosoma*, as multiple species often live in close sympatry or parapatry, and males or molecules are usually required for accurate identification.

Remarks

Idiosoma is by far the most widespread and speciose genus of Idiopidae in Australia, having experienced a remarkable diversification in the arid zone since the Miocene (Rix *et al.* 2017*a*). Unusual posterior abdominal modifications for phragmotic defence (e.g. Figs 97–99, 125–127), similar to *Galeosoma* Purcell, 1903 (Idiopidae) and *Cyclocosmia* Ausserer, 1871 (Ctenizidae), have putatively evolved twice independently within the genus in Western Australia (Rix *et al.* 2017*a*): once in the clade including *I. sigillatum*, *I. nigrum* Main, 1952 and related species (Figs 97, 98); and once in *I. galeosomoides* Rix, Main, Raven & Harvey, sp. nov. (Figs 99, 125–127). Burrow and burrow door morphologies vary widely according to lineage, habitat and substrate (Figs 106–114), with some species building supported palisade



Figs 106–114. Burrows of *Idiosoma* Ausserer. *106*, *Idiosoma nigrum* Main, 1952 from Minnivale Nature Reserve, Western Australia; *107*, *I.* sp. nr. *nigrum* from Meenaar Nature Reserve, Western Australia; *108*, *I. nigrum* from Minnivale Nature Reserve, Western Australia, showing phragmotic (abdominal) burrow plugging during excavation; *109*, *I.* sp. from near Laverton, Western Australia; *110*, *111*, *I.* sp. from Yorkrakine Rock Nature Reserve, Western Australia; *112*, *I.* sp. from Shenton Park, Perth, Western Australia; *113*, *I. cupulifex* (Main, 1957) from Lower Chittering, Western Australia; *114*, *I. castellum* (Main, 1986) from north of Kununoppin, Western Australia. Note the 'moustache' burrow twig-lines (*106*, *107*) characteristic of *I. nigrum* and its close relatives, the radiating twig-lines built by some arid species (*109*), and the palisade burrow of *I. castellum* (*114*). All images by M. Rix except: (*106*, *108*) by M. Harvey; (*109*) by Jeff Turpin, used with permission; (*114*) by M. Davis, used with permission.

burrows (Fig. 114) and others adorning their burrow entrances with twig-lines (Figs 106, 107, 109, 114). Species of *Idiosoma* are arid zone specialists, and are generally absent or extremely rare in the higher rainfall mesic zone, including on and east of the Great Dividing Range and in the Warren bioregion of far south-western Australia. Like other Aganippini, they have not been found in Tasmania.

The synonymy of *Idiosoma* with *Aganippe* and *Anidiops* (i.e. *An. manstridgei* Pocock, 1897 and related species, excluding *Gaius villosus* Rainbow, 1914 *contra* Main 1957: 424) is strongly supported on both morphological and molecular grounds, and indeed Pocock (1897: 112) recognised the morphological similarity between *Idiosoma* and *Aganippe* well over a century ago, but refrained from actually synonymising the two. Main (1985*b*: 15, 16) likewise alluded to the palpal morphology shared between *Aganippe* and *An. manstridgei* (Figs 132–144), but considered the absence of dorsal abdominal sigilla (e.g. Fig 86, 102, 133) in the latter to be of generic significance. We here recognise the digital retrolateral process on the male pedipalp of *Idiosoma* as both a synapomorphy and a diagnostic character of the genus, and thus transfer *An. manstridgei* and all valid species previously assigned to *Aganippe* to *Idiosoma*.

Idiosoma sigillatum (O. P.-Cambridge, 1870)

(Figs 83, 84, 87, 91, 93, 97)

Idiops sigillatus O. P.-Cambridge, 1870: 105, pl. 8, fig. 1.
Idiosoma sigillatum (O. P.-Cambridge): Ausserer, 1871: 150.
Idiosoma hirsutum Main, 1952: 132, fig. 2B. New synonymy.

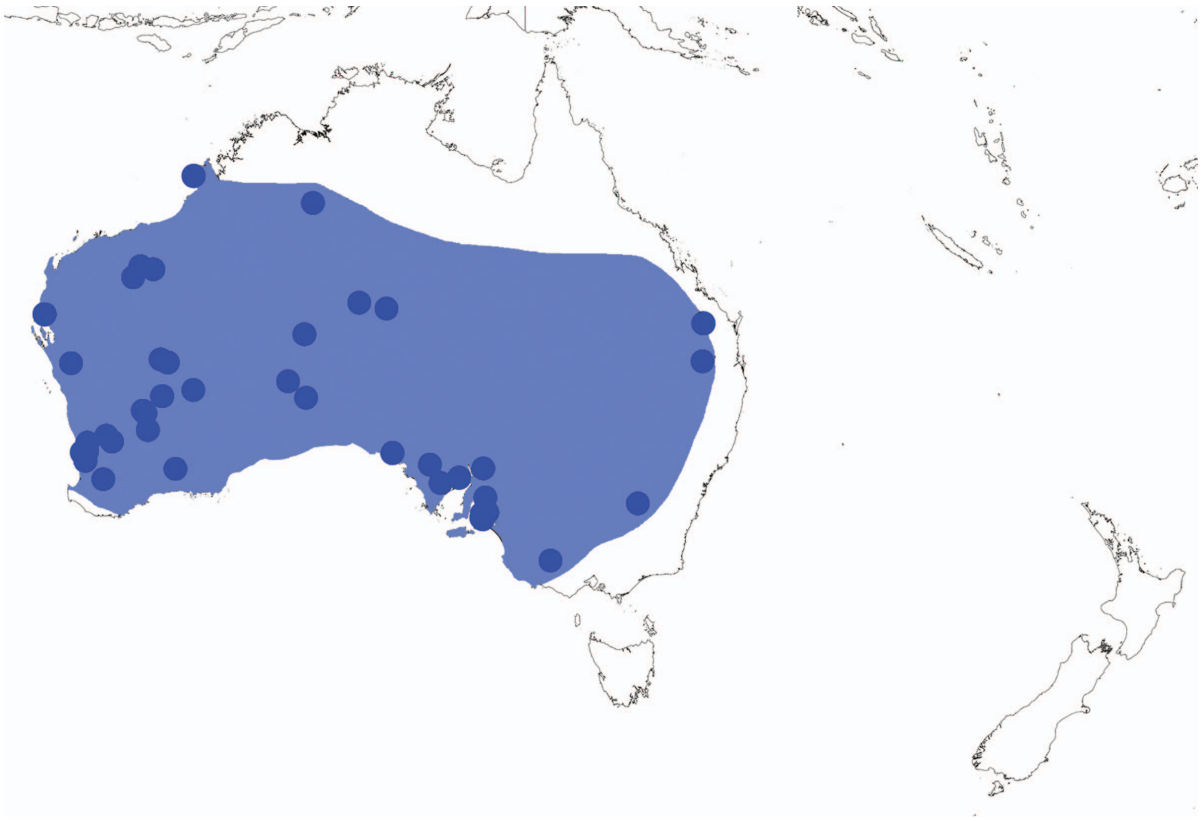


Fig. 115. Map showing the approximate extent of occurrence of the genus *Idiosoma* Ausserer in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al.* (2017*a*). Note the absence of this genus from the tropical north, and the mesic east, south-east and extreme south-west.

Material examined

Holotype (of *I. sigillatum*). Australia: Western Australia: ♂, Swan River [Perth] (OUM; examined [BYM]).

Holotype (of *I. hirsutum*). **Australia:** Western Australia: ♀, Victoria Park, Perth (WAM T2172; examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, Crawley, Perth (WAM T132564^{DNA_Voucher_ID}); 1 ♂, Duncraig, Perth (WAM T139480); 1 ♂, Curtin University, Kardinya, Perth (WAM T55925^{DNA_Voucher_127}).

Remarks

Idiosoma sigillatum, the type species of the genus, is a large black spider from the sandplains of the Western Australian Swan Coastal Plain (Fig. 97). It is the most common and easily recognisable idiopid spider around metropolitan Perth, and extends south to at least Bunbury. It builds a well-camouflaged burrow in sandy soils, with a distinctive 'moustache' of twig-lines and a flappy door that usually incorporates leaf litter debris. Due to widespread land clearing it is now locally extinct from much of its former range (see Main 1990; Rix *et al.* 2017*b*), although it can still be found in some bushland remnants (e.g. Kings Park in Perth). Like *I. nigrum* it has a phragmotic abdominal morphology for burrow plugging. *Idiosoma* '*hirsutum*' from the southern suburbs of Perth is conspecific with this species, and is here newly synonymised.

Idiosoma berlandi (Rainbow, 1914), comb. nov.

(Fig. 96)

Aganippe berlandi Rainbow, 1914: 199, figs 9–13.

Material examined

Holotype. Australia**:** New South Wales: ♂, Narrabri (AMS KS1668; examined [MGR, BYM]).

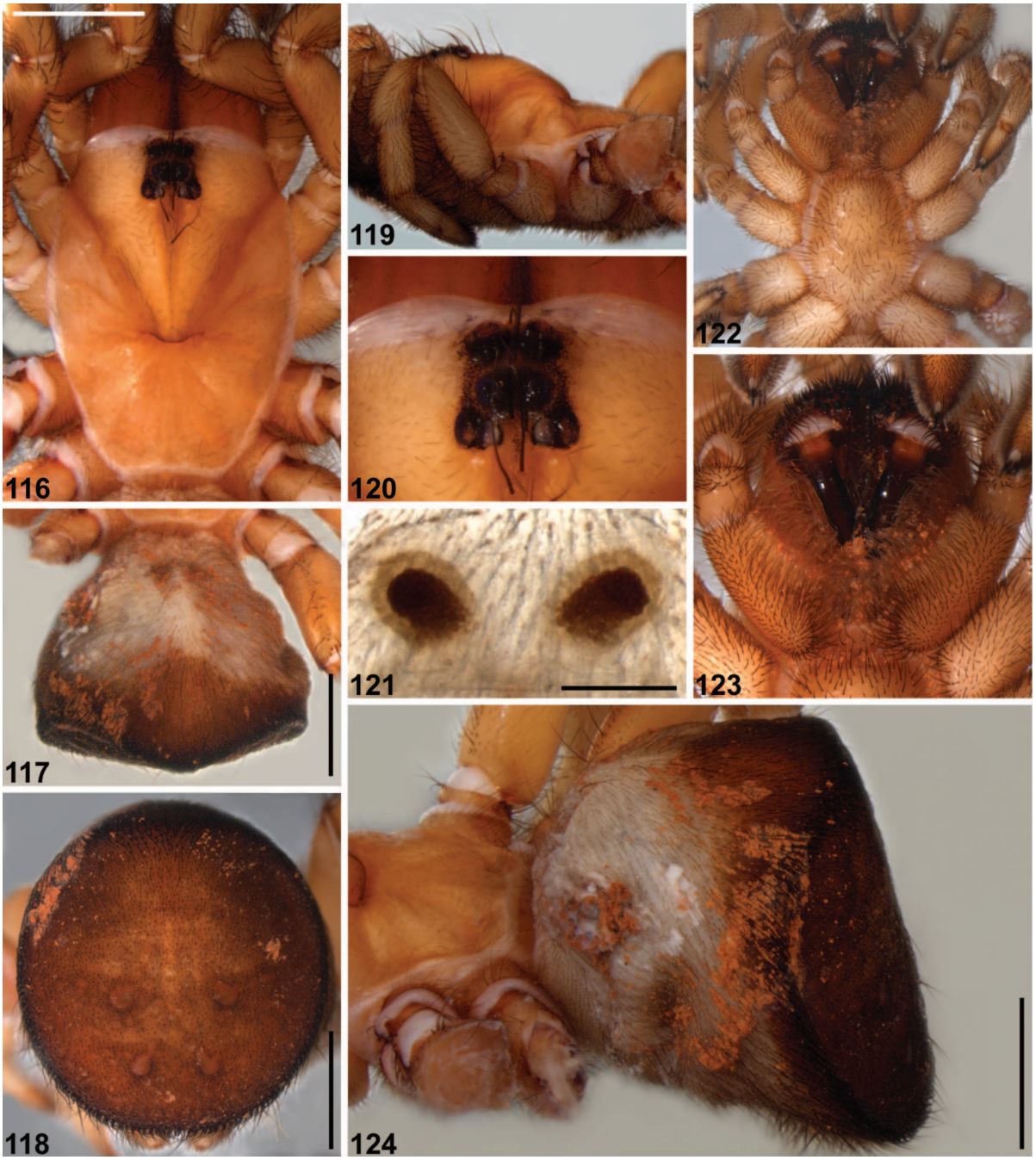
Remarks

Idiosoma berlandi is a medium-sized species from the southern Brigalow Belt region of New South Wales.

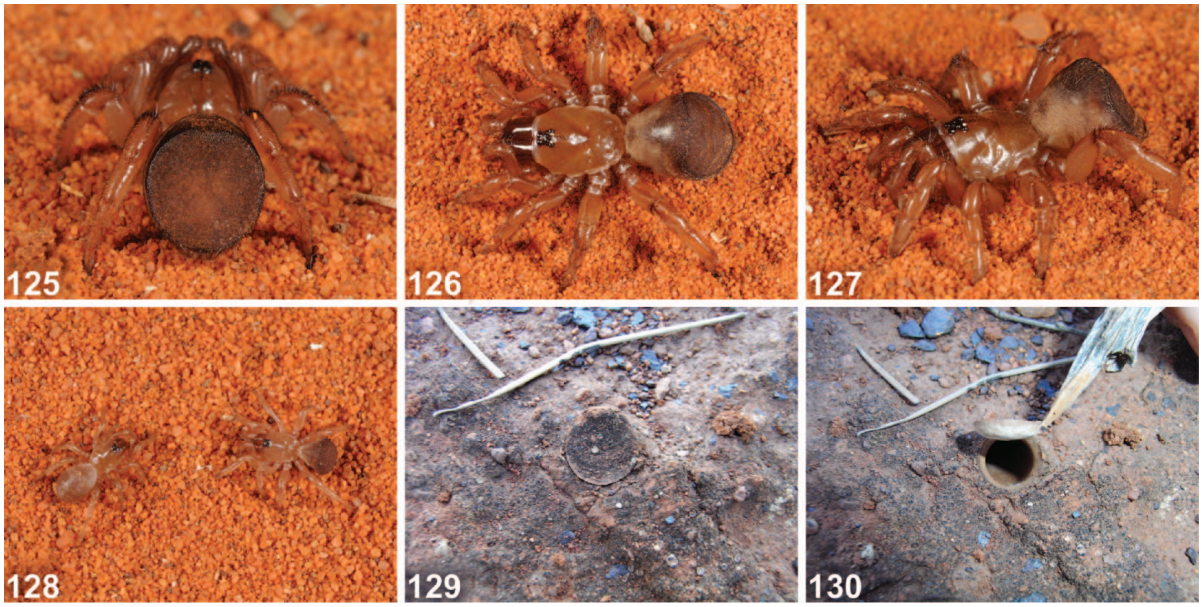
Idiosoma castellum (Main, 1986), comb. nov.

(Figs 89, 92, 95, 114)

Aganippe castellum Main, 1986: 101, figs 2, 4A–H.



Figs 116–124. *Idiosoma galeosomoides* Rix, Main, Raven & Harvey, sp. nov., female holotype (WAM T109160). *116*, *117*, Carapace and abdomen, dorsal view; *118*, abdomen, posterior view; *119*, cephalothorax, lateral view; *120*, eyes, dorsal view; *121*, spermathecae, dorsal view; *122*, sternum, ventral view; *123*, mouthparts, ventral view; *124*, abdomen and posterior cephalothorax, dorso-lateral view. Scale bars = 2.0 mm (*116–118*, *124*), 0.5 mm (*121*).



Figs 125–130. *Idiosoma galeosomoides* Rix, Main, Raven & Harvey, sp. nov. *125–128*, Images of live female (*125–127*) and early-instar juveniles (*128*) from Deception Hill, Western Australia; *129*, *130*, burrow of the same. All images by Z. Hamilton, used with permission.

Fig. 131. Map showing collection records of *Idiosoma galeosomoides* Rix, Main, Raven & Harvey, sp. nov. in south-western Western Australia, along with Interim Biogeographic Regionalisation of Australia (IBRA, Version 7.0) boundaries and select bioregion acronyms. Blue dots denote sequenced specimens. AVW, Avon Wheatbelt; COO, Coolgardie; MUR, Murchison; YAL, Yalgoo.

Figs 132–141. *Idiosoma manstridgei* (Pocock, 1897), male (WAM T96447), somatic morphology. *132*, *133*, Carapace and abdomen, dorsal view; *134*, cephalothorax, lateral view; *135*, eyes, dorsal view; *136*, mouthparts, ventral view; *137*, *138*, sternum and abdomen, ventral view; *139*, leg I, prolateral view; *140*, leg I tibia, clasping spurs, prolateral view; *141*, leg I tibia, proventral view. Scale bars = 2.0 mm.

Figs 142–144. *Idiosoma manstridgei* (Pocock, 1897), male (WAM T96447), pedipalp. *142*, Retrolateral view; *143*, retroventral view; *144*, prolateral view. Scale bar = 2.0 mm.

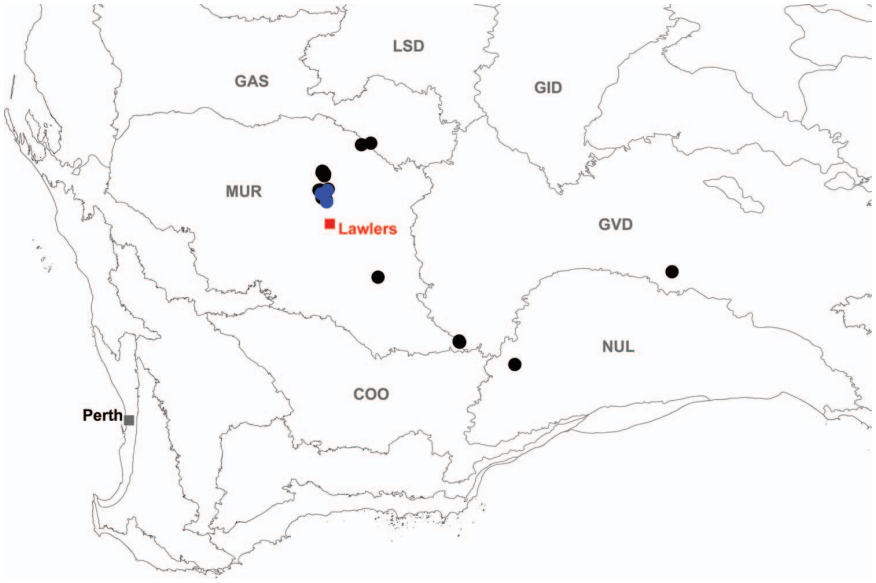


Fig. 145. Map showing collection records of *Idiosoma manstridgei* (Pocock, 1897) in Western Australia, along with Interim Biogeographic Regionalisation of Australia (IBRA, Version 7.0) boundaries and select bioregion acronyms. The original type locality, 'Lawlers', is shown in red; blue dots denote sequenced specimens. COO, Coolgardie; GAS, Gascoyne; GID, Gibson Desert; GVD, Great Victoria Desert; LSD, Little Sandy Desert; MUR, Murchison; NUL, Nullarbor.

f

Material examined

Holotype. Australia: Western Australia: ♂, Minnivale (WAM T16866; examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, Koolyanobbing Airstrip (WAM T97339[DNA_Voucher_249]).

Remarks

Idiosoma castellum, the 'tree-stem trapdoor spider', is a distinctive species from the Western Australian Wheatbelt. It builds a palisade burrow against the stems of bushes and small trees, with a radiating 'moustache' of twig-lines around the entrance (see Main 1986; Fig. 114). Males are without clasping spurs on the prolateral tibia I (Fig. 92). *Idiosoma castellum* is the sister species to the lineage including *I. nigrum* and *I. sigillatum*, with which it shares a 'moustache' twig-lining burrow morphology (Fig. 114).

Idiosoma cupulifex (Main, 1957), comb. nov.

(Fig. 113)

Aganippe cupulifex Main, 1957: 436, figs 7F, 9B, 12A, 13C.

Material examined

Holotype. Australia: Western Australia: ♂, Great Northern Highway near Chittering Lakes (WAM T3963; examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♀, Lower Chittering (WAM T133995[DNA_Voucher_42]).

Remarks

Idiosoma cupulifex is a medium-sized species from the northern jarrah forest near Perth. It builds a distinctive, outwardly domed burrow lid (Fig. 113), and can sometimes be found clustered in large numbers in suitable habitats.

Idiosoma galeosomoides Rix, Main, Raven & Harvey, sp. nov.

(Figs 99, 116–131)

http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:8ED43DD7-37E1-4BA1-8544-22ACFAB0DA54

Material examined

Holotype. Australia: Western Australia: ♀, Deception Hill, 77.9 km SW. of Lake Barlee, 112.55 km NNW. of Koolyanobbing (IBRA_COO), 29°51′19″S, 119°15′48″E, dug from burrow, 3.xii.2010, R. Teale, Z. Hamilton, V. Cartledge (WAM T109160[DNA_Voucher_73]).

Paratypes. **Australia:** Western Australia: 1 ♀, Deception Hill, 77.9 km SW. of Lake Barlee, 112.55 km NNW. of Koolyanobbing (IBRA_COO), 29°59′42″S, 119°15′25″E, dug from burrow, 1.xii.2010, R. Teale, Z. Hamilton, V. Cartledge (WAM T136970); 1 ♀, same data except 29°51′55″S, 119°16′37″E, 5.xii.2010 (WAM T136969); 1 ♀, same data except 152 km NNW. of Southern Cross, 29°51′31″S, 119°16′14″E, R. Teale, Z. Hamilton, J. Cairnes (WAM T103395); 1 ♀, same data except 151.3 km NNW. of Southern Cross, 29°51′59″S, 119°16′40″E (WAM T103396).

Other material examined. **Australia:** Western Australia: 1 ♀, Windarling, 92.5 km N. of Koolyanobbing (IBRA_COO), 30°00′45″S, 119°15′31″E, dug from burrow, 7.vii.2010, Z. Hamilton, J. Cairnes (WAM T103388); 13 juveniles, same data (WAM T103393); 1 ♀, same data except 93 km N. of Koolyanobbing, 30°00′38″S, 119°14′58″E, 6.vii.2010 (WAM T103391[DNA_Voucher_214]); 2 juveniles, same data (WAM T103394); 10 juveniles, same data (WAM T103397); 1 ♀, same data except 92.9 km N. of Koolyanobbing, 30°00′24″S, 119°14′15″E, 5.vii.2010 (WAM T103389); 1 ♀, same data except 93.6 km N. of Koolyanobbing, 30°00′23″S, 119°14′17″E, 5.vii.2010 (WAM T103392); 1 ♀, same data (WAM T103390).

Diagnosis

Idiosoma galeosomoides differs from all other described congeners by the presence of a modified phragmotic abdominal morphology (Figs 117, 118, 124–127): the abdomen is subtriangular in lateral view, with a circular posterior profile formed by a reinforced, sclerotised rim surrounding thickened, concave cuticle on the posterior face of the abdomen. However, one similar and very closely related undescribed species is known from the Avon Wheatbelt bioregion, and *I. galeosomoides* can be distinguished from this species by the more closely spaced (almost contiguous) ALE, and the more evenly circular profile of the posterior abdomen.

Description

Female holotype (*Figs 116–124*)

Total length 11.9. Carapace 5.1 long, 3.8 wide. Abdomen 5.1 long, 5.4 wide. Carapace tan with black ocular region (Fig. 116); fovea procurved (Fig. 116). Dorsal pars cephalica with three long, porrect post-ocular setae in staggered median arrangement (Fig. 116). Eye group (Fig. 120) trapezoidal, PLE–PLE/ALE–ALE ratio 1.4; 1.0× longer than wide; ALE separated by less than half their own diameter; AME separated by 1.3× their own diameter; PME separated by 1.5× their own diameter; PME and PLE almost contiguous, PME positioned in line with level of PLE. Maxillae with field of cuspules confined to inner corner (Fig. 123); labium without cuspules. Abdomen dark brown posteriorly and lighter beige-grey anteriorly (Figs 117, 124); trapezoidal in dorsal view (Fig. 117) and subtriangular in lateral view (Fig. 124), with truncate, heavily sclerotised and circular posterior profile (Fig. 118) formed by reinforced, sclerotised rim bearing a fringe of stout, strongly curved setae. Posterior face of abdomen with two pairs of large, sclerotised sigilla (sigilla pairs 2 and 3) in subquadrate trapezoidal arrangement (Fig. 118); sigilla pair 2 largest, separated by ~3.5× their own diameter; sigilla pair 3 separated by ~2.3× their own diameter. Legs variable shades of tan, with scopulae on tarsi I–II and metatarsi I–II; metatarsus I with row of four retroventral spine-like setae and 3 or 4 ventral spine-like setae; tarsus I with cluster of ~10 ventral and retroventral spine-like setae. Leg I: femur 2.8; patella 1.9; tibia 1.5; metatarsus 1.3; tarsus 1.1; total 8.7. Leg I femur–tarsus/carapace length ratio 1.7. Pedipalp tan with tarsal scopula; spine-like setae on prolateral and retrolateral tibia and tarsus, and ventral tarsus distally. Female genitalia (Fig. 121) with pair of simple, outwardly curved sac-like spermathecae, each composed of internal, sclerotised glandular chamber and membranous outer wall.

Distribution

This species is known only from south-western Western Australia in the southern Goldfields, south-west of Lake Barlee (Fig. 131).

Natural history and remarks

Idiosoma galeosomoides is a remarkable and instantly recognisable spider from arid south-western Australia, and while currently known only from female specimens, we have chosen to describe it here based on its morphological distinctiveness and the availability of molecular data from the type series (Rix *et al*. 2017*a*). Like African *Galeosoma*, it possesses a phragmotic abdominal morphology (Figs 117, 118, 124–127) formed by the sclerotised reinforcement of the posterior abdominal cuticle into a circular plug-like structure. This spider builds a thick, plug-like door without adornment (Figs 129, 130). A similar undescribed species is also known from the Avon Wheatbelt near Noongar.

Etymology

The specific epithet refers to the superficial resemblance of this species to members of the African idiopid genus *Galeosoma* Purcell, 1903.

Idiosoma manstridgei (Pocock, 1897), comb. nov.

(Figs 132–145)

Anidiops manstridgei Pocock, 1897: 114.

Material examined

Holotype. Australia: Western Australia: ♀, Lawlers (BMNH; examined [BYM]).

Reference material examined. **Australia:** Western Australia: 1 ♂, Albion Downs, 79.0 km NNW. of Leinster (IBRA_MUR), 27°14′42″S, 120°29′11″E, dry pitfall trap, 28.viii.–3.ix.2008, Z. Hamilton, R. Teale (WAM T96447[DNA_Voucher_266]).

Other material examined. **Australia:** Western Australia: 1 ♂, Albion Downs, 52.4 km NNW. of Leinster (WAM T96347[DNA_Voucher_268]); 1 ♂, same data (WAM T96339); 1 ♂, same data (WAM T96330); 1 ♂, same data (WAM T96344); 1 ♂, same data (WAM T96337); 1 ♂, same data except 75.0 km NNW. of Leinster (WAM T96333[DNA_Voucher_267]); 1 ♂, same data (WAM T96360); 1 ♂, same data (WAM T96332); 1 ♂, same data (WAM T96334); 1 ♂, same data except 55.7 km NNW. of Leinster (WAM T96434); 1 ♂, same data (WAM T96433); 1 ♂, same data (WAM T96435); 1 ♂, same data except 84.1 km NNW. of Leinster (WAM T96443); 1 ♂, same data except 70.0 km NNW. of Leinster (WAM T96345); 2 ♂, same data except 84.9 km NNW. of Leinster (WAM T96449); 1 ♂, same data except 60.4 km NNW. of Leinster (WAM T96338); 1 ♂, same data except 79.2 km NNW. of Leinster (WAM T96446); 1 ♂, same data except 70.1 km NNW. of Leinster (WAM T96331); 1 ♂, same data except 66.2 km NNW. of Leinster (WAM T96448); 1 ♂, Lorna Glen Station (WAM T90769); 1 ♂, same data (WAM T76092); 5 ♂, same data (WAM T76093); 1 ♂, Cyclone, ~200 km N. of Forrest (WAM T136234); 1 ♂, Glenorn Homestead (WAM T26868); 1 ♂, Kanandah Homestead (WAM T26882); 1 ♂, Queen Victoria Spring (WAM T20645); 1 ♂, same data (WAM T44216); 1 ♂, same data (WAM T27052); 12 ♂, Lake Way Station, Honeymoon Well (WAM T80599); 3 ♂, same data (WAM T80591); 8 ♂, same data (WAM T80596); 1 ♂, same data (WAM T80600); 1 ♂, same data (WAM T80601); 1 ♂, same data (WAM T80602); 1 ♂, same data (WAM T80595); 2 ♂, same data (WAM T80605); 1 ♂, same data (WAM T80594); 1 ♂, same data (WAM T80604); 3 ♂, same data (WAM T80597); 2 ♂, same data (WAM T80598); 3 ♂, same data (WAM T80593); 1 ♂, same data (WAM T80603).

Diagnosis

Idiosoma manstridgei can be distinguished from all other described congeners by the absence of sclerotised sigilla on the dorsal abdomen (Fig. 133). However, similar undescribed congeners in the *Anidiops manstridgei*-group (see 'Remarks', below; Figs 85, 86, 88, 94, 102) are known from other areas, and males of this species can be distinguished from these taxa by the dark colour of the dorsal abdomen, which is characteristically uniform slate-grey with faint lighter banding posteriorly (Fig. 133; cf. Fig. 86), by the absence of a pronounced mound adjacent to the RTA (Figs 142, 143; cf. Fig. 94), and by the shape and proportions of the eye group (Fig. 135).

Description

Male (*WAM T96447*) (*Figs 132–144*)

Total length 16.0. Carapace 7.6 long, 6.0 wide. Abdomen 6.4 long, 4.4 wide. Carapace dark tan, darkest anteriorly, with black ocular region (Fig. 132); fovea slightly procurved (Fig. 132). Dorsal pars cephalica with three porrect post-ocular setae in straight median arrangement (Fig. 132); lateral margins of carapace with uniformly spaced fringe of porrect black setae (Fig. 132). Eye group (Fig. 135) trapezoidal, PLE–PLE/ALE–ALE ratio 1.8; 0.7× as long as wide; ALE separated by less than half their own diameter; AME separated by 0.8× their own diameter; PME separated by 5.6× their own diameter; PME and PLE separated by slightly less than diameter of AME, PME positioned slightly posterior to level of PLE. Maxillae and labium without cuspules. Abdomen oval, dark slate-grey in dorsal view (Fig. 133), with faint tan mottling and lighter tan sigilla spots, the latter forming paired bands posteriorly. Dorsal surface of abdomen covered with stiff, porrect black setae, each with slightly raised, dark brown sclerotic base; sclerotised sigilla absent. Legs variable shades of tan, with scopulae on tarsi I–II; tibia I (Figs 139–141) stout, about twice width of metatarsus I in lateral view, bearing large prolateral clasping spurs; tarsus I (Fig. 139) slightly attenuate proximally. Leg I: femur 7.0; patella 3.5; tibia 4.6; metatarsus 5.9; tarsus 3.1; total 24.1. Leg I femur–tarsus/carapace length ratio 3.2. Pedipalpal tibia 2.6× longer than wide, bowed prolaterally, with porrect digitiform process on retroventral margin distal to RTA (Figs 142, 143); RTA short, rounded, burr-like, with field of spinules directed retroventrally (Figs 143, 144); tibia otherwise without spinules. Cymbium densely setose but without field of spinules (Fig. 142). Embolus over twice length of bulb (Fig. 143), gradually tapering distally but with slightly broader tip and small, triangular embolic apophysis sub-distally (Fig. 143).

Distribution

Widespread in arid inland Western Australia, from the central Murchison north to the southern Gascoyne and east to the Great Victoria Desert and Nullarbor Plain (Fig. 145).

Remarks

Anidiops manstridgei has long posed a problem at the generic level, and as the type species of the genus *Anidiops* its identity is of central importance. Unfortunately, the holotype specimen is a female from Lawlers, in the remote Western Australian Murchison bioregion (Fig. 145). Rather than designating a neotype, we have addressed this issue by using available

evidence to deduce the likely identification of the holotype. This was done by first determining the *Anidiops manstridgei*-group lineage in Rix *et al*. (2017*a*; Fig. 1), using two female specimens that closely matched the somatic morphology of the holotype (the latter extremely distinctive due its lack of abdominal sigilla and presence of a strongly trapezoidal eye group with bulging, anteriorly directed AME; see Main 1985*b*: fig. 20; Fig. 135). We then isolated other sequenced males belonging to this molecular clade, and assessed male morphologies characteristic of the lineage. Finally, male *Idiosoma* specimens from across Australia were examined to determine the distribution of the lineage and, in doing so, a single dominant species was recorded from the central Murchison bioregion. This species, represented by sequenced males, belongs to the *Anidiops manstridgei*-group molecular clade, shares the important diagnostic morphological characters of that clade, and is found near Lawlers, at Albion Downs in the central Murchison (Fig. 145). We therefore consider this species to be conspecific with the holotype female described by Pocock (1897), and in the interests of stability we here base our concept of this species on a reference male from Albion Downs (see 'Reference material examined', above).

Main (1985*b*) recognised the close similarity in male pedipalp morphology between her concept of *An. manstridgei* and species of *Aganippe* (= *Idiosoma*), but erroneously considered the absence of dorsal sigilla in the former to be of generic significance. Based on thorough molecular sampling, it is now clear that the degree of sclerotisation of the dorsal sigilla varies enormously among *Idiosoma*, from asigillate species in the *An. manstridgei*-group (Figs 86, 102, 133) to strongly sigillate taxa (Figs 84, 97, 98, 101, 118). As a result, we hereby transfer *An. manstridgei* to *Idiosoma* (and thus synonymise *Anidiops* with the genus *Idiosoma*).

Idiosoma montanum (Faulder, 1985), comb. nov.

(Fig. 90)

Aganippe montanus Faulder, 1985: 85, figs 5a–c, 6a–c, 7a–c, 8a, b.

Material examined

Holotype. Australia: New South Wales: ♂, Young (AMS KS5055; examined [MGR]).

Remarks

Idiosoma montanum is a medium-sized species from the Western Slopes region of central eastern New South Wales.

Idiosoma nigrum Main, 1952

(Figs 106, 108)

Idiosoma nigrum Main, 1952: 133, pl. 1, figs 2–5, fig. 2C.

Material examined

Holotype. Australia: Western Australia: ♀, Wongan Hills (WAM T3960; examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, North Bungulla, Lind Road (WAM T139514); 1 ♂, Walk Walkin, via Koorda (WAM T3301); 1 ♀, Minnivale Nature Reserve (WAM T132737^{DNA_Voucher_62}).

Remarks

Idiosoma nigrum, the 'shield-backed trapdoor spider' (Fig. 108), is a distinctive and well-known species that is currently listed as threatened under both the Western Australian *Wildlife Conservation Act 1950* and the Commonwealth *Environmental Protection and Biodiversity Conservation Act* – the only idiopid in Australia to be afforded such a high level of legislative protection. As a result, its identification and distribution are of crucial importance, and the subject of detailed ongoing research (M. G. Rix, unpubl. data). This spider builds a well-camouflaged burrow with a thin lid and a 'moustache' of twig-lines around the entrance (Fig. 106), and like *I. sigillatum*, it has a strongly developed phragmotic abdominal morphology for defensive burrow plugging (Fig. 108). The core range of the species is the western and central Wheatbelt of south-western Western Australia.

Idiosoma smeatoni (Hogg, 1902), comb. nov.

Aganippe smeatoni Hogg, 1902: 126, fig. 23, pl. 13, fig. 7.

Material examined

Syntypes. **Australia:** South Australia: 3 ♂, Blakiston (SAM NN459–461; examined [MGR, BYM]).

Select material examined. **Australia:** South Australia: 1 ♀, Adelaide Botanical Gardens (SAM^{DNA_Voucher_31}).

Remarks

Idiosoma smeatoni is one of the most abundant species of *Idiosoma* in the Adelaide metropolitan region. However, its identity requires some clarification, as molecular data show that there is a *smeatoni*-like complex in south-eastern South Australia, likely composed of at least three species. They are all dark spiders that build unadorned wafer-like burrow doors typical of *Idiosoma*.

Idiosoma subtriste (O. P.-Cambridge, 1877), comb. nov.

Aganippe subtrisis O. P.-Cambridge, 1877: 28, pl. 6, fig. 3.

Aganippe pulleinei Hogg, 1902: 128, fig. 24, pl. 13, figs 3–4 (synonymised by Main, 1957: 428).

Idiommata schomburgki Karsch, 1878: 820 (synonymised by Main, 1985*b*: 12).

Material examined

Holotype (of *Ag. subtristis*). Australia: South Australia: ♀, Adelaide (BMNH; examined [BYM]).

Syntypes (of *Ag. pulleinei*). **Australia:** South Australia: 1 ♂ lectotype, Blakiston (BMNH; examined [BYM]); 2 ♂ paralectotypes (presumed), Blakiston and Hallet (*sic* 'Hallets') Cove (SAM NN159; examined [MGR, BYM]).

Holotype (of *Idiom. schomburgki*). Australia: South Australia: ♂, Adelaide (ZMB; examined [RJR]).

Select material examined. **Australia:** South Australia: 1 ♂, Morphett Vale (SAM^{DNA_Voucher_102}); 1 ♀, North Plympton (SAM^{DNA_Voucher_45}).

Remarks

Idiosoma subtriste, the type species of the genus *Aganippe*, is the most abundant *Idiosoma* in the Adelaide metropolitan region. Although the holotype specimen is a female, a neotype

seems unnecessary for nomenclatural stability, given the type locality (Adelaide) and thus the confidence that can be placed in its identification. However, like the sympatric *I. smeatoni*, its identity at broader geographic scales requires further analysis, as molecular data show that there is a *subtriste*-like complex distributed throughout south-eastern South Australia. Males of this group have a distinctive yellowish-brown carapace and legs and a relatively broad eye group, and the spiders build unadorned wafer-like burrow doors typical of *Idiosoma*, sometimes in suburban habitats.

Idiosoma winsori (Faulder, 1985), comb. nov.

(Fig. 100)

Aganippe winsori Faulder, 1985: 89, fig. 9A–C.

Material examined

Holotype. Australia: Victoria: ♂, Grampians National Park, near Reed [*sic* 'Reid's'] Lookout track (AMS KS5894; examined [MGR]).

Select material examined. **Australia:** Victoria: 1 ♀, Grampians National Park, Reed Lookout Road (WAM T131983^{DNA_Voucher_54}).

Remarks

Idiosoma winsori is a large dark brown spider from Victoria (Fig. 100), similar and closely related to *I. smeatoni* from South Australia. It builds an unadorned wafer-like burrow door, and is common in the Grampians National Park.

Genus ***Bungulla*** Rix, Main, Raven & Harvey, gen. nov.

(Figs 1, 146–175)

http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:8D97916B-6E04-45C2-918E-9ECC8DB5AE5F

Type species: Bungulla bertmaini Rix, Main, Raven & Harvey, sp. nov.

Diagnosis

Species of *Bungulla* can be distinguished from all other Arbanitinae by the absence of an RTA on the male pedipalp (Figs 156–159, 172, 173).

Males, females and juveniles of this genus can also be identified (on the basis of six molecular exemplar specimens; see Fig. 162) by the following seven nuclear nucleotide substitutions: *MRPL45* C(658; rarely homoplastic in *Euoplos*); *XPNPEP3* A(246), C(382; rarely homoplastic in *Idiosoma*), T (484); *HAT1* C(387; rarely homoplastic in *Blakistonia*); and *28S* A(644), G(1405).

Description

Small to medium-sized idiopid spiders, pale tan to dark chocolate-brown in colour (Figs 146–149, 163, 164). Carapace narrowly or broadly oval (Figs 146, 148, 163); fovea straight or procurved, rarely everted (similar to Main, 1957: fig. 6). Eye group trapezoidal, anterior eye row strongly procurved (Figs 150–153, 166). Chelicerae with rastellum; maxillae usually with cuspules in males and females (Fig. 167); labial cuspules absent. Abdomen oval, dorsal surface covered with stiff, porrect black setae in males (Figs 147, 149, 164); sclerotised sigilla absent. Legs of both sexes with scopulae on tarsi I–II and also on metatarsi I–II of females. Male tibia I without prolateral clasping spurs or paired macrosetae (Figs 154, 155, 171). Male pedipalp without RTA; cymbium usually with field of strong spinules dorsally (Figs 156–159, 172–174). Female genitalia with pair of simple, sac-like spermathecae, each cylindrical, spherical or laterally expanded distally.

Distribution

Western Australia, from the south-western forests and Wheatbelt, north to the Pilbara (Fig. 162).

Composition

Bungulla includes two described species (Table 1). Numerous undescribed species are also known from collections (M. G. Rix and M. S. Harvey, unpubl. data).

Remarks

Bungulla is an unambiguously monophyletic assemblage of numerous species, strongly supported by both molecular and morphological characters. Most are relatively small trapdoor spiders, although larger (and darker) species are known from some areas (Figs 146, 147). While seemingly common and diverse throughout much of arid and semiarid Western Australia, little is known of their biology or burrow-building behaviour (Figs 160, 161), due largely to the requirement of males for morphological identification. *Bungulla* appears to be the sister-lineage to all other Aganippini (Fig. 1), although this relationship is weakly supported. Females are similar in general appearance to species of *Eucyrtops*.

Etymology

The generic name is a noun in apposition, taken from North Bungulla Nature Reserve (via Tammin) in the Western Australian central Wheatbelt. North Bungulla is the site of the longest-running demographic study of a mygalomorph spider, conducted from 1973 to 2015 (see Main 1978, 1987). The gender is feminine.

Bungulla bertmaini Rix, Main, Raven & Harvey, sp. nov.

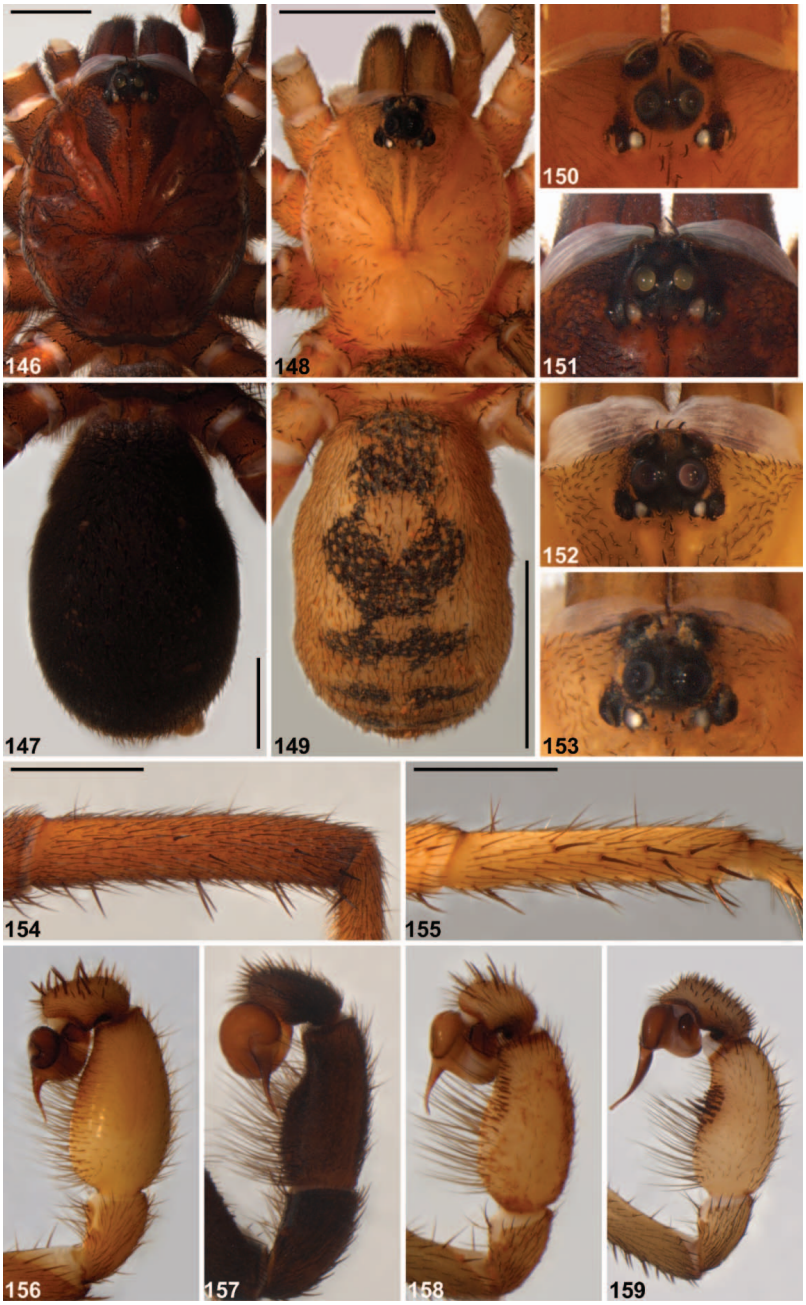
(Figs 152, 159, 163–175)

http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:DF2F280B-340F-41C8-AF8C-740A2DDF3B92

Material examined

Holotype. Australia: Western Australia: ♂, Deception [Hill], 102.5 km N. of Koolyanobbing (IBRA_COO), 29°55′10″S, 119°15′26″E, leaf litter, 1.vii.2010, Z. Hamilton, J. Cairnes (WAM T103988^{DNA_Voucher_93}).

Other material examined. **Australia:** Western Australia: 1 ♂, Mt Ida, 100 km WSW. of Leonora, site MI–08–8C (IBRA_MUR), 29°12′59″S, 120°26′10″E, active search, 29.vii.2008, M. Quinn, G. Murray (WAM T110235^{DNA_Voucher_202}); 1 ♂, Mt Gibson iron-ore mine, Banded Ironstone Range, Extension Hill east facing (IBRA_AVW), 29°34′27″S, 117°09′39″E, wet pitfall traps, 31.v.– 11.vi.2005, S. Thompson (WAM



Figs 146–159. Morphology of *Bungulla* Rix, Main, Raven & Harvey, gen. nov. *146–149*, Male carapace and abdomen, dorsal view: *146*, *147*, *Bun.* sp. from Torndirrup National Park, Western Australia (WAM T139595); *148*, *149*, *Bun.* sp. from Albion Downs, Western Australia (WAM T96268). *150–153*, Eyes, dorsal view: *150*, male *Bun. riparia* (Main, 1957) (WAM T139594); *151*, male *Bun.* sp. from Torndirrup National Park, Western Australia (WAM T139595); *152*, male *Bun. bertmaini* Rix, Main, Raven & Harvey, holotype male; *153*, male *Bun.* sp. from Albion Downs, Western Australia (WAM T96268). *154*, *155*, Male leg I tibia, prolateral view: *154*, *Bun.* sp. from Torndirrup National Park, Western Australia (WAM T139595); *155*, *Bun. riparia* (WAM T139594). *156–159*, Male pedipalp, retrolateral view: *156*, *Bun. riparia* (WAM T139594); *157*, *Bun.* sp. from Torndirrup National Park, Western Australia (WAM T139595); *158*, *Bun.* sp. from Albion Downs, Western Australia (WAM T96268); *159*, *Bun. bertmaini* Rix, Main, Raven & Harvey (holotype). Scale bars = 2.0 mm.

Figs 160, 161. Burrow of *Bungulla* Rix, Main, Raven & Harvey, gen. nov. *160*, *161*, *Bun.* sp. from John Forrest National Park, Western Australia, with an Australian two-dollar coin (diameter 20 mm) for scale in (*161*). Images by M. Rix.

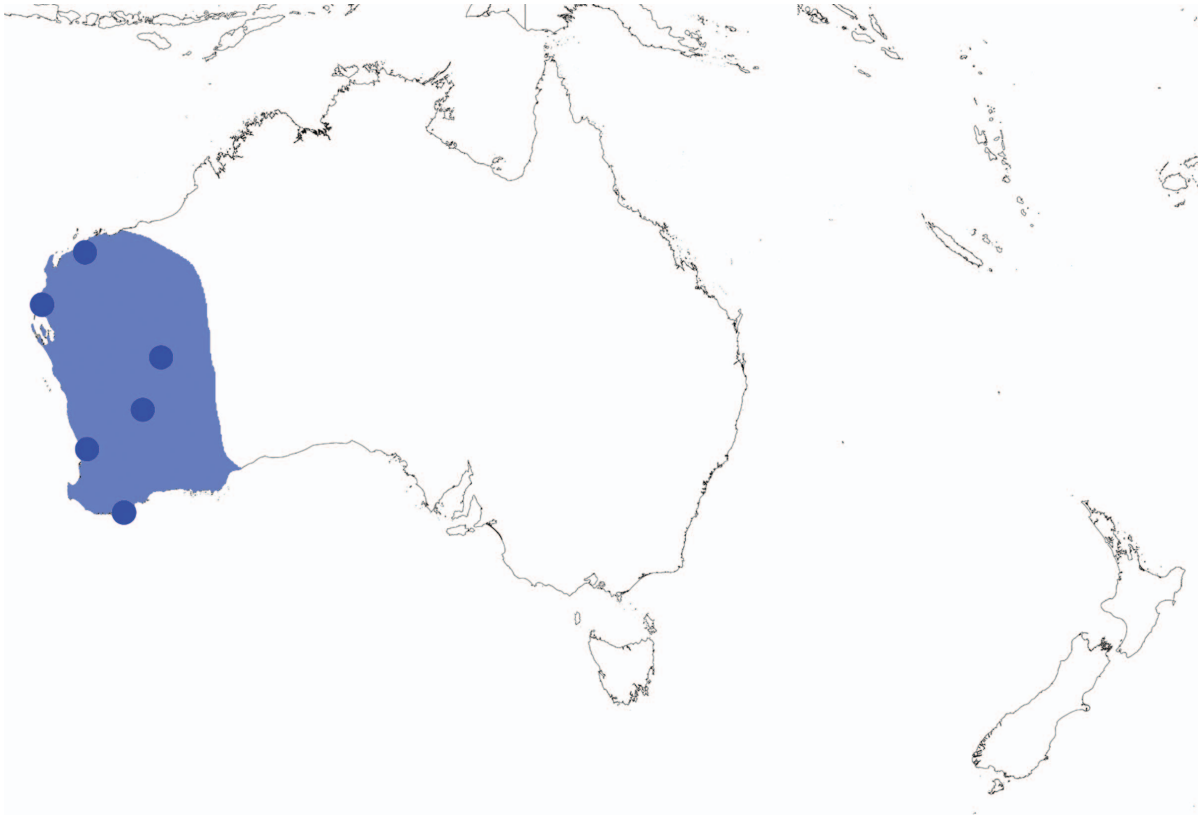
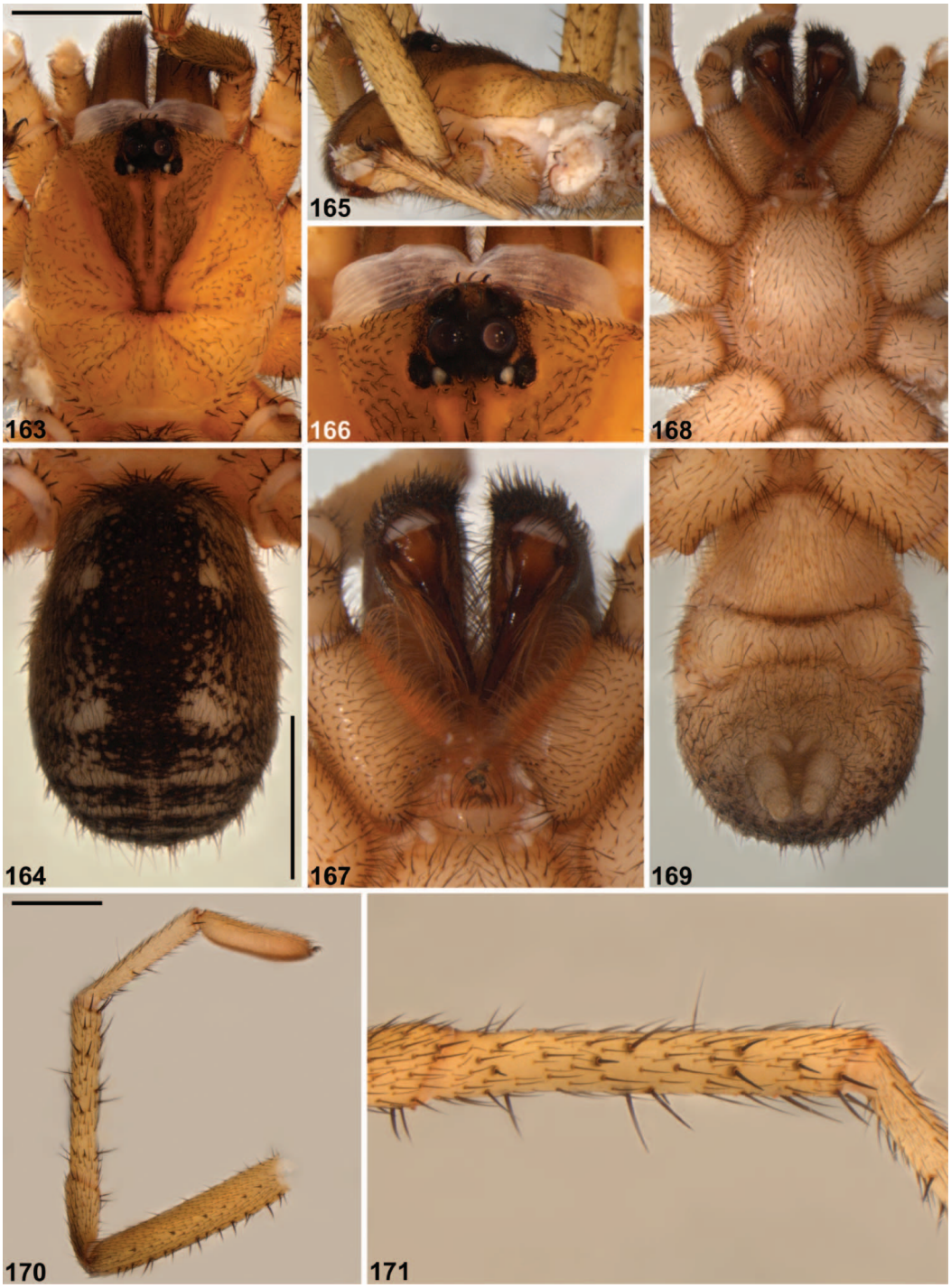


Fig. 162. Map showing the approximate extent of occurrence of the genus *Bungulla* Rix, Main, Raven & Harvey, gen. nov. in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al.* (2017*a*). Note the absence of this genus from central and eastern Australia.



Figs 163–171. *Bungulla bertmaini* Rix, Main, Raven & Harvey, sp. nov., male holotype (WAM T103988), somatic morphology. *163*, *164*, Carapace and abdomen, dorsal view; *165*, cephalothorax, lateral view; *166*, eyes, dorsal view; *167*, mouthparts, ventral view; *168*, *169*, sternum and abdomen, ventral view; *170*, leg I, prolateral view; *171*, leg I tibia, prolateral view. Scale bars = 2.0 mm.

Figs 172–174. *Bungulla bertmaini* Rix, Main, Raven & Harvey, sp. nov., male holotype (WAM T103988), pedipalp. *172*, Retrolateral view; *173*, retroventral view; *174*, prolateral view. Scale bar = 2.0 mm.

Fig. 175. Map showing collection records of *Bungulla bertmaini* Rix, Main, Raven & Harvey, sp. nov. in Western Australia, along with Interim Biogeographic Regionalisation of Australia (IBRA, Version 7.0) boundaries and select bioregion acronyms. Blue dots denote sequenced specimens. AVW, Avon Wheatbelt; COO, Coolgardie; MUR, Murchison; YAL, Yalgoo.

T72327); 1 ♂, same data except Ironstone Slope, Extension Hill west facing, 29°34′38″S, 117°09′35″E (WAM T72326); 1 ♂, same data except sandplains 4 (D), control site (N. of road), 29°34′34″S, 117°07′34″E, 30.v.–11.vi.2005 (WAM T71637); 1 ♂, same data except sandplains 1 (A), impact site (S. of road), 29°34′33″S, 117°06′35″E (WAM T71636).

Diagnosis

Bungulla bertmaini can be distinguished from the only other described species of *Bungulla*, *Bun. riparia* (Main, 1957), by the presence of a dense field of spinules on the retrolateral palpal tibia (Figs 172, 173). However, similar undescribed congeners are known from other areas, and this species can be distinguished from these taxa by the colour of the dorsal abdomen, which is darkly speckled with lighter sigilla spots and posterior banding (Fig. 164), by the distribution and arrangement of spinules on the palpal tibia (Figs 172, 173), by the uniform field of short spinules on the dorsal cymbium (Figs 172–174), by the shape of the distal embolus (Figs 172–174), and by the shape and proportions of the eye group (Fig. 166).

Description

Male holotype (*Figs 163–174*)

Total length 10.6. Carapace 4.6 long, 4.1 wide. Abdomen 4.5 long, 3.1 wide. Carapace tan with black ocular region, contrasting short dark setae and darker grey-brown patterning on pars cephalica (Fig. 163); fovea slightly procurved (Fig. 163). Dorsal pars cephalica with eight porrect post-ocular setae, in staggered median arrangement (Fig. 163); postero-lateral margins of carapace above coxa IV with short fringe of 3–5 porrect black setae (Fig. 163). Eye group (Fig. 166) trapezoidal, PLE–PLE/ALE–ALE ratio 1.5; 0.8× as long as wide; ALE separated by slightly more than their own diameter; AME separated by 0.9× their own diameter; PME separated by 3.8× their own diameter; PME and PLE separated by slightly less than half diameter of AME, PME positioned marginally anterior to level of PLE. Maxillae with field of cuspules confined to inner corner (Fig. 167); labium without cuspules. Abdomen oval, dark brown-black in dorsal view (Fig. 164), lighter dorso-laterally, with beige-grey mottling and prominent beige-grey sigilla spots, the latter forming paired bands posteriorly. Dorsal surface of abdomen covered with stiff, porrect black setae, each with slightly raised, dark brown sclerotic base; sclerotised sigilla absent. Legs variable shades of tan, with scopulae on tarsi I–II; tibia I (Figs 170, 171) unmodified, without clasping spurs. Leg I: femur 4.9; patella 2.3; tibia 3.9; metatarsus 3.4; tarsus 2.5; total 16.9. Leg I femur–tarsus/carapace length ratio 3.7. Pedipalpal tibia 2.0× longer than wide; RTA absent (Figs 172, 173); tibia with compact field of spinules retroventrally, with single long spinule medio-ventrally, two slightly shorter adjacent spinules, and oval field of successively shorter spinules (Figs 172, 173). Cymbium sparsely setose, with field of stout, uniformly distributed spinules on dorsal surface (Figs 172–174). Embolus twice length of bulb (Fig. 174), gradually tapering distally, but with broader flanged tip (Fig. 174); embolic apophysis absent.

Distribution

Known only from northern inland south-western Australia, from Mount Gibson east to the southern Murchison bioregion (Fig. 175).

Natural history and remarks

Little is known of the biology of *Bungulla bertmaini*, and females are unknown.

Etymology

The specific epithet is a patronym in honour of the late Albert (Bert) Russel Main (1919–2009), in recognition of his extraordinary contributions to zoology and conservation biology.

Bungulla riparia (Main, 1957), comb. nov.

(Figs 150, 155, 156)

Eucyrtops riparia Main, 1957: 419, figs 3A, 4D–F, 7B, 8A (NB. figs 5D, 8D–E probably not conspecific).

Material examined

Holotype. Australia: Western Australia: ♀, S. of Mount Misery, W. of Moora (WAM T3961; examined [BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, Mount Misery, W. of Moora (WAM T139594).

Remarks

Bungulla riparia was the only previously described species in this genus, and occurs in the north-western Wheatbelt of southern Western Australia.

Genus ***Eucanippe*** Rix, Main, Raven & Harvey, gen. nov.

(Figs 1, 176–204)

http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:4A02B23C-0911-43D0-9F7D-C63962050738

Type species: Eucanippe bifida Rix, Main, Raven & Harvey, sp. nov.

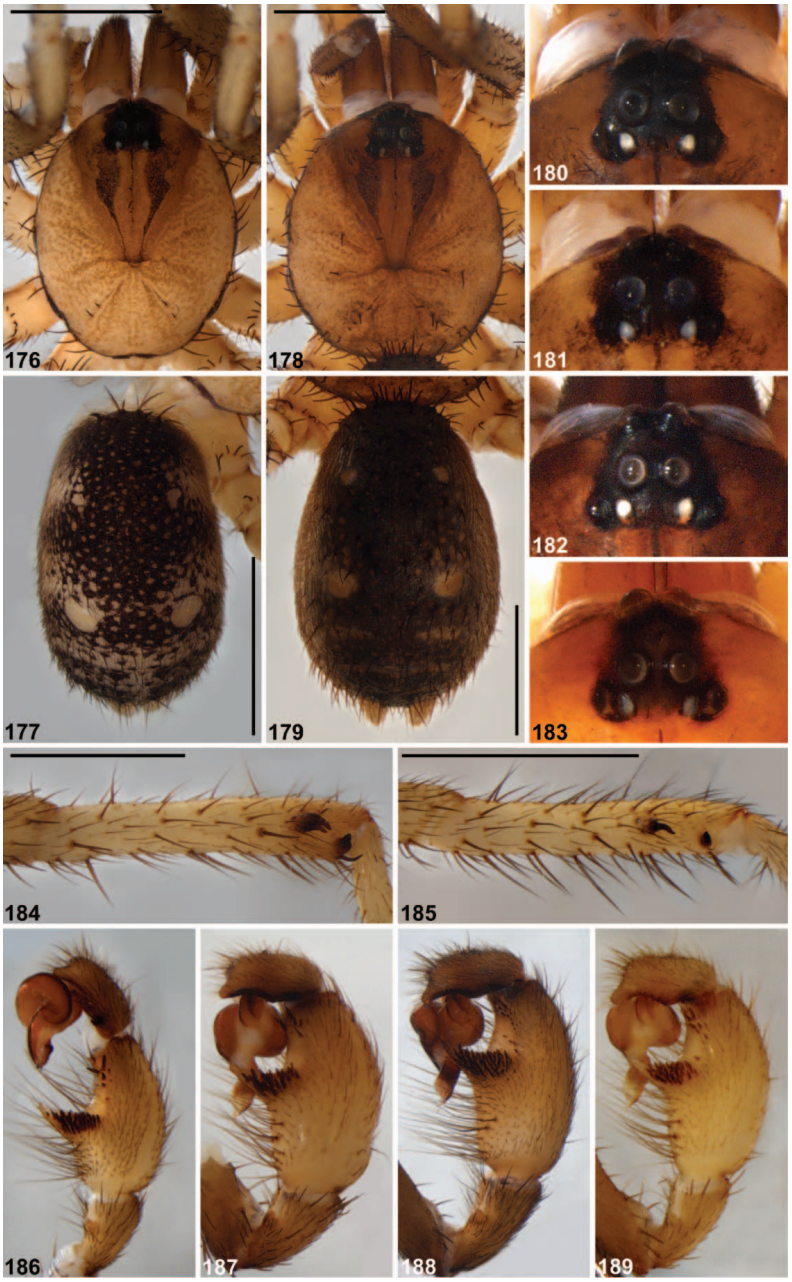
Diagnosis

Species of *Eucanippe* can be distinguished from all other Arbanitinae by the presence of a uniquely bifurcate distal embolus (Figs 186–189, 201–203).

Males, females and juveniles of this genus can also be tentatively identified (on the basis of a limited molecular taxon sample of two specimens; see Fig. 190) by the unique ‘GC’ motif at positions 123–124 of nuclear RPF2, and by the following 10 nuclear nucleotide substitutions: *MRPL45* C(726); *RPF2* A(270), C(440), G(693); *XPNPEP3* T(322), A(577); *HAT1* C(48); *ITS1* A (33); *28S* C(708), G(1399).

Description

Small idiopid spiders, variably tan to dark grey-brown in colour (Figs 176–179, 191, 192). Male carapace narrowly or broadly oval (Figs 176, 178, 191), usually with rows of short, porrect



Figs 176–189. Morphology of *Eucanippe* Rix, Main, Raven & Harvey, gen. nov. *176–179*, Male carapace and abdomen, dorsal view: *176*, *177*, *Eucan.* sp. from Mount Mason, Western Australia (WAM T110226); *178*, *179*, *Eucan.* sp. from Stirling Range National Park, Western Australia (WAM T41782). *180–183*, Eyes, dorsal view: *180*, male *Eucan. bifida* Rix, Main, Raven & Harvey, sp. nov. (holotype); *181*, *Eucan.* sp. from Mount Mason, Western Australia (WAM T110226); *182*, male *Eucan.* sp. from Wellstead, Western Australia (WAM T117264); *183*, male *Eucan.* sp. from Kojonup, Western Australia (WAM T139596). *184*, *185*, Male leg I tibia, prolateral view: *184*, *Eucan.* sp. from Stirling Range National Park, Western Australia (WAM T41782); *185*, *Eucan.* sp. from Mount Mason, Western Australia (WAM T110226). *186–189*, Male pedipalp, retrolateral view: *186*, *Eucan.* sp. from Mount Mason, Western Australia (WAM T110226); *187*, *Eucan.* sp. from Stirling Range National Park, Western Australia (WAM T41782); *188*, *Eucan.* sp. from Wellstead, Western Australia (WAM T117264); *189*, *Eucan.* sp. from Kojonup, Western Australia (WAM T139596). Scale bars = 2.0 mm.

Fig. 190. Map showing the approximate extent of occurrence of the genus *Eucanippe* Rix, Main, Raven & Harvey, gen. nov. in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al.* (2017*a*). Note the restricted distribution of this genus in south-western Australia.

spinules on furrows of posterior pars thoracica (Figs 176, 178, 191); fovea straight or slightly procurved, never everted. Male eye group trapezoidal, anterior eye row strongly procurved (Figs 180–183, 185). Male chelicerae with rastellum; maxillae usually with cuspules (Fig. 195); labial cuspules absent. Male abdomen oval, dorsal surface covered with stiff, porrect black setae in males (Figs 177, 179, 192); single pair of large sclerotised sigilla present. Legs of males with scopulae on tarsi I–II. Male tibia I with small to large prolateral clasping spurs or paired macrosetae (Figs 184, 185, 199). Male pedipalp with conical RTA, usually with aspinose distal process; cymbium with or without spinules dorsally; embolus with finely bifurcate tip (Figs 186–189, 201–203). Females unknown.

Distribution

Western Australia, mostly in the greater south-west, Goldfields and Murchison regions, south-east to Eucla (Fig. 190).

Composition

Eucanippe includes one described species (Table 1). Several other undescribed species are also known from collections (M. G. Rix and M. S. Harvey, unpubl. data).

Remarks

The presence of a distinct undescribed genus in Western Australia has long been recognised, but this lineage was never described, despite initial confusion with *Aganippe* (= *Idiosoma*) (see Main 1957: 435, fig. 13A, B). Like many *Idiosoma*, species of *Eucanippe* possess a pair of strongly sclerotised sigilla on the dorsal abdomen (Figs 177, 179, 192), and are the sister-group to that genus (Fig. 1). However, unlike *Idiosoma*, very little is known of their biology: their burrows are unknown, and identifiable females have never been found.

Etymology

The generic name is an arbitrary combination of letters based on a contraction of '*Eucyrtops*' and '*Aganippe*'. The gender is feminine.

Eucanippe bifida Rix, Main, Raven & Harvey, sp. nov.

(Figs 180, 191–204)

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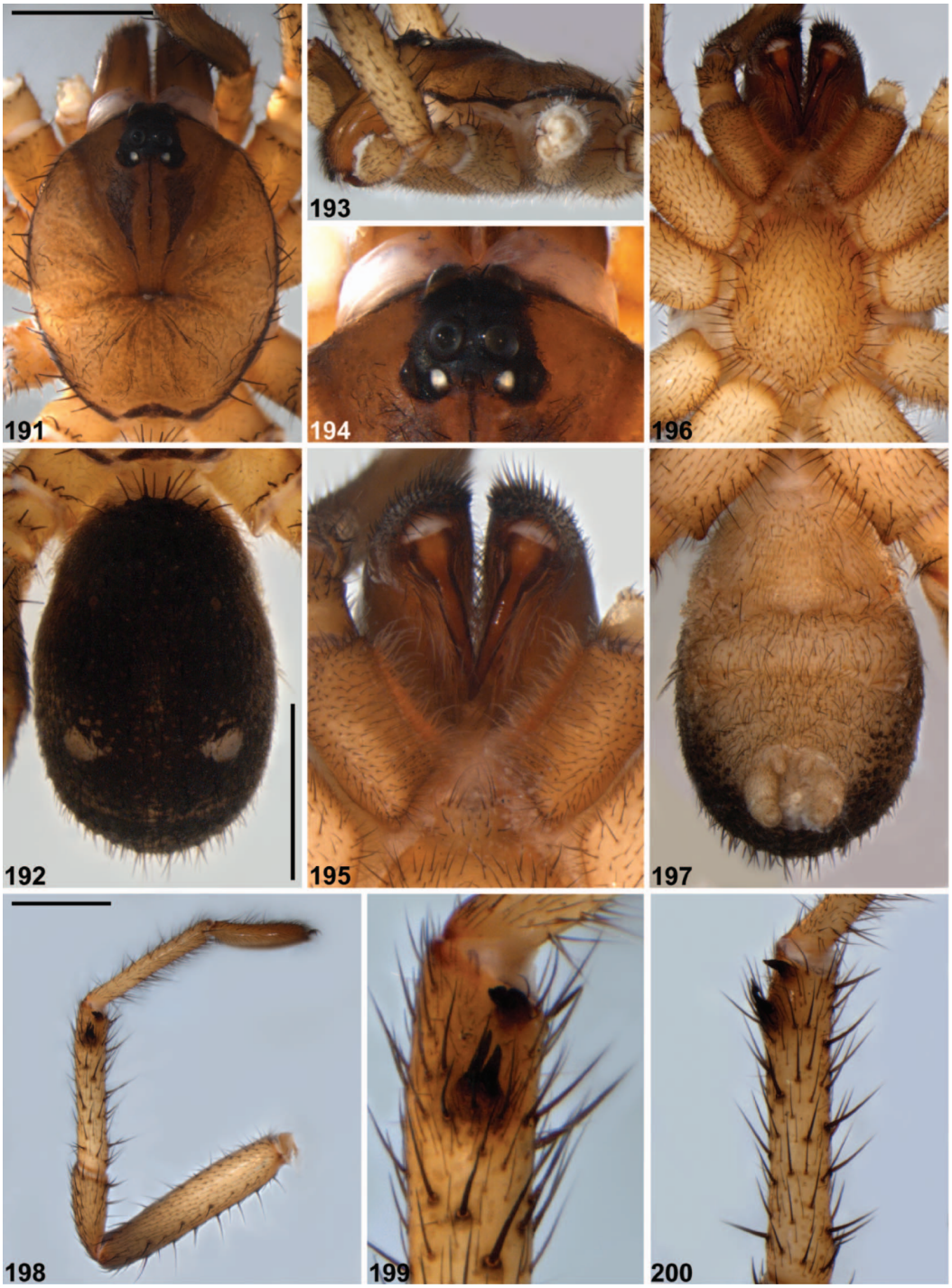


Figs 191–200. *Eucanippe bifida* Rix, Main, Raven & Harvey, sp. nov., male holotype (WAM T72649), somatic morphology. *191*, *192*, Carapace and abdomen, dorsal view; *193*, cephalothorax, lateral view; *194*, eyes, dorsal view; *195*, mouthparts, ventral view; *196*, *197*, sternum and abdomen, ventral view; *198*, leg I, prolateral view; *199*, leg I tibia, clasping spurs, prolateral view; *200*, leg I tibia, proventral view. Scale bars = 2.0 mm.

Figs 201–203. *Eucanippe bifida* Rix, Main, Raven & Harvey, sp. nov., male holotype (WAM T72649), pedipalp. *201*, Retrolateral view; *202*, retroventral view; *203*, prolateral view. Scale bar = 2.0 mm.

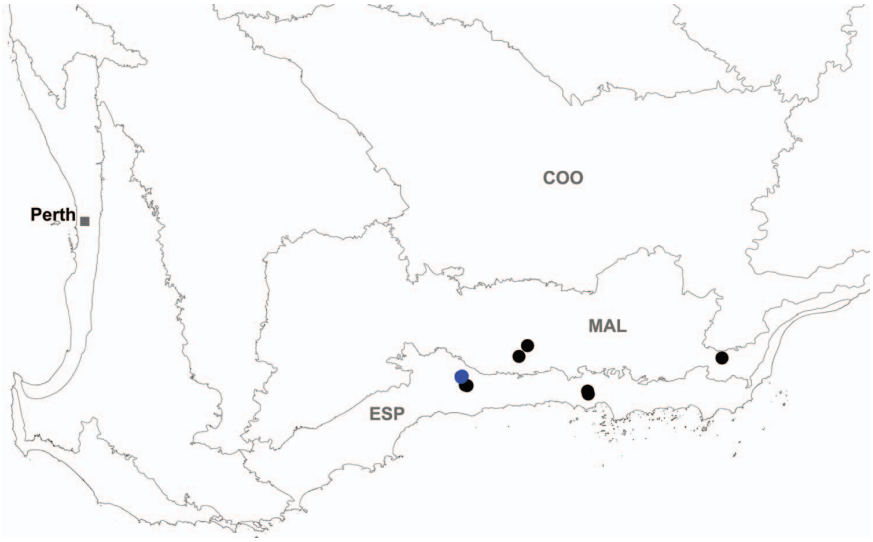


Fig. 204. Map showing collection records of *Eucanippe bifida*, sp. nov. in south-western Western Australia, along with Interim Biogeographic Regionalisation of Australia (IBRA, Version 7.0) boundaries and select bioregion acronyms. Blue dots denote sequenced specimens. COO, Coolgardie; ESP, Esperance Plains; MAL, Mallee.

Material examined

Holotype. Australia: Western Australia: ♂, 24.3 km E. of Ravensthorpe, site RNOCTS1 (IBRA_ESP), 33°34′45″S, 120°18′37″E, dry pitfall, 26.viii.2005, R. Teale, Z. Hamilton (WAM T72649[DNA_Voucher_213]).

Paratypes. **Australia:** Western Australia: 1 ♂, 25.5 km E. of Ravensthorpe, site RNOCTS3 (IBRA_ESP), 33°34′06″S, 120°19′11″E, dry pitfall, 25.viii.2005, R. Teale, Z. Hamilton (WAM T72656[DNA_Voucher_74]); 1 ♂, same data (WAM T72657); 1 ♂, same data (WAM T72655); 1 ♂, same data (WAM T72658); 1 ♂, same data (WAM T72654).

Other material examined. **Australia:** 1 ♂, Western Australia: 25.5 km E. of Ravensthorpe, site RNOCTS3 (IBRA_ESP), 33°34′06″S, 120°19′11″E, dry pitfall, 24.viii.2005, R. Teale, Z. Hamilton (WAM T72659); 1 ♂, same data except 26.viii.2005 (WAM T72653); 1 ♂, same data (WAM T72660); 1 ♂, same data except 24.4 km E. of Ravensthorpe, site RNOCTS2, 33°34′22″S, 120°18′28″E, 25.viii.2005 (WAM T72650); 1 ♂, same data (WAM T72651); 1 ♂, same data except 24.6 km E. of Ravensthorpe, site RNOCTS1, 33°34′45″S, 120°18′37″E, 26.viii.2005 (WAM T72669); 1 ♂, same data except 30.1 km SE. of Ravensthorpe, site CMS4, 33°39′30″S, 120°21′30″E, 26.viii.2005 (WAM T72671); 1 ♂, same data except ~37 km SE. of Ravensthorpe, site CMS2, 33°39′46″S, 120°22′40″E, 23–28.viii.2005 (WAM T72670); 1 ♂, Junana Rock, Cape Arid National Park, NW. of Mount Ragged, site 3 (IBRA_MAL), 33°23′S, 123°24″E, 5.iv.–23.v.1986, B. Main (WAM T139584); 1 ♂, N. of Edwards Rd, SE. of Lake King, site GP 2 (IBRA_MAL), 33°22′01″S, 120°59′43″E, wet pitfalls, 15.x.1999–1.xi.2000, P. Van Heurck, CALM Survey (WAM T139585); 1 ♂, same data (WAM T139586); 1 ♂, Shark Lake Rd, Helms Arboretum Reserve, site ES 1 (IBRA_ESP), 33°44′49″S, 121°48′55″E, wet pitfalls, 15.x.1999–1.xi.2000, P. Van Heurck, CALM Survey (WAM T139587); 1 ♂, same data (WAM T139590); 1 ♂, Lake Morgan, Helms Arboretum Reserve, site ES 3 (IBRA_ESP), 33°43′09″S, 121°48′29″E, 15.x.1999–1.xi.2000, P. Van Heurck, CALM Survey (WAM T139588); 1 ♂, N. of Rollond Rd, near junction with Neds Corner Rd, site GP 3 (IBRA_MAL), 33°15′28″S, 121°05′47″E, wet pitfalls, 15.x.1999–1.xi.2000, P. Van Heurck CALM Survey (WAM T139589).

Diagnosis

Eucanippe bifida is the only described species of *Eucanippe*, and can therefore be distinguished from all other Australian Idiopidae by the uniquely bifurcate embolus (Figs 201–203). However, similar undescribed congeners are known from other areas, and this species can be distinguished from these taxa by the conspicuous absence of an aspinose distal process on the short RTA (Figs 201–203; cf. Figs 186–189).

Description

Male holotype (*Figs 191–203*)

Total length 9.6. Carapace 4.5 long, 3.6 wide. Abdomen 4.0 long, 2.8 wide. Carapace dark mottled tan, darkest anteriorly, with black ocular region, darker grey-brown patterning on pars cephalica and black rim (Fig. 191); fovea straight (Fig. 191). Dorsal pars cephalica with five porrect post-ocular setae, in straight median arrangement (Fig. 191); lateral margins of carapace with sparse fringe of porrect black setae (Fig. 191). Eye group (Fig. 194) trapezoidal, PLE–PLE/ALE–ALE ratio 1.5; 0.9× as long as wide; ALE separated by slightly less than one-third their own diameter; AME separated by 0.7× their own diameter; PME separated by 2.9× their own diameter; PME and PLE separated by slightly less than half diameter of AME, PME positioned slightly anterior to level of PLE. Maxillae with field of cuspules confined to inner corner (Fig. 195); labium without cuspules. Abdomen oval, dark grey in dorsal view (Fig. 192), with faint tan mottling, prominent pair of beige-grey sigilla spots and faint banding posteriorly. Dorsal surface of abdomen covered with stiff, porrect black setae, each with slightly raised, dark brown sclerotic base; single pair of large sclerotised sigilla present (sigilla pair 2), separated by approximately 3× their own diameter (Fig. 192). Legs variable shades of tan, with scopulae on tarsi I–II; tibia I (Figs 198–200) bearing small prolateral clasping spurs. Leg I: femur 4.3; patella 2.0; tibia 3.3; metatarsus 3.0; tarsus 1.9; total 14.5. Leg I femur–tarsus/carapace length ratio 3.2. Pedipalpal tibia stout, 1.7× longer than wide; RTA short, conical, with dense field of retrolateral spinules extending along entire length (Figs 201, 202); tibia also with long field of spinules extending along retroventral edge, distal to base of RTA (Figs 201, 202). Cymbium setose, with only a few long spinules anteriorly (Figs 201, 202). Embolus slightly over twice length of bulb (Figs 201, 202), sharply tapering distally, with broad twisted morphology, sub-distal flange and finely bifurcate tip (Figs 201–203); embolic apophysis absent.

Distribution

Known only from southern Western Australia (Esperance Plains and southern Mallee bioregions), from the Ravensthorpe Range east to Cape Arid National Park (Fig. 204).

Natural history and remarks

Based on pitfall trap survey data, *Eucanippe bifida* may be relatively common through the Esperance Plains bioregion; however, nothing is known of its biology and females are unknown.

Etymology

The specific epithet is derived from the Latin adjective ‘bifidus’ (noun: forked; see Brown 1956), in reference to the distally bifurcate embolus on the male pedipalp.

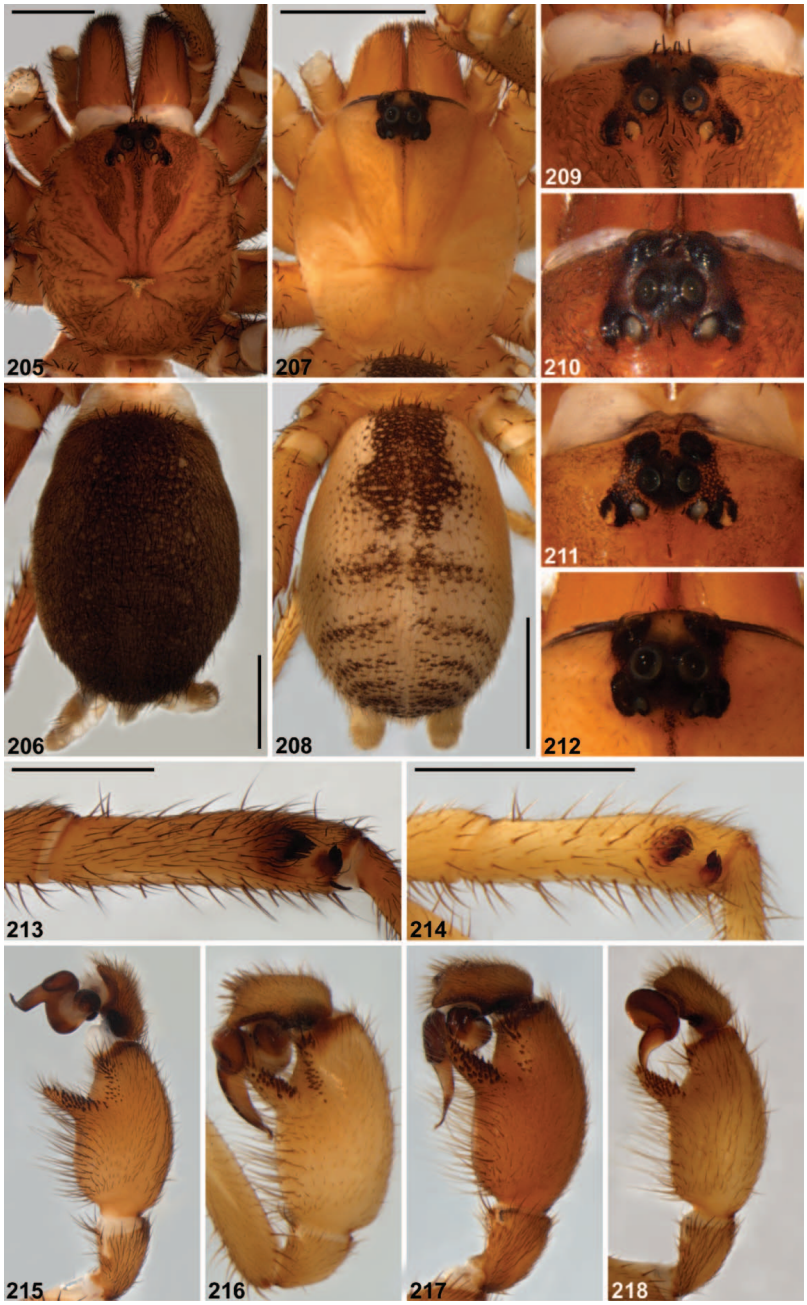
Genus ***Eucyrtops*** Pocock, 1897

(Figs 1, 205–237)

Eucyrtops Pocock, 1897: 113. Type species *Aganippe latior* O. P.-Cambridge, 1877, by original designation. Removed from synonymy of *Aganippe* O. P.-Cambridge, 1877 (*contra* Hogg, 1902: 125) by Main, 1957: 416.

Diagnosis

Species of *Eucyrtops* can be distinguished from all other Arbanitinae by the presence of a trapezoidal (rarely subquadrate) eye group with a strongly procurved anterior eye row (Figs 209–212, 227), combined with the presence of a strongly developed RTA (Figs 215–218, 234), the presence of an unmodified (i.e. non-bifurcate) distal embolus (Figs 215–218, 234), and the absence of a median retrolateral digital process and usually also a pronounced distal retrolateral tibial apophysis on the male pedipalp (Figs 215–218, 234, 235).



Figs 205–218. Morphology of *Eucyrtops* Pocock. *205–208*, Male carapace and abdomen, dorsal view: *205*, *206*, *Eucy*. sp. from north-east of Tammin, Western Australia (WAM T39963); *207*, *208*, *Eucy. eremaeus* Main, 1957 (WAM T139597). *209–212*, Eyes, dorsal view: *209*, male *Eucy*. sp. from north-east of Tammin, Western Australia (WAM T39963); *210*, male *Eucy*. sp. from Stirling Range National Park, Western Australia (WAM T139598); *211*, male *Eucy*. sp. from north of Beaufort River, Western Australia (WAM T139599); *212*, male *Eucy. eremaeus* (WAM T139597). *213*, *214*, Male leg I tibia, prolateral view: *213*, *Eucy*. sp. from north-east of Tammin, Western Australia (WAM T39963); *214*, *Eucy. eremaeus* (WAM T139597). *215–218*, Male pedipalp, retrolateral view: *215*, *Eucy*. sp. from north-east of Tammin, Western Australia (WAM T39963); *216*, *Eucy. eremaeus* (WAM T139597); *217*, *Eucy*. sp. from Stirling Range National Park, Western Australia (WAM T139598); *218*, *Eucy*. sp. from north of Beaufort River, Western Australia (WAM T139599). Scale bars = 2.0 mm.

Figs 219–222. Burrow and images of live *Eucyrtops* Pocock. *219*, *221*, *222*, Female *Eucy.* sp. from Stirling Range National Park, Western Australia; *220*, male *Eucy. latior* (O. P.-Cambridge, 1877) from Hovea, Western Australia. All images by M. Harvey except: (*220*) by V. Framenau, used with permission.

Some anomalous *Eucyrtops* have a similar subquadrate eye group to species of *Blakistonia* (e.g. *E. eremaeus* Main, 1957; Fig. 212), but can be distinguished by the presence of a more strongly attenuate base to the RTA (Fig. 216). Species of *Eucyrtops* are unusual among Aganippini in that they are most easily identified by the absence of those morphological synapomorphies characteristic of other genera.

Males, females and juveniles of this genus can also be identified (on the basis of seven molecular exemplar specimens; see Fig. 223) by the unique deletion of three amino acid residues (serine–glutamine–serine; 9 bp) at positions 88–96 of nuclear *MRPL45*, and by the following 15 nuclear nucleotide substitutions: *MRPL45* A(314), C(324), A(420; homoplastic in *Cantuaria stewarti*), T(624; homoplastic in *Cataxia bolganupensis*); *RPF2* A(132; homoplastic in *Arbanitis villosus*), C(519; homoplastic in *Cataxia pallida*); *XPNPEP3* G(153), G(383), T(496), C(504; rarely homoplastic in *Idiosoma*); *HAT1* T(183; homoplastic in *Arbanitis robertsi*), T(228), G(570); *H3* G(183; rarely homoplastic in *Idiosoma*); *28S* A or G(491).

Description

See Main (1985*b*: 14).

Distribution

Western Australia, mostly in the greater south-west, Goldfields and Murchison regions (Fig. 223).

Composition

Eucyrtops includes two described species (Table 1). Numerous undescribed species are also known from collections (M. G. Rix and M. S. Harvey, unpubl. data).

Remarks

Eucyrtops is a relatively small and geographically restricted genus endemic to the southern half of Western Australia (Fig. 223). Most species are medium-sized and dark in colour (Figs 205, 206, 219, 220), but a few strongly arid-adapted

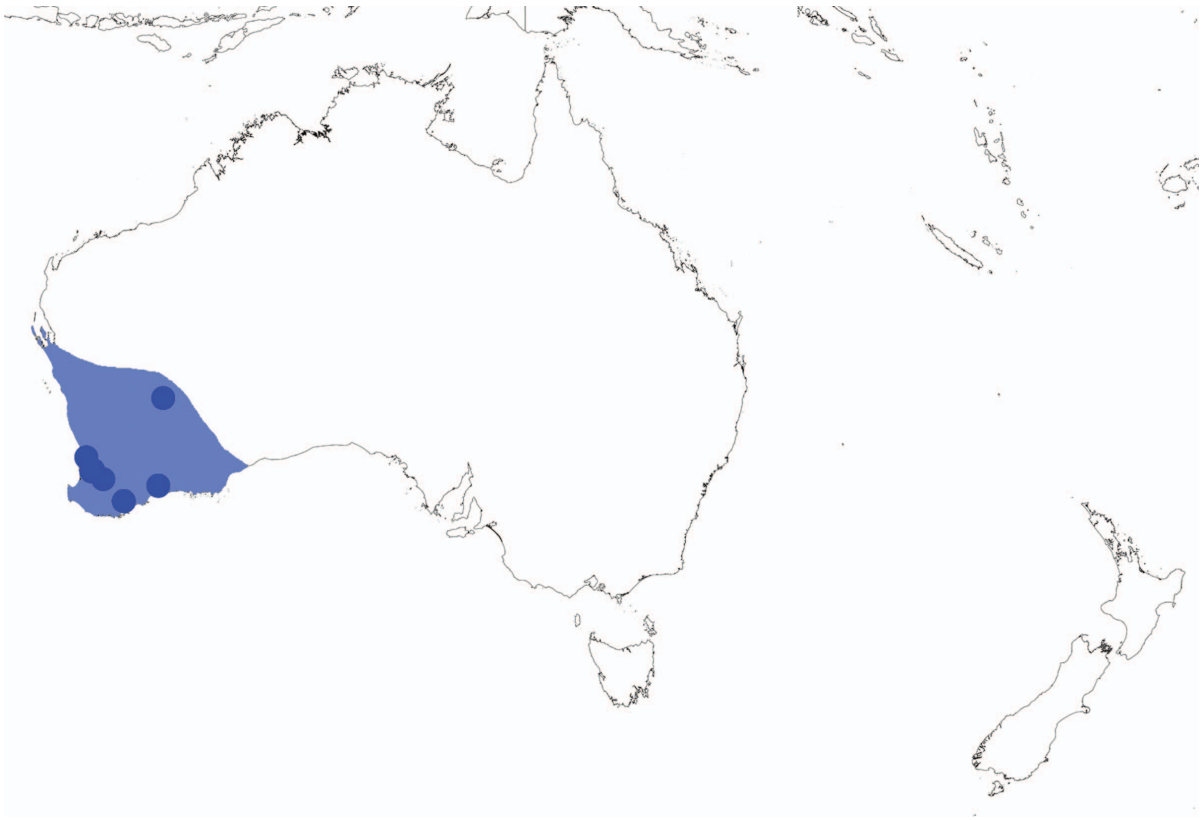


Fig. 223. Map showing the approximate extent of occurrence of the genus *Eucyrtops* Pocock in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al*. (2017*a*). Note the restricted distribution of this genus in south-western Australia.

species are smaller and paler (e.g. *Eucy. eremaeus* from the Murchison bioregion; Figs 207, 208). Most species are found in the south-western jarrah forests, Avon Wheatbelt and along the Western Australian south coast, and the genus is common in the Darling Range east of Perth. The sister-lineage to *Eucyrtops* is *Gaius* (Fig. 1), both of which possess a strongly developed RTA.

Although the genus was treated as feminine by Main (1957), Article 30 of the ICZN (ICZN 1999) rules that genus-group names ending in '-ops' are to be treated as masculine. Therefore, we alter *Eucyrtops eremaea* to *Eucy. eremaeus*.

Eucyrtops latior (O. P.-Cambridge, 1877)

(Figs 220, 224–237)

Aganippe latior O. P.-Cambridge, 1877: 29, pl. 6, fig. 4.
Eucyrtops latior (O. P.-Cambridge): Pocock, 1897: 113.
Aganippe latior O. P.-Cambridge: Rainbow & Pulleine, 1918: 92.
Eucyrtops latior (O. P.-Cambridge): Main, 1957: 416, figs 2A–B, 4A–C, 5C, 5E, 6, 7A, 24A.

Material examined

Holotype. Australia: Western Australia: ♀, 'Perth' [no specific locality] (BMNH; examined [BYM]).

Reference material examined. **Australia:** Western Australia: 1 ♂, Stoneville (IBRA_JAF), 31°52′S, 116°10′E, 31.v.2001, J. Burn (WAM T44160).

Other material examined. **Australia:** Western Australia: 1 ♂, Wungong Dam (WAM T104308^{DNA_Voucher_198}); 1 ♂, Roleystone (WAM T27113); 1 ♂, N. of Jarrahdale (WAM T31783); 1 ♂, NE. of Jarrahdale (WAM T44658).

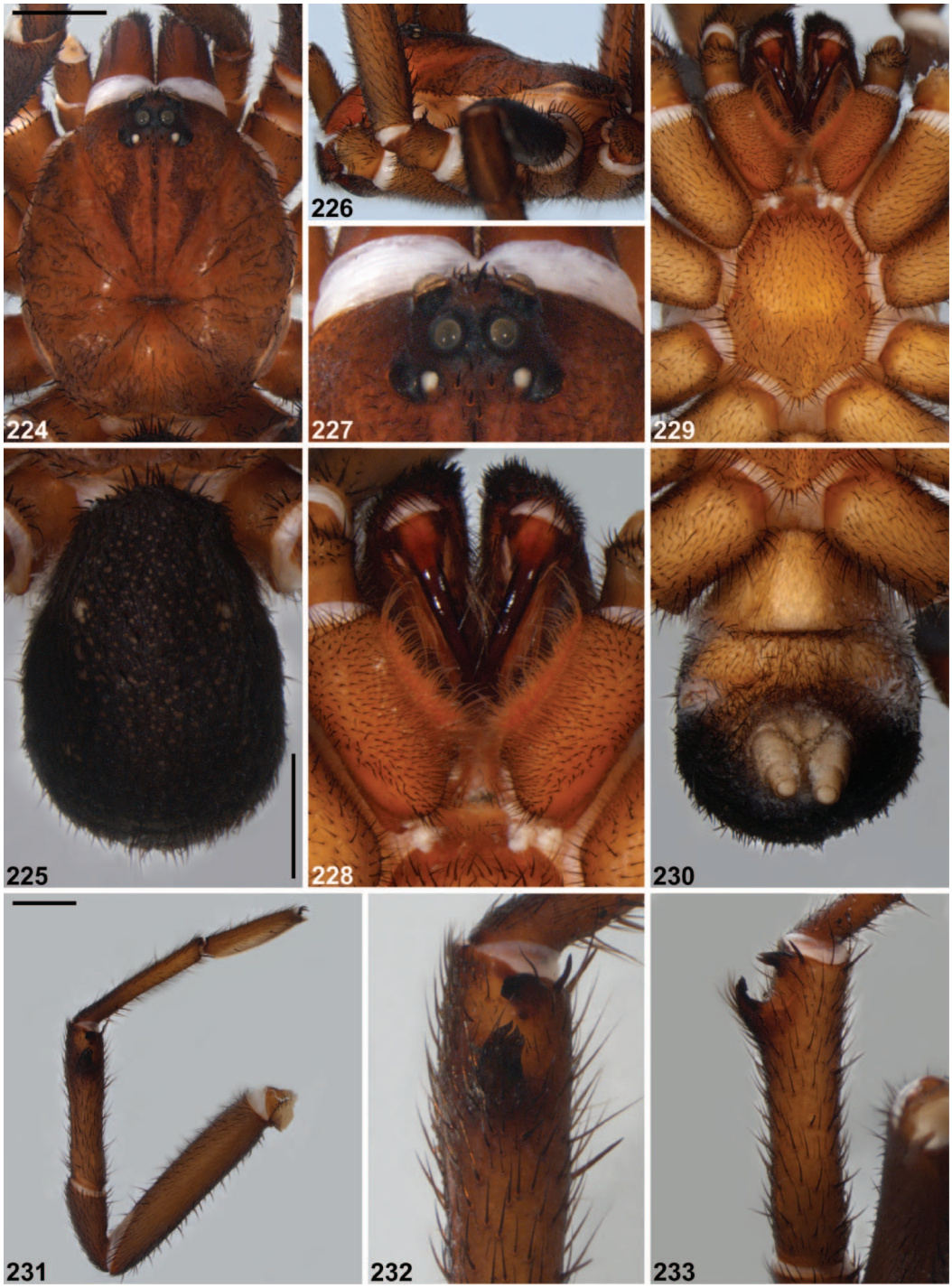
Diagnosis

Eucyrtops latior can be distinguished from the only other described species of *Eucyrtops*, *E. eremaeus* Main, 1957, by the presence of a trapezoidal eye group (Fig. 227; cf. Fig. 212) and dark body coloration (Figs 224, 225; cf. Figs 207, 208). However, similar undescribed congeners are known from other areas, and males of this species can be distinguished from these taxa by the combined presence of a relatively long, thin RTA, which is sparsely setose and provided with relatively few spinules (Fig. 234), by the relatively widely spaced ALE (Fig. 227), and by the shape and proportions of the eye group (Fig. 227).

Description

Male (WAM T44160) (Figs 224–236)

Total length 14.6. Carapace 7.0 long, 5.9 wide. Abdomen 5.9 long, 4.2 wide. Carapace dark chocolate-brown, with black ocular



Figs 224–233. *Eucyrtops latior* (O. P.-Cambridge, 1877), male (WAM T44160), somatic morphology. *224*, *225*, Carapace and abdomen, dorsal view; *226*, cephalothorax, lateral view; *227*, eyes, dorsal view; *228*, mouthparts, ventral view; *229*, *230*, sternum and abdomen, ventral view; *231*, leg I, prolateral view; *232*, leg I tibia, clasping spurs, prolateral view; *233*, leg I tibia, proventral view. Scale bars = 2.0 mm.

Figs 234–236. *Eucyrtops latior* (O. P.-Cambridge, 1877), male (WAM T44160), pedipalp. *234*, Retrolateral view; *235*, retroventral view; *236*, prolateral view. Scale bar = 2.0 mm.

Fig. 237. Map showing collection records of *Eucyrtops latior* (O. P.-Cambridge, 1877) in south-western Western Australia, along with Interim Biogeographic Regionalisation of Australia (IBRA, Version 7.0) boundaries and select bioregion acronyms. The original type locality, 'Perth', is shown in red; blue dots denote sequenced specimens. AVW, Avon Wheatbelt; JAF, Jarrah Forest; SWA, Swan Coastal Plain.

region and darker grey-brown patterning on pars cephalica (Fig. 224); fovea straight (Fig. 224). Dorsal pars cephalica with six porrect post-ocular setae in anteriorly staggered (1–2) then straight (3–6) median arrangement (Fig. 224); lateral margins of carapace with fringe of porrect black setae above coxae I–II and coxa IV (Fig. 224). Eye group (Fig. 227)

trapezoidal, PLE–PLE/ALE–ALE ratio 1.5; 0.7× as long as wide; ALE separated by slightly more than 1.5× their own diameter; AME separated by 1.1× their own diameter; PME separated by 4.2× their own diameter; PME and PLE separated by slightly less than half diameter of AME, PME positioned slightly anterior to level of PLE. Maxillae with field of cuspules confined to inner corner (Fig. 228); labium without cuspules. Abdomen oval, charcoal-coloured in dorsal view (Fig. 225), with faint tan mottling and small beige-grey sigilla spots. Dorsal surface of abdomen covered with stiff, porrect black setae, each with slightly raised, dark brown sclerotic base; sclerotised sigilla absent. Legs variably dark brown, with scopulae on tarsi I–II; tibia I (Figs 231–233) bearing large prolateral clasping spurs. Leg I: femur 6.9; patella 3.2; tibia 5.0; metatarsus 4.9; tarsus 3.0; total 23.0. Leg I femur–tarsus/carapace length ratio 3.3. Pedipalpal tibia 1.9× longer than wide; RTA long and pointed, gradually tapering distally, with sparse field of retrolateral spinules extending along entire length (Figs 234, 235); tibia also with long field of spinules extending along retroventral edge, distal to base of RTA (Figs 234, 235). Cymbium sparsely setose, with field of long spinules anteriorly (Figs 234–236). Embolus twice length of bulb (Figs 234–236), gradually tapering distally but with slightly broader tip and very small, triangular embolic apophysis subdistally (Fig. 236).

Remarks

The holotype of *Eucyrtops latior* is a degraded pinned female from an imprecise location (‘Perth’) and, as the type species of the genus *Eucyrtops*, its identification requires clarification. To address this, we examined available collections from the Greater Perth region, and determined the identity and distribution of *Eucyrtops* species in the northern Darling Range east of Perth (where the genus occurs and from where the original holotype specimen probably originated). One species is common and dominant in this region, and agrees with the holotype female in somatic morphology. On the strength of this evidence, we here base our concept of this species on a reference male from Stoneville, 12 km east of Perth (see ‘Reference material examined’, above), which is further conspecific with an available molecular (male) exemplar from Wungong Dam, 12 km south-east of Perth. This species is a medium-sized, dark brown to black trapdoor spider (Figs 220, 224, 225) that has a patchy distribution in the northern Jarrah Forest bioregion (Fig. 237).

Eucyrtops eremaeus Main, 1957

(Figs 207, 208, 212, 214, 216)

Eucyrtops eremaea Main, 1957: 421, fig. 8C.

Material examined

Holotype. Australia: Western Australia: ♂, Cardinia Creek, E. of Malcolm (WAM T3962; examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, Mt Ida, 100 km WSW. of Leonora (WAM T110236^{DNA_Voucher_203}); 1 ♂, Cardinia Creek, E. of Malcolm (WAM T139597).

Remarks

Eucyrtops eremaeus is unusual among species of *Eucyrtops* in being small and relatively pale. It has a distinctive bi-coloured abdomen and dark brown anterior margin of the carapace (Figs 207, 208), and is found in the northern Goldfields (Murchison bioregion).

Genus ***Gaius*** Rainbow, 1914, status revised

(Figs 1, 238–256)

Gaius Rainbow, 1914: 195. Type species *Gaius villosus* Rainbow, 1914, by monotypy. Here removed from synonymy of *Anidiops* Pocock, 1897 (*contra* Main, 1957: 424).

Diagnosis

Species of *Gaius* can be distinguished from all other Arbanitinae by the combined presence of a trapezoidal eye group with a strongly procurved anterior eye row (Figs 242–245), the presence of a strongly developed distal retrolateral tibial apophysis (dRTA) on the male pedipalp (Figs 248–251), the presence of dense setation on the body and legs (Figs 238–251), and the presence in most species of a massive RTA (Figs 248, 250, 251). Species of *Gaius* are most similar (and closely related) to species of *Eucyrtops*, from which they can be distinguished by the much larger body size (Figs 238–241), more densely setose body and legs (Figs 238–251) and presence of a large dRTA (Figs 248–251).

Males, females and juveniles of this genus can also be identified (on the basis of seven molecular exemplar specimens; see Fig. 256) by the unique ‘CGA’ motif at positions 139–141 of nuclear *ITS2*, by the unique ‘AG’ motif at positions 757–758 of nuclear *28S* rRNA, by the unique ‘TCCAA’ or ‘TCAAA’ motif at positions 1912–1917 of *28S* rRNA, and by the following 14 nuclear nucleotide substitutions: *MRPL45* G(111), T(363; rarely homoplastic in *Arbanitis*), C (454), T(465; homoplastic in *Cantuaria mestoni*), G(620), A (717); *RPF2* G(126), G(309; rarely homoplastic in *Idiosoma*); *XPNPEP3* C(264), T(383), T(648); *HAT1* C(197), T(237); *ITS1* C(403).

Description

See Main (1985*b*: 15, in part).

Distribution

Western Australia, from the southern Wheatbelt and western Nullarbor, north to the Pilbara and Little Sandy Desert (Fig. 256).

Composition

Gaius includes one described species (Table 1). Several undescribed species are also known from collections (M. G. Rix and M. S. Harvey, unpubl. data).

Figs 238–251. Morphology of *Gaius* Rainbow. *238–241*, Male carapace and abdomen, dorsal view: *238*, *239*, *G. villosus* Rainbow, 1914 (WAM T41700); *240*, *241*, *G.* sp. from Kalgoorlie, Western Australia (WAM T30021). *242–245*, Eyes, dorsal view: *242*, male *G. villosus* (WAM T41700); *243*, male *G.* sp. from Kalgoorlie, Western Australia (WAM T30021); *244*, male *G.* sp. from Wiluna, Western Australia (WAM T132589); *245*, male *G.* sp. from Collie, Western Australia (WAM T27005). *246*, *247*, Male leg I tibia, prolateral view: *246*, *G. villosus* (WAM T41700); *247*, *G.* sp. from Kalgoorlie, Western Australia (WAM T30021). *248–251*, Male pedipalp, retrolateral view: *248*, *G. villosus* (WAM T41700); *249*, *G.* sp. from Kalgoorlie, Western Australia (WAM T30021); *250*, *G.* sp. from Collie, Western Australia (WAM T27005); *251*, *G.* sp. from Wiluna, Western Australia (WAM T132589). Scale bars = 5.0 mm.

Figs 252–255. Burrows and images of live *Gaius* Rainbow. *252*, *254*, Female *G. villosus* Rainbow, 1914 from Minnivale Nature Reserve, Western Australia; *253*, male *G. villosus* from Minnivale Nature Reserve, Western Australia; *255*, female *G.* sp. from near Zuytdorp, Western Australia, with Australian one-dollar coin (diameter 25 mm) for scale. Note the radiating burrow twig-lines characteristic of this genus. Images (*252*, *254*, *255*) by M. Harvey; (*253*) by V. Framenau, used with permission.

Remarks

Gaius is a relatively small genus of very large trapdoor spiders endemic to Western Australia (Fig. 256). All are dark in colour (Figs 238–241, 252, 253) and include some of the largest Mygalomorphae in Australia outside of the Theraphosidae. They build characteristic burrows with radiating twig-lines and flappy doors (Figs 254, 255), always with an internal sock-like silken collar that can be collapsed and pulled down by the spider in defence. The sister-lineage to *Gaius* is *Eucyrtops* (Fig. 1), both of which possess a strongly developed RTA. Long-term demographic work at North Bungulla Nature Reserve (Main 1978, 1987) has clarified the biology and life history characteristics of the single described species, *Gaius villosus*. Males and females mature at around eight years of age, and males emerge after the first summer storms. Females can live for over 40 years in the wild (B. Y. Main, unpubl. data).

Gaius villosus Rainbow, 1914

(Figs 238, 239, 242, 246, 248, 252–254)

Gaius villosus Rainbow, 1914: 195, figs 6–8.
Anidiops villosus (Rainbow): Main, 1957: 426, figs 3C, 5B.

Material examined

Holotype. Australia: Western Australia: ♀, Minnivale (AMS KS6259; examined [BYM]).

Select material examined. **Australia:** Western Australia: 1 ♀, Minnivale Nature Reserve (WAM T132736^{DNA_Voucher_AN}); 1 ♂, Minnivale, lot 10 Dowell Street (WAM T41700); 1 ♂, 1.5 km NNW. of Wongan Hills (WAM T71695^{DNA_Voucher_216}).

Remarks

Gaius villosus (Figs 252, 253) is a very large trapdoor spider from the Wheatbelt of south-western Australia. Like other

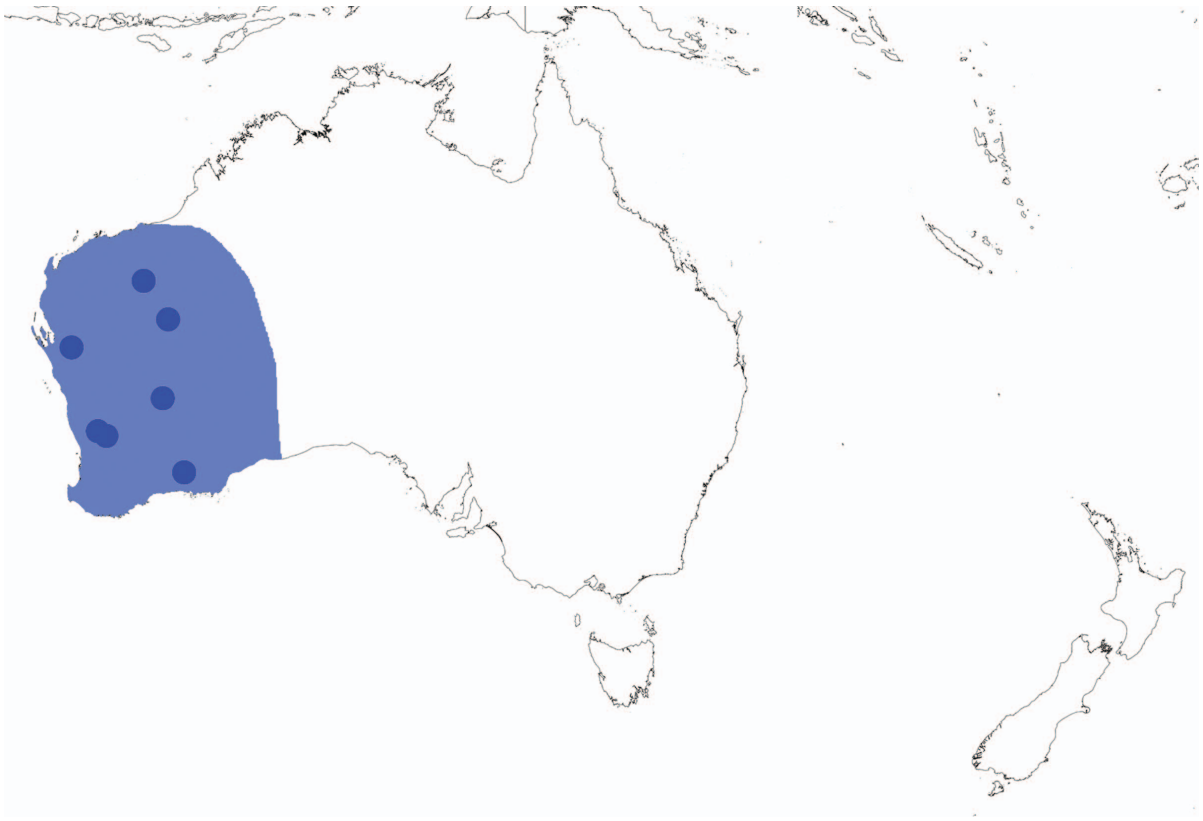


Fig. 256. Map showing the approximate extent of occurrence of the genus *Gaius* Rainbow in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al*. (2017*a*). Note the absence of this genus from central and eastern Australia.

species of *Gaius*, it builds a radiating skirt of twig-lines around the burrow entrance (Fig. 254) and is common in some areas. Main (1978, 1987) summarised the biology and demographic characteristics of this species at North Bungulla Nature Reserve, north-west of Kellerberrin.

Tribe **CATAXIINI** Rainbow, 1914, status revised

Cataxeae Rainbow, 1914: 222. Type genus *Cataxia* Rainbow, 1914. Here removed from synonymy of Arbanitini Simon, 1903 (*contra* Raven, 1985: 139).

Homogoneae Rainbow, 1914: 188 (synonymised with Arbanitini Simon, 1903 by Raven, 1985: 139). New synonymy.

Diagnosis

As for *Cataxia* (see below).

Distribution

As for *Cataxia* (see below).

Included genera

Cataxia Rainbow, 1914.

Remarks

As for *Cataxia* (see below).

Genus ***Cataxia*** Rainbow, 1914

(Figs 1, 257–288)

Cataxia Rainbow, 1914: 222. Type species *Cataxia maculata* Rainbow, 1914, by monotypy.

Homogona Rainbow, 1914: 189. Type species by monotypy *H. pulleinei* Rainbow, 1914 (synonymised by Raven, 1985: 154 *contra* Main, 1993: 600).

Neohomogona Main, 1985*b*: 42. Type species by original designation *N. bolganupensis* Main, 1985*b* (synonymised by Raven, 1985: 175 *contra* Main, 1993: 600).

Diagnosis

Species of *Cataxia* can be distinguished from all other Arbanitinae by the combined absence of scopulae on the anterior legs of females, the presence of a non-hirsute, glabrous carapace (Figs 271–276), and a relatively narrow carapace profile in dorsal view (Figs 257, 259, 272, 275). Males of *Cataxia* are most similar to (and often sympatric with) species of *Arbanitis*, with which they share a rectangular

Figs 257–270. Morphology of *Cataxia* Rainbow. *257–260*, Male carapace and abdomen, dorsal view: *257*, *258*, *Cat.* sp. nr. *maculata* from Fairies Knob, Queensland (QMB S39845); *259*, *260*, *Cat. bolganupensis* (Main, 1985*b*) (WAM T95754). *261–264*, Eyes, dorsal view: *261*, male *Cat.* sp. nr. *maculata* from Fairies Knob, Queensland (QMB S39845); *262*, male *Cat.* sp. nr. *babindaensis* from The Crater National Park, Queensland (QMB S54435); *263*, male *Cat. pulleinei* (Rainbow, 1914) (QMB); *264*, male *Cat. bolganupensis* (WAM T95754). *265*, *266*, Male leg I tibia, prolateral view: *265*, *Cat. maculata* Rainbow, 1914 (SAM NN22839); *266*, *Cat.* sp. from Stirling Range National Park, Western Australia (WAM T130332). *267–270*, Male pedipalp, retrolateral view: *267*, *Cat. maculata* (SAM NN22839); *268*, *Cat.* sp. nr. *babindaensis* from The Crater National Park, Queensland (QMB S54435); *269*, *Cat. pulleinei* (QMB); *270*, *Cat. bolganupensis* (WAM T95754). Scale bars = 2.0 mm.

Figs 271–276. Images of live *Cataxia* Rainbow. *271*, Female *Cat. maculata* Rainbow, 1914 from Eidsvold, Queensland; *272*, female *Cat. spinipectoris* Main, 1969 from Boyce Estate, Toowoomba, Queensland; *273*, female *Cat. pallida* (Rainbow & Pulleine, 1918) from Eidsvold, Queensland; *274*, female *Cat. pulleinei* (Rainbow, 1914) from Lismore, Queensland; *275*, female *Cat. victoriae* Main, 1985*a* from Grampians National Park, Victoria; *276*, female *Cat.* sp. from Stirling Range National Park, Western Australia. All images by M. Rix except: (*276*) by M. Harvey.

eye group (Figs 261–264) and usually also a distal retrolateral tibial apophysis on the male pedipalp (Figs 267, 268). Male *Cataxia* can be distinguished from similar sympatric species of *Arbanitis* by the presence of a non-hirsute, glabrous carapace (Figs 257, 259) and the presence of scopulae on only the anterior leg tarsi.

Males, females and juveniles of this genus can also be identified (on the basis of 12 molecular exemplar specimens; see Fig. 288) by the following 10 nuclear nucleotide substitutions: *MRPL45* A(141; homoplastic in *Cantuaria stewarti*), A(378; rarely homoplastic in *Idiosoma*), T(256; homoplastic in *Euoplos tasmanicus*), C(450); *XPNPEP3* G(342), C(471), C (585; rarely homoplastic in *Idiosoma*), A(606), G(682); *HAT1* G(264).

Description

See Main (1969: 193), Main (1983: 83) and Main (1985*b*: 17, 42, 43).

Distribution

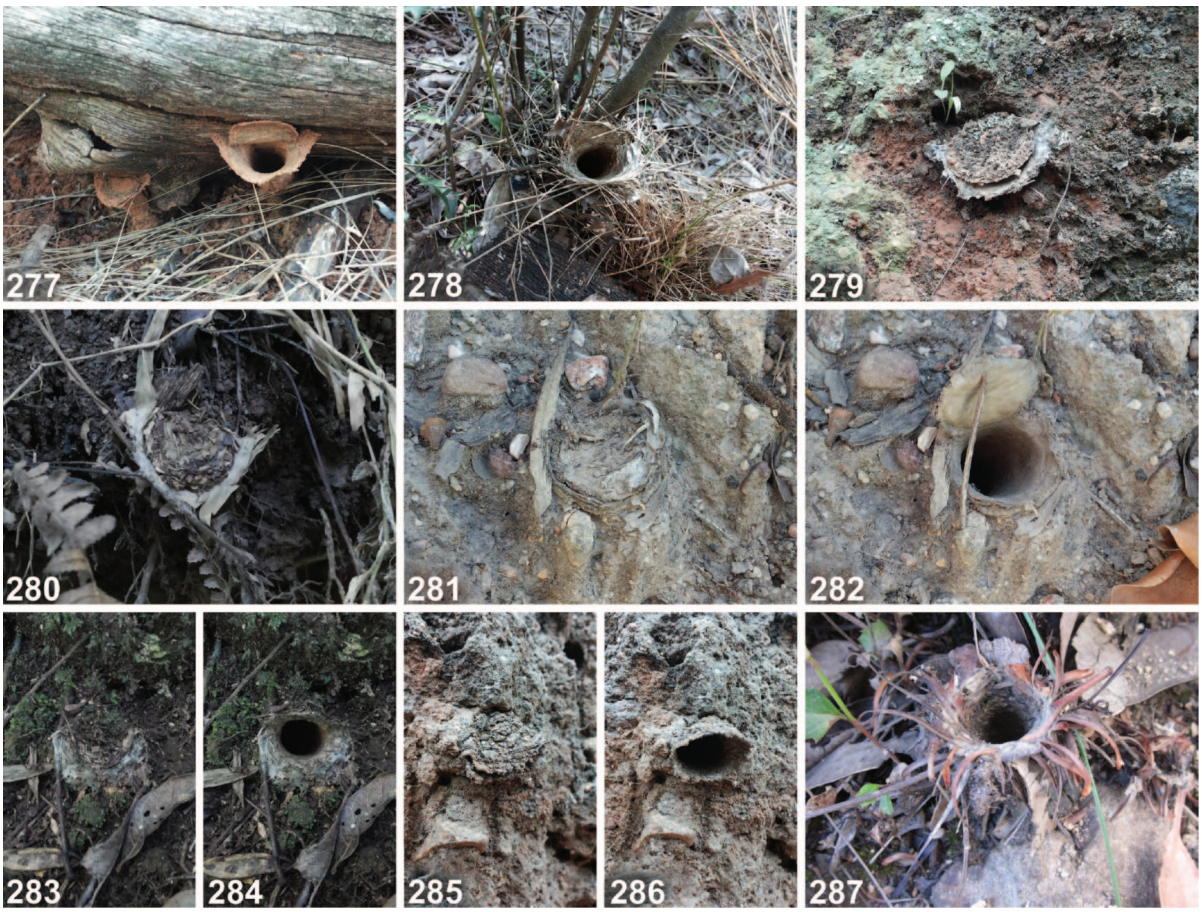
Tropical and subtropical eastern Australia, Victoria and the extreme south-west of Western Australia (Fig. 288). Absent from Tasmania, South Australia and the central arid zone, and rare in central-eastern New South Wales.

Composition

Cataxia includes 11 described species (Table 1).

Remarks

Cataxia is entirely restricted to the Australasian temperate, eastern tropical and south-western mesic zones (Fig. 288). While not as diverse and generally nowhere near as common as *Arbanitis*, the genus is (along with *Euoplos*) an important component of the idiopid fauna of mesic eastern Australia, where populations are usually found in rainforest or wet sclerophyllous habitats. Several species (e.g. *Cat. maculata*, *Cat. pallida*) have adapted to drier woodland or dry rainforest habitats in Queensland. Species of *Cataxia* exhibit the greatest range of burrow morphologies found among Australian Idiopidae (Figs 277–287), from typical hinged doors (Figs 277–282) to sock-like burrow entrances (Figs 283–286) and even fully open holes in Western Australian taxa (Fig. 287). Variously ornate palisade burrow morphologies are typical of many species (Figs 277–279), with tube-like burrows analogous to those of *Arbanitis robertsi* built by some taxa (e.g. *Cat. maculata*; Figs 277, 278). *Cataxia* is a very well-supported monophyletic clade, which appears to be sister to the tribe Arbanitini (but with weak support) (Fig. 1). Because of this weak sister-group support, and evidence in some molecular analyses for an alternate sister-group relationship with Aganippini, the genus is included in its own tribe. Although the three major sub-lineages – congruent with the older generic concepts of *Cataxia* s. s., *Homogona* and *Neohomogona* – are reciprocally monophyletic, these taxa are all so similar morphologically that they are united here into a single genus (*sensu* Raven 1985).



Figs 277–287. Burrows of *Cataxia* Rainbow. *277*, *278*, *Cat. maculata* Rainbow, 1914 from west of Eidsvold, Queensland; *279*, *Cat.* sp. from Mapleton National Park, Queensland; *280*, *Cat.* sp. from Conondale National Park, Queensland; *281*, *282*, *Cat. pallida* (Rainbow & Pulleine, 1918) from Eidsvold, Queensland; *283*, *284*, *Cat. pulleinei* (Rainbow, 1914) from near Binna Burra, Lamington National Park, Queensland; *285*, *286*, *Cat. victoriae* (Main, 1985*a*) from Grampians National Park, Victoria; *287*, *Cat. stirlingi* (Main, 1985*b*) from Bluff Knoll, Stirling Range National Park, Western Australia. Note the hinged, thin doors characteristic of this genus (*277–282*), the palisade burrows (*277*, *278*) of *Cat. maculata*, the flush burrow of *Cat. pallida* (*281*) with its stronger, wafer-like door (*282*), the everted sock-like burrows of *Cat. pulleinei* (*283*, *284*) and *Cat. victoriae* (*285*, *286*), and the ornate, open palisade burrow of *Cat. stirlingi* (*287*). All images by M. Rix.

Cataxia maculata Rainbow, 1914

(Figs 265, 267, 271, 277, 278)

Cataxia maculata Rainbow, 1914: 223, figs 32–35.
Arbanitis inornatus Rainbow & Pulleine, 1918: 119, pl. 22, fig. 70 (synonymised by Main, 1969: 193).
Cataxia tetrica Rainbow & Pulleine, 1918: 133, pl. 23, fig. 83 (synonymised by Main, 1969: 193).

Material examined

Syntypes (of *Cat. maculata*). **Australia:** Queensland: 3 juveniles, Upper Burnett River [NB. approx. Eidsvold] (AMS KS6335; examined [BYM]).

Syntypes (of *A. inornatus*). **Australia:** Queensland: 1 ♀, 1 juvenile, Eidsvold (AMS KS6264; examined [BYM]).

Holotype (of *Cat. tetrica*). Australia: Queensland: ♀, Eidsvold (AMS KS1630; examined [BYM]).

Select material examined. **Australia:** Queensland: 1 ♀, Eidsvold, off Lochaber Road (WAM T133278^{DNA_Voucher_CA2}); 2 ♂, Eidsvold (SAM NN22839–40).

Remarks

Cataxia maculata (Fig. 271), the type species of the genus, is a medium-sized spider from eastern southern-central Queensland, where it is moderately common in the Eidsvold region. It sometimes goes by the name of ‘moon spider’, a reference to the moon-like profile of the burrow door (Main 1969) (Figs 277, 278). The spiders are mostly found in dry rainforest habitats and surrounding sclerophyllous woodlands, where they build distinctive palisade burrows against logs and tree roots, each with an expanded lower ‘lip’ and a friable flappy door (Figs 277, 278). The burrow walls are usually incorporated with fine grains

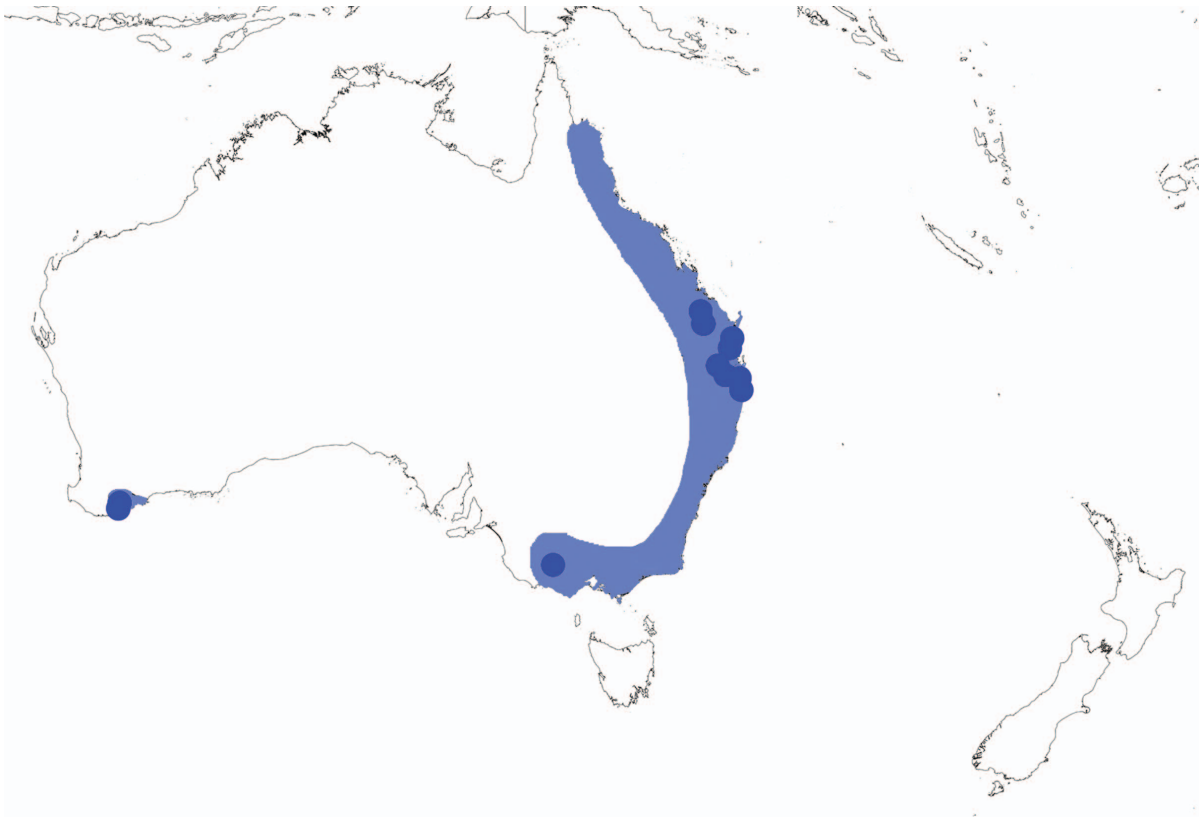


Fig. 288. Map showing the approximate extent of occurrence of the genus *Cataxia* Rainbow in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al*. (2017*a*). Note the absence of this genus from the arid interior.

of soil (Fig. 277), but are sometimes made from fine grass stems (Fig. 278).

Cataxia bolganupensis (Main, 1985)

(Figs 259, 260, 264, 270)

Neohomogona bolganupensis Main, 1985*b*: 43, figs 158–164, 169–177, 181–186, 205, 220–222.
Cataxia bolganupensis (Main): Raven, 1985: 175 (*contra* Main, 1993: 600).

Material examined

Holotype. Australia: Western Australia: ♂, track on Nancy Peak (above Bolganup Dam), Porongurup National Park (WAM T16395; examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♀, Porongurup National Park, track just E. of Tree-in-the-Rock Day Use Area (WAM T131631^{DNA_Voucher_34}); 1 ♂, Porongurup National Park, south end of Millinup Pass (WAM T95754).

Remarks

Cataxia bolganupensis is one of only a small handful of *Cataxia* known from extreme south-western Western Australia; these species previously formed the genus *Neohomogona*. It is endemic to the tall, wet karri (*Eucalyptus diversicolor*) forests of the Porongurup Range, 37 km north of Albany, where it is locally common, but extremely patchy. This spider builds an ornate open-holed palisade burrow with a radiating skirt of leaves and twigs around the entrance (similar to Fig. 287).

Cataxia pallida (Rainbow & Pulleine, 1918)

(Figs 273, 281, 282)

Armadalia pallida Rainbow & Pulleine, 1918: 132, pl. 23, fig. 82.
Cataxia pallida (Rainbow & Pulleine): Main, 1985*b*: 18, figs 30–34.

Material examined

Holotype. Australia: Queensland: juvenile, Eidsvold (AMS KS6269; examined [BYM]).

Select material examined. **Australia:** Queensland: 1 ♀, Eidsvold, off Hollywell Road (WAM T133263^{DNA_Voucher_82}).

Remarks

Cataxia pallida is a large species from eastern southern-central Queensland, where around Eidsvold it can sometimes be found in the vicinity of *Cat. maculata*. This spider is among the palest of *Cataxia* in body coloration, with a rich orange-brown

cephalothorax and legs (Fig. 273). They are unusual among *Cataxia* in building solid, non-descript wafer-like doors that are flush with the ground (Figs 281, 282), usually in hard, consolidated banks or soil.

Cataxia pulleinei (Rainbow, 1914)

(Figs 263, 269, 274, 283, 284)

Homogona pulleinei Rainbow, 1914: 190, figs 1–5.
Cataxia pulleinei (Rainbow): Raven, 1985: 154 (*contra* Main, 1993: 600).

Material examined

Holotype. Australia: New South Wales: ♀, Lismore (AMS KS6394; examined [BYM]).

Select material examined. **Australia:** New South Wales: 1 ♂, Lismore (QMB); 1 ♀, Rotary Rainforest Reserve, Lismore, off Rotary Drive (WAM T133297[DNA_Voucher_35]). Queensland: 1 ♀, Lamington National Park, Binna Burra, start of Coomera Circuit Track (WAM T133277[DNA_Voucher_84]); 1 ♀, Main Range National Park, Cunningham's Gap, track to Mount Mitchell (WAM T133302[DNA_Voucher_87]).

Remarks

Cataxia pulleinei is a medium-sized to large species from south-eastern Queensland and north-eastern New South Wales, where it is restricted to rainforest habitats. It is a handsome black spider (Fig. 274) that builds a distinctive 'sock-like' burrow with a lower 'lip' around the entrance and an upper flap (which does not have a defined hinge) (Figs 283, 284). The burrow can therefore be open or pulled closed by the spider as necessary. It is a common species along the scenic rim of Queensland and New South Wales, and is often found in sympatry with *Euoplos* and *Arbanitis* species in suitable habitats. Main (1983) summarised the taxonomy and natural history of this species.

Cataxia spinipectoris Main, 1969

(Fig. 272)

Cataxia spinipectoris Main, 1969: 201, figs 2, 8, 23–26.

Material examined

Holotype. Australia: Queensland: ♀, Toowoomba (QMB W2876; examined [BYM]).

Select material examined. **Australia:** Queensland: 1 ♀, University of Queensland Boyce Estate, Toowoomba, off Range Street (WAM T133288[DNA_Voucher_86]); 1 ♀, Conondale National Park, off Booloumba Creek Road, near Lobster Creek (WAM T133318[DNA_Voucher_88]).

Remarks

Cataxia spinipectoris (Fig. 272) is similar to *Cat. maculata* in appearance, but is found further south in Queensland and builds a burrow without a pronounced palisade morphology.

Cataxia victoriae (Main, 1985)

(Figs 275, 285, 286)

Homogona victoriae Main, 1985*a*: 16, figs 1–7.
Cataxia victoriae (Main): Raven, 1985: 154 (*contra* Main, 1993: 600).

Material examined

Holotype. Australia: Victoria: ♀, Barney's Creek, Grampians National Park (NMV K163; examined [BYM]).

Select material examined. **Australia:** Victoria: 1 ♀, Grampians National Park, off Mafeking Road (WAM T131987[DNA_Voucher_80]).

Remarks

Cataxia victoriae (Fig. 275) is closely related to *Cat. pulleinei*, and like that species it builds a 'sock-like' burrow with an upper flap that does not possess a true hinge (Figs 285, 286). It is endemic to Victoria.

Tribe **EUOPLINI** Rainbow, 1914, status revised

Euoploae Rainbow, 1914: 217. Type genus *Euoplos* Rainbow, 1914. Here removed from synonymy of Arbanitini Simon, 1903 (*contra* Raven, 1985: 139).

Diagnosis

As for *Euoplos* (see below).

Distribution

As for *Euoplos* (see below).

Included genera

Euoplos Rainbow, 1914.

Remarks

As for *Euoplos* (see below).

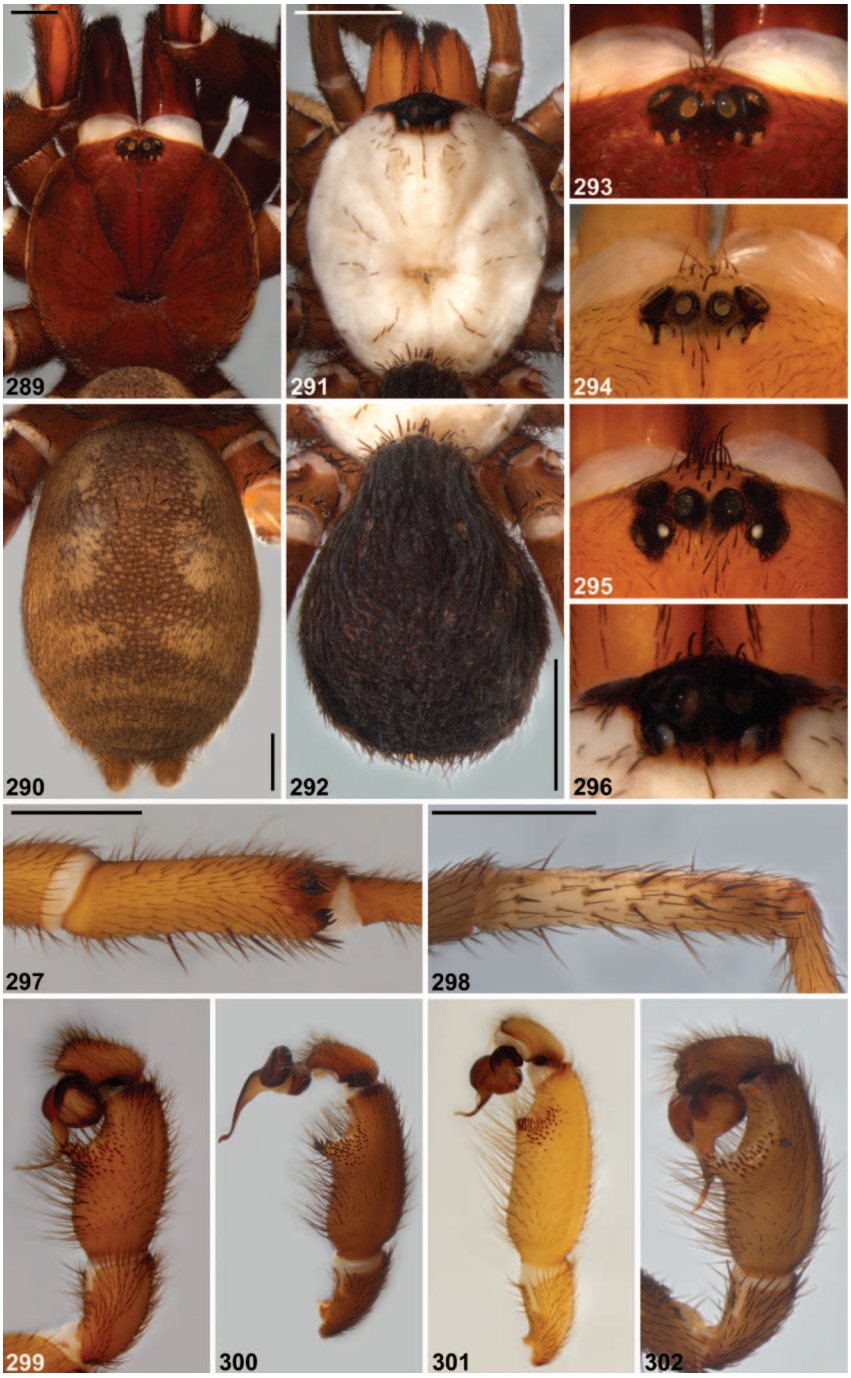
Genus ***Euoplos*** Rainbow, 1914

(Figs 1, 289–321)

Euoplos Rainbow, 1914: 217. Type species *Euoplos spinnipes* Rainbow, 1914, by monotypy.
Evoplos Bonnet, 1956: 1813, 1892 (unjustified emendation).
Tambouriniana Rainbow & Pulleine, 1918: 120. Type species by monotypy *Tam. variabilis* Rainbow & Pulleine, 1918 (synonymised with *Arbanitis* L. Koch, 1874 by Main, 1964: 28; with *Euoplos* Rainbow, 1914 by Raven & Wishart, 2006: 552).
Albaniana Rainbow & Pulleine, 1918: 122. Type species by subsequent designation of Petrunkevitch (1928) *Alb. inornata* Rainbow & Pulleine, 1918 (synonymised with *Arbanitis* L. Koch, 1874 by Main, 1985*b*: 22; with *Euoplos* Rainbow, 1914 by Raven & Wishart, 2006: 552).
Bancroftiana Rainbow & Pulleine, 1918: 127. Type species by monotypy *Ban. speciosa* Rainbow & Pulleine, 1918 (synonymised with *Arb*anitis L. Koch, 1874 by Main, 1985*b*: 22; with *Euoplos* Rainbow, 1914 by Raven & Wishart, 2006: 552).
Armadalia Rainbow & Pulleine, 1918: 129. Type species by subsequent designation of Petrunkevitch (1928) *Arm. ornata* Rainbow & Pulleine, 1918 (synonymised with *Arbani*tis L. Koch, 1874 by Main, 1985*b*: 22; with *Euoplos* Rainbow, 1914 by Raven & Wishart, 2006: 552).

Diagnosis

Species of *Euoplos* can be distinguished from all other Arbanitinae by the combined presence of a small, rectangular eye group (Figs 293–296), the presence of a uniquely broad carapace profile in dorsal view (Figs 289, 291, 304–306, 310,



Figs 289–302. Morphology of *Euoplos* Rainbow & Pulleine. *289–292*, Male carapace and abdomen, dorsal view: *289*, *290*, *Euo. spinnipes* Rainbow, 1914 (QMB S8755); *291*, *292*, *Euo. mcmillani* (Main, 2000) (holotype). *293–296*, Eyes, dorsal view: *293*, male *Euo. spinnipes* (QMB S8755); *294*, male *Euo. inornatus* (Rainbow & Pulleine, 1918) (WAM T139592); *295*, male *Euo. tasmanicus* (Hickman, 1928) (WAM T139591); *296*, male *Euo. mcmillani* (holotype). *297*, *298*, Male leg I tibia, prolateral view: *297*, *Euo. tasmanicus* (WAM T139591); *298*, *Euo. mcmillani* (holotype). *299–302*, Male pedipalp, retrolateral view: *299*, *Euo. tasmanicus* (WAM T139591); *300*, *Euo. spinnipes* (QMB S8755); *301*, *Euo. inornatus* (WAM T139592); *302*, *Euo. mcmillani* (holotype). Scale bars = 2.0 mm.

Figs 303–311. Images of live *Euoplos* Rainbow & Pulleine. *303*, Female *Euo. spinnipes* Rainbow, 1914 from Eidsvold, Queensland; *304*, female *Euo.* sp. from Conondale National Park, Queensland; *305*, female *Euo.* sp. from Serpentine Falls National Park, Western Australia; *306*, female *Euo. inornatus* (Rainbow & Pulleine, 1918) from Armadale, Western Australia; *307*, male *Euo.* sp. from Grass Valley, Western Australia; *308*, female *Euo. ornatus* (Rainbow & Pulleine, 1918) from west of Eidsvold (Queensland); *309*, female *Euo.* sp. from south of Goomboorian, Queensland; *310*, female *Euo.* sp. from near Young, New South Wales; *311*, female *Euo. tasmanicus* (Hickman, 1928) from Porter Hill, Hobart, Tasmania. Note the broad carapace and small, tightly rectangular eye group of most *Euoplos* species, and the ornate abdominal colouration of some taxa (*304*, *305*, *310*). Note also the remarkable white carapace of the males of some species from south-western Western Australia (*307*). All images by M. Rix except: (*306*) by M. Harvey and (*307*) by V. Framenau, used with permission.

311), and the presence (usually) of ventrally incrassate anterior leg tarsi on males.

Males, females and juveniles of this genus can also be identified (on the basis of 17 molecular exemplar specimens; see Fig. 321) by the unique deletion of a single amino acid residue (3 bp) at positions 556–558 of mitochondrial *CYB*, and by the following 23 nuclear nucleotide substitutions: *MRPL45* A(114), A(192), T(235), A(276), C(295), G(307), G(325), T(450), C(561), G(681), A(687); *RPF2* G(91), A(273), A(471), T(540), A(588), A(646); *XPNPEP3* T(473), C(518); *HAT1* G(302), C(350), G(369); *H3* G(261).

Description

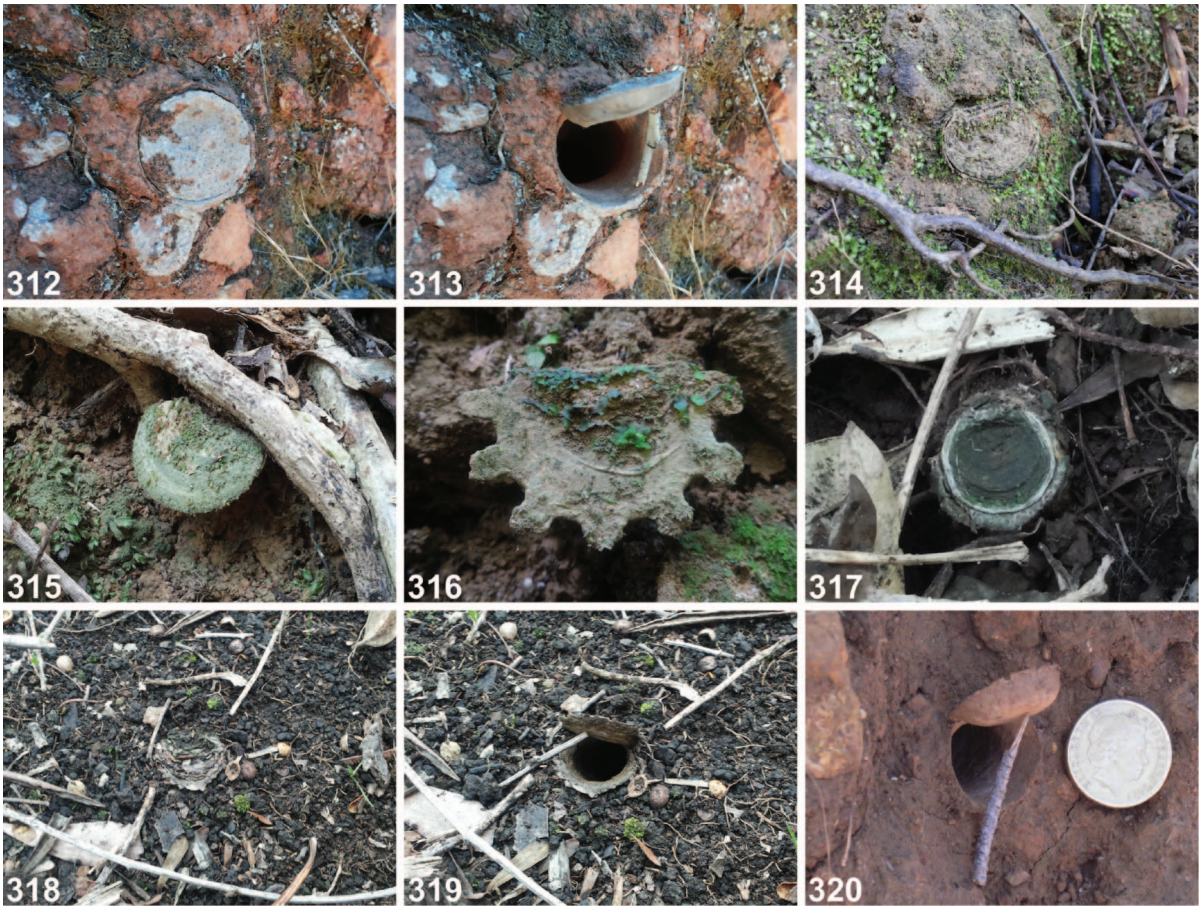
See Main (1977: 70) and Main (1985*b*: 23).

Distribution

Widely distributed in eastern and south-eastern Australia, from tropical Queensland (Cape York Peninsula) south to Tasmania, and Western Australia from the southern Warren bioregion north to the Pilbara (Fig. 321). Absent from the east of Western Australia, South Australia and the central arid zone; rare in southern New South Wales and Victoria.

Composition

Euoplos includes 12 described species (Table 1). This genus has had a confusing taxonomic history, with numerous junior generic and specific synonyms in the literature (many of these originating from Rainbow and Pulleine 1918), and a long history of confusion with the genus *Arbanitis*. Indeed, species of *Euoplos* were included in *Arbanitis* for many decades, until Raven and



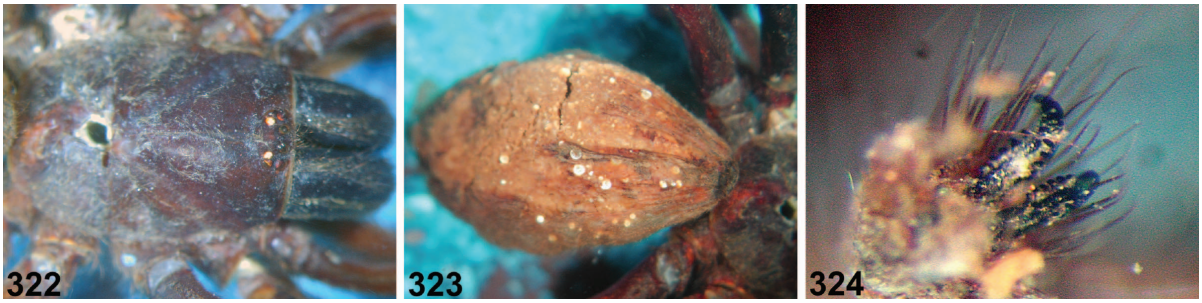
Figs 312–320. Burrows of *Euoplos* Rainbow & Pulleine. *312*, *313*, *Euoplos* sp. from near Young, New South Wales; *314*, *Euo.* sp. from south of Goomboorian, Queensland; *315*, *Euo.* sp. from south of Goomboorian, Queensland; *316*, *Euo.* sp. from west of Goomboorian, Queensland; *317*, *Euo.* sp. from near Binna Burra, Lamington National Park, Queensland; *318*, *319*, *Euo. tasmanicus* (Hickman, 1928) from Porter Hill, Hobart, Tasmania; *320*, *Euo.* sp. from Serpentine Falls National Park, Western Australia (with Australian two-dollar coin of diameter 20 mm for scale). Note the thick, plug-like doors and bevelled burrow entrances characteristic of most species (*313*, *320*); the much thinner, wafer-like door of *Euo. tasmanicus* (*319*); and the highly derived, palisade burrows found in several undescribed species from south-eastern Queensland (*315*, *316*). Note also the sophisticated incorporation of lichen (*312*), moss (*314–316*) or leaf litter fragments (*318*) into the external doors, and the presence of burrow 'growth rings' in some individuals (*317*). All images by M. Rix except: (*316*) by J. Wilson, used with permission.

Wishart (2006) radically relimited *Arbanitis* following the rediscovery of the holotype male of *A. longipes*. As a result, Raven and Wishart (2006) transferred the then 14 Australian *Arbanitis* species (excluding *A. longipes*) into *Euoplos*, and moved all of the New Zealand taxa back into *Cantuaria* (from *Misgolas*). However, several these transfers required subsequent clarification. First, *Mygale annulipes* C. L. Koch, 1842 is here transferred from *Euoplos* to *Stanwellia* (Nemesiidae), as the holotype female (ZMB 2095) is clearly not at idiopid (Figs 322–324). *Armadalia zorodes* Rainbow & Pulleine, 1918 from Mount Lofty (South Australia) and *Arbanitis maculipes* Hogg, 1903 from 'Tasmania' are designated as *nomina dubia*, as the female holotypes cannot be confidently identified or associated with a named species. Finally, another *nomen dubium*, *Macrothele aculeata* Urquhart, 1893, has no known holotype, no type locality beyond 'Tasmania', and the original description of the male is not adequate for identification.

Remarks

Euoplos is the sister-lineage to all other Australasian Arbanitinae, with unequivocal molecular support for its monophyly (Fig. 1). It is an abundant genus in subtropical (mesic) eastern Queensland, and one of only three idiopid genera found in Tasmania (Fig. 321). In Western Australia, an endemic lineage has independently adapted to xeric habitats in

Fig. 321. Map showing the approximate extent of occurrence of the genus *Euoplos* Rainbow & Pulleine in Australia, overlaid with sampling points for specimens sequenced in the molecular analysis of Rix *et al.* (2017*a*). Note the absence of this genus from the arid interior.



Figs 322–324. *Mygale annulipes* C. L. Koch, 1842, female holotype (ZMB 2095), somatic morphology, imaged *in situ* in Berlin. *322*, Carapace, dorsal view; *323*, abdomen, dorsal view; *324*, claws, anterior view, showing double row of teeth.

the Wheatbelt, mid-west and Pilbara, where species are usually extremely rare; males of some of these species have a remarkable glabrous white carapace morphology (Figs 291, 307). Most *Euoplos* build thick, circular,, plug-like doors to their burrows (Figs 312–314, 317, 320), although several species in eastern Australia (e.g. *E. tasmanicus* (Hickman, 1928)) build a more pliable, flappy or wafer-like door (Figs 318, 319). At least two undescribed species from south-eastern Queensland build an unusual palisade burrow with a lip-like entrance and convex, D-shaped lid (Figs 315, 316); one of these species also incorporates remarkable ornate edging to its burrow lid (Fig. 316).

Euoplos spinnipes Rainbow, 1914

(Figs 289, 290, 293, 300, 303)

Euoplos spinnipes Rainbow, 1914: 219, figs 28–31.
Arbanitis spinnipes (Rainbow): Main, 1985*b*: 28, figs 56–59, 75, 76, 199.
Euoplos spinnipes Rainbow: Raven & Wishart, 2006: 552.

Material examined

Holotype. Australia: Queensland: ♀, Upper Burnett River [NB. approx. Eidsvold] (AMS KS1612; examined [BYM]).

Select material examined. **Australia:** Queensland: 1 ♂, Oakey Creek, Gayndah (QMB S53835); 2 ♂, 1 ♀, Mount Goonaneman, via Childers (QMB S8755); 1 ♀, Eidsvold, Lochaber Road (WAM T133276^{DNA_Voucher_EU2}).

Remarks

Euoplos spinnipes (Fig. 303), the type species of the genus, is a large spider from eastern south-central Queensland and northern south-eastern Queensland. It builds a thick, plug-like door, and has a distinctive reddish-brown cephalothorax in life (Fig. 303).

Euoplos inornatus (Rainbow & Pulleine, 1918)

(Figs 294, 301, 306)

Albaniana inornata Rainbow & Pulleine, 1918: 122, pl. 22, fig. 72.
Albaniana flavomaculata Rainbow & Pulleine, 1918: 125, pl. 22, fig. 76 (synonymised by Main, 1985*b*: 25).
Armadalia setosa Rainbow & Pulleine, 1918: 130, pl. 15, fig. 16, pl. 22, fig. 80 (synonymised by Main, 1985*b*: 25).
Arbanitis inornatus (Rainbow & Pulleine): Main, 1985*b*: 25, figs 45–50, 66, 67, 72, 79, 81, 82, 89, 94, 95, 104, 197, 217, 218.
Euoplos inornatus (Rainbow & Pulleine): Raven & Wishart, 2006: 552.

Material examined

Holotype (of *Alb. inornata*). Australia: Western Australia: ♀, Albany Road, Narrogin [NB. approx. Armadale *sensu* Main, 1985b] (AMS KS1621; examined [MGR, BYM]).

Holotype (of *Alb. flavomaculata*). **Australia:** Western Australia: ♀, Albany Road, Narrogin [NB. approx. Armadale *sensu* Main, 1985b] (AMS KS1622; examined [BYM]).

Holotype (of *Arm. setosa*). **Australia:** Western Australia: juvenile, Armadale (AMS KS7174; examined [BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, Chittering Valley Road, E. of Bullsbrook (WAM T139592); 1 ♂, same data (WAM T139593); 1 ♀, Lions Park, off Carradine Road, E. of Albany Highway/Armadale Road intersection (WAM T 129360^{DNA_Voucher_36}); 1 juvenile, Mount Henry Reserve, S. end of Mount Henry Peninsula, Salter Point, Perth (WAM T132845^{DNA_Voucher_272}).

Remarks

Euoplos inornatus (Fig. 306), and probably also *Euo. festivus* (Rainbow & Pulleine, 1918), is unusual among Western Australian *Euoplos* in being a member of an otherwise eastern Australian clade. It is restricted to relatively mesic (usually riparian) habitats in the northern Jarrah Forest bioregion, and builds a thick, plug-like door in consolidated banks (similar to Fig. 320). It is largely found along the western Darling Range east of Perth, with two outlying populations on the Swan Coastal Plain at Kings Park (Mt Eliza) and on the Mount Henry Peninsula.

Euoplos mcmillani (Main, 2000)

(Figs 291, 292, 296, 298, 302)

Arbanitis mcmillani Main, 2000: 93, figs 1, 2A–N.
Euoplos mcmillani (Main): Raven & Wishart, 2006: 552.

Material examined

Holotype. Australia: Western Australia: ♂, Eneabba, rehabilitation site 7 of R.G.C. (Westralian) Mineral Sands (WAM T24582, examined [MGR, BYM]).

Select material examined. **Australia:** Western Australia: 1 ♂, Cooljarloo, 15 km NW, of Cataby (WAM T110280^{DNA_Voucher_112}); 1 ♂, 6.4 km SE, of Cooljarloo (WAM T135188^{DNA_Voucher_256}).

Remarks

Euoplos mcmillani is one of the 'white-headed trapdoor spiders', a group of related species from southern Western Australia with a remarkable glabrous white carapace morphology (which sometimes earns them the erroneous common name of 'albino trapdoor spiders') (Fig. 291). Related species (Fig. 307) are known from the central and northern Wheatbelt and from elsewhere on the Geraldton Sandplains (Main 2000; M. G. Rix and M. S. Harvey, unpubl. data); *Euo. mcmillani* is currently known only from the Kwongan heathlands around Eneabba and Cooljarloo, north of Perth. Nothing is known of the biology of this species, *Euo. ballidu* (Main, 2000) or any other white-headed taxa, and females are unknown. It is a relatively small species, and belongs to the Western Australian 'arid zone clade' of *Euoplos* (Rix *et al*. 2017*a*).

Euoplos ornatus (Rainbow & Pulleine, 1918)

(Fig. 308)

Albaniana ornata Rainbow & Pulleine, 1918: 123, pl. 22, fig. 73.
Armadalia ornata Rainbow & Pulleine, 1918: 129, pl. 22, fig. 79 (synonymised by Main, 1985*b*: 27).
Bancroftiana speciosa Rainbow & Pulleine, 1918: 127, pl. 22, figs 77, 78 (synonymised by Main, 1985*b*: 27).
Arbanitis ornatus (Rainbow & Pulleine): Main, 1985b: 27, figs 51–55, 64, 65, 70, 71, 74, 77, 78, 83, 84, 88, 92, 93, 105, 198.
Euoplos ornatus (Rainbow & Pulleine): Raven & Wishart, 2006: 552.

Material examined

Holotype (of *Alb. ornata*). Australia: Queensland: ♀, Eidsvold (AMS KS1623; examined [BYM]).

Holotype (of *Arm. ornata*). Australia: Queensland: ♀, Eidsvold (AMS KS6268; examined [BYM]).

Holotype (of *Ban. speciosa*). Australia**:** Queensland: ♂, Eidsvold (AMS KS7176; examined [BYM]).

Select material examined. **Australia:** Queensland: 1 ♀, ~50 km W. of Eidsvold off Eidsvold-Theodore Rd (WAM T133261^{DNA_Voucher_37}).

Remarks

Euoplos ornatus (Fig. 308) is a medium-sized species known from eastern south-central Queensland, which builds a thick, plug-like door that can sometimes be adorned with leaf litter fragments.

Euoplos similaris (Rainbow & Pulleine, 1918)

Arbanitis similaris Rainbow & Pulleine, 1918: 112, pl. 22, fig. 60.
Euoplos similaris (Rainbow & Pulleine): Raven & Wishart, 2006: 553.

Material examined

Holotype. Australia: Queensland: ♀, Kedron Brook, Brisbane (AMS KS6267; examined [BYM]).
Select material examined. **Australia:** Queensland: 1 ♀, Kedron Brook, Stafford, Brisbane, off Shand Street (WAM T133299[DNA_Voucher_123]).

Remarks

Euoplos similaris is a medium-sized species from the Brisbane region of south-eastern Queensland. It builds a thick, plug-like door, usually in consolidated banks in riparian or rainforest habitats.

Euoplos tasmanicus (Hickman, 1928)

(Figs 295, 297, 299, 311, 318, 319)

Aganippe tasmanica Hickman, 1928: 158, pls 21, 22, fig. 1.
Arbanitis tasmanicus (Hickman): Main, 1957: 427.
Euoplos tasmanicus (Hickman): Raven & Wishart, 2006: 553.

Material examined

Holotype. Australia: Tasmania: ♀, Prince of Wales Bay, Derwent Park (QVM 1957/13/21; not examined).
Select material examined. **Australia:** Tasmania: 1 ♂, 1 ♀, Sandy Bay, Hobart (WAM T139591); 1 ♀, Porter Hill, Hobart (WAM T133326[DNA_Voucher_119]).

Remarks

Euoplos tasmanicus (Fig. 311) is a medium-sized species from Tasmania, and belongs to a lineage that is sister to all other *Euoplos* species. It builds a thin, relatively pliable flappy or wafer-like door (Figs 318, 319), sometimes near the high tide mark of the Derwent River (see Hickman 1928).

Euoplos variabilis (Rainbow & Pulleine, 1918)

Tambouriniana variabilis Rainbow & Pulleine, 1918: 121, pl. 14, fig. 12, pl. 22, fig. 71.
Tambouriniana variabilis flavomaculata Rainbow & Pulleine, 1918: 22 (synonymised by Bonnet, 1959: 4237).
Albaniana villosa Rainbow & Pulleine, 1918: 124, pl. 22, fig. 75 (synonymised by Main, 1985*b*: 29).
Arbanitis variabilis (Rainbow & Pulleine): Main, 1964 [undated]: 28.
Euoplos variabilis (Rainbow & Pulleine): Raven & Wishart, 2006: 553.

Material examined

Holotype (of *Tam. variabilis*). Australia: Queensland: ♀, Mount Tamborine (AMS KS6409; examined [BYM]).
Holotype (of *Tam. variabilis flavomaculata*). Australia: Queensland: ♀, Mount Tamborine (AMS KS1638; examined [BYM]).
Holotype (of *Alb. villosa*). Australia: Queensland: ♀, Mount Tamborine (AMS KS1620; examined [BYM]).
Select material examined. **Australia:** Queensland: 1 ♀, Tamborine National Park, Mount Tamborine, Joalah Section (WAM T133307[DNA_Voucher_38]).

Remarks

Euoplos variabilis is a large to very large species from the greater Brisbane region of south-eastern Queensland. It builds a thick, plug-like door, usually in consolidated banks in riparian or rainforest habitats.

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APPENDIX 6.3: Where have all the spiders gone? The decline of a poorly known invertebrate fauna in the agricultural and arid zones of southern Australia (2017, Austral Entomology 56, 14–22).

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My contribution to this paper was 5%.

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Review

Where have all the spiders gone? The decline of a poorly known invertebrate fauna in the agricultural and arid zones of southern Australia

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Abstract Earth is currently experiencing the sixth mass extinction of complex multi-cellular life, the first at the hands of a single species. The documented extinctions of iconic (mostly vertebrate and plant) taxa dominate the discourse, while poorly known invertebrate species are disappearing 'silently', sometimes without having ever been described. Here, we highlight the decline of elements of the trapdoor spider (Mygalomorphae: Idiopidae) fauna of southern Australia – a taxonomically poorly documented yet diverse assemblage of long-lived fossorial predators. We show that a number of trapdoor spider species may be threatened after a century of intensive land clearing and stocking, and that remaining populations in some areas may be experiencing serious contemporary population declines. So, how do we conserve this fauna? We suggest that baseline systematic studies are crucial, and that follow-up surveys, including integrative citizen science solutions, should be used to assess where remnant populations still exist, and whether they can persist into the future. Detailed population genetic research on a handful of carefully chosen taxa could be broadly informative, and ongoing natural history studies remain invaluable. Although solutions may be limited in the face of ongoing habitat degradation and other threats, urgently quantifying declines has implications not just for spiders but for mitigating against the mass extinction of poorly known invertebrate taxa across the globe.

Key words Aganippini, Arachnida, Araneae, biodiversity hotspot, south-western Australia.

INTRODUCTION

> 'One hundred and fifty nine years [*sic*, in 1990] of [European] settlement in Western Australia has made a travesty of the natural landscape.' (Main 1990: 397)

The observations and predictions of Main (1990) on the degradation of the biota of south-western Western Australia (SWWA) make for difficult reading. A biodiversity hotspot (Myers *et al.* 2000; Rix *et al.* 2015), SWWA has experienced such destructive degradation since European settlement that a suite of natural ecosystems are now 'so drastically diminished or have experienced such profound degradation and regime changes that their ecology is fundamentally altered' (Laurance *et al.* 2011: 1477). Those fragments that remain face numerous threats (Environmental Protection Authority 2007). The same is true for much of southern Australia, where a mosaic of different ecosystems has experienced widespread land clearing and modification for agriculture, along with historical or contemporary grazing by stock. Unsurprisingly, this degradation has severely affected the region's biota, with well-documented contemporary extinctions or declines among mammals, birds and plants (e.g. Woinarski *et al.* 2015). These threatened and often iconic vertebrate and plant taxa have dominated the conservation biology discourse worldwide (Régnier *et al.* 2015); their declines are usually easily detectable and often generate an emotive public response. It is, however, the invertebrate animals – 'the little things that run the world' (Wilson 1987) – that may be affected most. Indeed, the scale of the ongoing decline of poorly known invertebrate faunas may be grossly underestimated by standard assessment practices (Régnier *et al.* 2015).

Arachnids are rarely the subject of public sympathy, and the widespread fear of these animals is an impediment to their conservation (Yen 1995). Despite this, spiders have featured heavily in the invertebrate conservation literature, none more so than members of the infraorder Mygalomorphae – a worldwide lineage including tarantulas and trapdoor spiders. Mygalomorph spiders (Fig. 1) are mostly fossorial and are renowned for their longevity, habitat specificity and generally poor vagility (Hedin *et al.* 2013). They have been of

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Fig. 1. Representative aganippine Idiopidae: (a and b) Female and burrow of an *Aganippe* sp. from Watarrka National Park (Northern Territory); (c) open burrow of an *Aganippe* sp. from near Eidsvold (Queensland); (d–f) female and burrow of *Idiosoma nigrum* Main, 1952 from Meenaar Nature Reserve (Western Australia); (g and h) female and burrow of *Anidiops villosus* (Rainbow, 1914) from Minnivale Nature Reserve (Western Australia); (i) burrow of female *Eucyrtops* sp. from John Forrest National Park (Western Australia). Images a–f and i are by M. Rix; images g and h are by M. Harvey.

conservation significance in many regions of the world (e.g. Arnedo & Ferrández 2007) and are also widely studied for their utility in systematics research (Cooper *et al.* 2011; Hedin *et al.* 2015). Indeed, mygalomorph life histories are often suitable for revealing fine-scale phylogeographic signal; these life history characteristics, in turn, make many species susceptible to threatening processes. The Australian mygalomorph spider fauna is no exception and is replete with a diversity of short-range endemic species (Harvey 2002). Some taxa (e.g. Idiopidae) seem especially vulnerable to threatening processes, and various studies have documented this vulnerability in Australia over several decades (e.g. Main 1987, 1995; Harvey *et al.* 2015; Mason *et al.* 2016).

In this essay, we document the potential decline of elements of the trapdoor spider fauna of the agricultural and arid zones of southern Australia (Fig. 2). This geographical region covers a vast area south of the Tropic of Capricorn, characterised by low annual rainfall (i.e. the arid zone) or low summer rainfall (in the temperate Mediterranean-climate regions; Fig. 2). The heavily cleared agricultural lands of south-western and south-eastern Australia occur within these zones (Fig. 2), usually in transitional rainfall habitats. By drawing on multiple lines of evidence and focussing on Idiopidae (Fig. 1) of the Western Australian Wheatbelt (Gibson *et al.* 2004; Fig. 2), we show that a number of trapdoor spider species may be threatened after a century of intensive land clearing and stocking, and that remaining populations in some areas may be experiencing serious contemporary population declines. We also highlight what data are required to determine if any species may have already been lost. This work is necessarily qualitative in nature – a case study to highlight the challenges faced in documenting the status of poorly known invertebrate taxa, especially those that exhibit: (1) low recruitment and/or long generation times; (2) limited vagility; (3) a high degree of habitat specificity; and (4) are low on the conservation radar. Clearly, most of these same life history characteristics can make populations fundamentally susceptible to habitat disturbance (see Owens & Bennett 2000; Harcourt *et al.* 2002). In the case of the Wheatbelt's trapdoor spiders, we have a decades-long perspective for some species for specific localities (e.g. Main 1987); for other regions across southern Australia, there is a need to infer, *post hoc*, the extent to which populations may have been affected.

IDIOPIDAE

The mygalomorph spiders of Australia include over 400 described species in nine families (World Spider Catalog 2015).

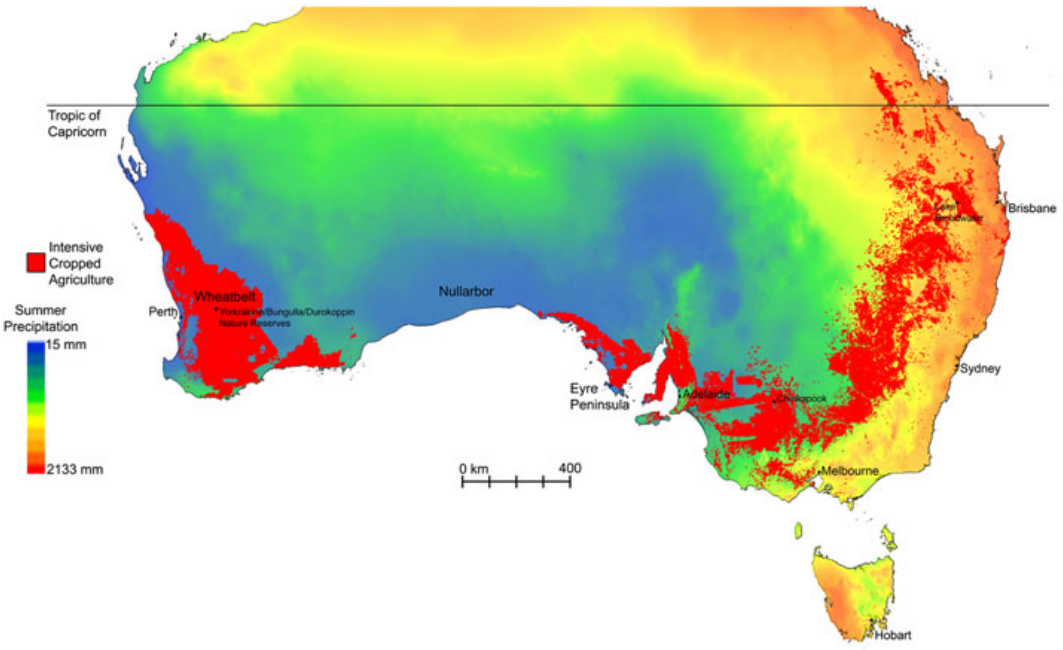

Fig. 2. Map of Australia south of the Tropic of Capricorn, showing the south-western Australian Wheatbelt and other localities mentioned in the text. Summer precipitation is mapped to show the low rainfall inland arid zone and low summer rainfall Mediterranean climate zones of southern Western Australia, South Australia and western Victoria. Red areas denote cleared lands used for intensive cropped agriculture; note the extent of the south-western Australian Wheatbelt agricultural zone. Map layers are created by the Atlas of Living Australia website (https://www.ala.org.au/), reproduced under a Creative Commons Attribution 3.0 Australia Licence.

Unfortunately, our knowledge of the natural history of most taxa is scant, and it is thus difficult to make reasonable inferences about the conservation status of most groups. However, for the trapdoor spiders of the Idiopidae (Fig. 1), a longer history of research and field work indicates a fauna of recognised conservation significance (Main 1987). Idiopidae in Australia are currently represented by nine valid genera and over 100 described species (World Spider Catalog 2015); at least 100–200 undescribed species are known from museum collections (MGR & MSH unpubl. data). The large tribe Aganippini (*Aganippe*, *Anidiops*, *Eucyrtops*, and *Idiosoma*; Fig. 1) and members of at least two other genera (*Blakistonia* and *Euoplos*) have radiated within the Australian arid and semi-arid zones and are most abundant south of the Tropic of Capricorn. Although the distributions of the vast majority of taxa are not known in detail, molecular and morphological research have shown that the family is replete with short-range endemic species (Harvey 2002) or otherwise more broadly distributed species with strong microhabitat fidelity, with the greatest generic diversity in southern Western Australia. Species for which data are available are long-lived (8 to >40 years; Main 1987, unpubl. data), with long generation times (10+ years), limited vagility, low recruitment, strong site fidelity (Main 1987) and usually deep genetic structuring between populations (MGR unpubl. data). One species (*Idiosoma nigrum* Main, 1952; Fig. 1d–f) is currently listed as threatened under both Australian State (Western Australian) and Commonwealth legislation.

THE CHALLENGE: DETECTING DECLINES IN A POORLY KNOWN FAUNA

The conservation biology discourse has long been dominated by a focus on vertebrates and plants; under one measure of assessment of conservation status – relative representation on the International Union for the Conservation of Nature (IUCN) Red List – invertebrates remain 'essentially unevaluated overall' (Régnier *et al.* 2015: 1; see also Cardoso *et al.* 2011, 2012). By definition, a poorly known fauna lacks rigorous empirical or quantitative assessment at the species and population levels, and this, in turn, renders such groups difficult to adjudicate from a conservation perspective. The Australian aganippine Idiopidae are largely undocumented taxonomically, with only 18 of 100–200 species described; museum collections of these taxa are only now being analysed by using both morphological and molecular data. The problem is further amplified in long-lived species with long generation times and low recruitment, in that short-term empirical ecological approaches can fail to detect the symptoms of long-term – and potentially catastrophic – threatening processes. This is especially true of invertebrate faunas, where a lack of iconic species or a dearth of taxonomic documentation can result in an inability to attract conservation funding, thus preventing future quantitative research. For example, the disappearance of small mammals in the Wheatbelt has resulted in this region being classed as a landscape that has already reached a tipping point (Laurance *et al.* 2011). While this classification seems justified, numerous

endemic invertebrates persist in remnant habitats of the Wheatbelt and continue to contribute critical ecosystem functions.

The question then becomes: Within a realistic timeframe, how do we infer or interpret potential population declines in poorly documented and understudied invertebrate taxa with long generation times? And how do we determine if population declines are occurring in widespread common species or more restricted and potentially threatened rare species? For trapdoor spiders in Australia, we highlight these problems by bringing together three lines of evidence, as follows: (1) previous research on idiopid demographics, natural history, systematics and conservation; (2) personal observations and anecdotes resulting from field work by experienced researchers; and (3) museum and other collection records. As stated above, this is therefore a largely qualitative synthesis, but one which builds on existing information to reveal, and where possible interpret, a complex problem across a vast geographical area. As a case study, we focus on the Wheatbelt of SWWA but extend our observations and conclusions to cover much of southern Australia (Fig. 2).

WHERE HAVE ALL THE SPIDERS GONE?

The many small, remnant reserves in the agricultural zones of southern Australia (Fig. 2) typically consist of a denuded series of habitat islands in a sea of cropped or stocked farmland. Weeds are a perennial problem, vertebrate pest species are ubiquitous, bird assemblages are depauperate, and small marsupials are usually absent (McKenzie *et al.* 2003). In many areas, dryland salinity and plant diseases such as *Phytophthora* are causing enormous changes to floristics and the structure of vegetation communities, some of which are themselves threatened or home to threatened species (Barrett & Yates 2015; https://www.environment.gov.au/biodiversity/threatened/communities). Other vast tracts of central Australia, while still covered with some primary vegetation, have been denuded by 150 years of stocking with cattle and sheep and the impacts of grazing by rabbits, feral donkeys, camels and goats (Environmental Protection Authority 2007).

What are less obvious in the remnant habitats of southern Australia are the many cryptic invertebrates that survive in these fragments. Indeed, a careful inspection of the ground may reveal burrows belonging to fossorial spider taxa, including highly camouflaged idiopid trapdoors (Fig. 1b,c,e,f,h,i), the latter a once ubiquitous occurrence in many places (e.g. Main 1967). Most of these Idiopidae are members of the diverse tribe Aganippini (Fig. 1). In some of the larger reserve systems, seemingly healthy population clusters of burrows can still be found in suitable habitats. However, surveys in smaller reserves or roadside remnants have shown that these spiders are often increasingly difficult to find. The 'lone matriarch' phenomenon, whereby at most one or a very few large burrows with resident older females are active in the absence of any others (with smaller juvenile burrows conspicuously absent), is now a familiar occurrence (for a full description of the matriarch concept in trapdoor spider demographics, see Main 1987). In some places, only defunct (i.e. empty) burrows can be found.

But where have all the spiders gone? What evidence is there of population declines, and does this equate to species actually being (or becoming) threatened? In the Wheatbelt of SWWA and other habitats, one of us (BYM) has documented some of these declines over 65 years, using a combination of demographic and other ecological approaches, combined with taxonomic appraisal and field work across the surrounding landscape. At North Bungulla Nature Reserve (BNR; Fig. 2), trapdoor spiders have been surveyed and their demographic characteristics assessed for over 40 years (Main 1978, 1987, unpubl. data). The results of this work provide evidence for idiopid declines, as well as quantitative life history information implicated in the likely causes of these declines. Indeed, surveys on a private property near BNR with some remnant bush and a variety of other land uses revealed that three of the nine species present in the 1950s may have disappeared by 1980, and of these, most were rare and none were common as in the previous census (Main 1987). Similarly, a pitfall trap survey at nearby Durokoppin Nature Reserve in the late 1980s and early 1990s revealed 10 species in this one reserve; another pitfall trap survey a decade later captured only three species, one of which was not sampled in the first survey (Appendix A in the Supporting Information). Site sampling methods for the two Durokoppin surveys were not precisely replicated, but given the small size of the reserve (1030 ha), these recapture data may be indicative of population declines for some species during the intervening 10 years.

Museum collection records offer another important source of data with which to compare modern distributions. In the case of Idiopidae, these historical collections can be used to track the extirpation of populations following land clearing, as shown by Main (1990). In this study, Western Australian Museum records of *Idiosoma sigillatum* (O. P. Cambridge, 1870) from the Perth region were tracked by location and date of collection. As Perth suburbs expanded throughout the 20th Century, collections (usually public submissions) were made with the advancing front of development; in the aftermath of urbanisation, these records became the so-called 'phantoms' of extinct populations. While small populations of *I. sigillatum* still exist in some reserves in the Perth metropolitan region, and in other remnant woodlands, the species is now locally extinct across the majority of its former range and can be assessed as 'vulnerable' by using standard IUCN Red List criteria (Appendix B in the Supporting Information). Clearly, museum collection records provide crucial data necessary to determine which taxa occurred in a particular area, and whether those species still exist.

Some of the strongest evidence for recent declines comes from an accumulation of field work by the authors and other workers over recent decades. While qualitative in nature, these observations are nonetheless informative, given the historical perspective upon which they are founded. One example is Yorkrakine Rock Nature Reserve – a habitat island in the Wheatbelt (Fig. 2). Main (1967) documented the natural history of this woodland remnant and described in detail the populations of four species of trapdoor spiders present at the time of writing.

Two visits to this site and many combined hours of searching by two of us (MGR and MSH) in 2014 revealed just two adult female idiopid specimens – one *Aganippe* sp. and one *Anidiops villosus* (Rainbow, 1914) (Fig. 1g,h). No other active burrows were located. Although burrows can sometimes be difficult to locate due to their camouflage (Fig. 1), recruitment has undoubtedly been reduced at Yorkrakine Rock relative to the 1960s. Similar lone matriarchs have been recorded at a number of sites across Australia, including at Lake Broadwater Conservation Park, south-eastern Queensland (2014; 1x *Aganippe* sp.), and in a small patch of remnant scrub near Chinkapook, western Victoria (2013; 1x *Blakistonia* sp.; Fig. 2). Both sites are highlighted here as they were surveyed by at least two of the authors for at least five hours, and are surrounded by cleared agricultural lands; in each case, old doors and other defunct burrows were present. While subsequent survey work at Lake Broadwater has revealed a small 9 ha area within the park where a population of two species of Idiopidae can be found, active burrows are yet to be located anywhere else in the reserve, despite follow-up searches. Given the predictions of Main (1987), who calculated that populations of *A. villosus* were only viable long-term if there were at least 20 matriarchs present (and that populations probably also require habitat-connected satellite populations for occasional recruitment during adverse conditions), the persistence of these species at such localities seems doubtful.

There is also evidence for trapdoor spider population declines in the largely uncleared but often heavily stocked arid zone. A 2014 survey, along a ~1400 km transect following the southern edge of the Nullarbor (Eyre Highway) by two of us (SEH and MSH), revealed just 18 idiopid specimens, despite dedicated field work across hundreds of kilometres over 10 days, including at many sites that provided fertile collecting for three or four genera in the 1950s to 1980s (these <1990 specimens now stored in the BYM collection, Western Australian Museum; Fig. 3; Appendix C in the Supporting Information). At least one genus commonly recorded then (*Eucyrtops*) was not located in 2014, another (*Blakistonia*) was unexpectedly sparse (Fig. 4), and sympatry at sites was uncommon; this was surprising, given the ease with which idiopids could be located from the same areas in the 1950s (Fig. 3). Likewise, in arid central Australia, three field trips in 2013 and 2014 by one or more of us (MGR, SEH, MSH and ADA) revealed an almost complete absence of active idiopid burrows; many of these landscapes were severely degraded due to stocking by various introduced herbivores. Taken together, these data provide evidence for a problem that may not simply be restricted to the cleared agricultural zones, but rather to temperate arid and semi-arid southern Australia in general.

WHAT FACTORS ARE IMPLICATED IN POPULATION DECLINES?

Understanding the factors implicated in the decline of a poorly known fauna is by definition difficult and subjective. However, setting out what we know, what we think we know and what we need to ascertain is critical for informing research priorities.

The most significant threatening processes to Australian trapdoor spiders are undoubtedly land clearing, stocking by sheep and cattle and the impacts of other feral grazing animals. Parts of the Wheatbelt and southern South Australia are among the most cleared landscapes in Australia (Bradshaw 2012), the result of destroying 'a million wild acres a year' during post-WWI and post-WWII resettlement schemes (Gaynor 2015). Likewise, vast areas of the Australian arid zone have been stocked since the earliest phases of European settlement. Most of the clearing in southern Australia was historical rather than ongoing, and there have been intense efforts to transfer remaining remnants into conservation estates. Nonetheless, it is implicit that land clearing on this scale has major conservation implications for range-restricted or habitat-restricted taxa, as reflected in 'geographical range' being a primary consideration in IUCN Red List species assessments (Criterion B), which use 'extent of occurrence' and 'area of occupancy' data. Stocking was and remains destructive in many areas, and as witnessed by one of us (BYM) in the Wheatbelt, most existing reserves (many of which were gazetted only in the late 20th Century) were previously open to use by stock, largely for shade or water. What appear today to be carefully protected remnants have actually had a long history of disturbance, and it is now clear that trapdoor spider burrows are severely affected (and usually destroyed) by trampling by stock. This problem remains ongoing in the vast unfenced rangelands of the Australian arid zone and is likely implicated in the scarcity of Idiopidae across some of these areas.

Salinity is another threat to inland ecosystems, at all levels. The wholesale changes to vegetation and soil chemistry wrought by an increasingly saline water table affect the entire biota (George *et al.* 1997). There is no evidence that Idiopidae previously adapted to non-saline environments can persist in newly saline landscapes, although several species are naturally adapted to salt-lake environs in other regions (Main 1982). Dryland salinity is perhaps the most significant threat to the biota of the inland Australian agricultural zone (Keighery 2004) and remains a particular threat to dispersal-limited trapdoor spiders, given that it is so difficult to mitigate. Understanding how idiopid populations are affected and at what salinity threshold individual fitness is reduced are thus important questions for future research.

Despite its central role in the ecology and evolution of the Australian biota, fire (and its potential increase in frequency with progressing climate change) may be another threatening process in the arid and semi-arid zones, especially in small reserves where hot-burn fires may be 'total instead of patchy' (Main 1987: 36). Data exist on idiopid post-fire mortality, and in some cases, nearly 50% of adults can die within 3 months after a fire; juveniles are more severely affected with no short-term recruitment (Main 1995). Without recruitment from adjacent unburnt areas, the long-term survival of successively degraded populations may be affected, potentially leading to local population extinction.

Other potential threats are less clear or may have indirect effects, and they are listed below in no particular order. Firstly, the effects of drought (and increased drought frequency), agricultural herbicides and pesticides on trapdoor spiders are little known, although the latter may be worthy of urgent

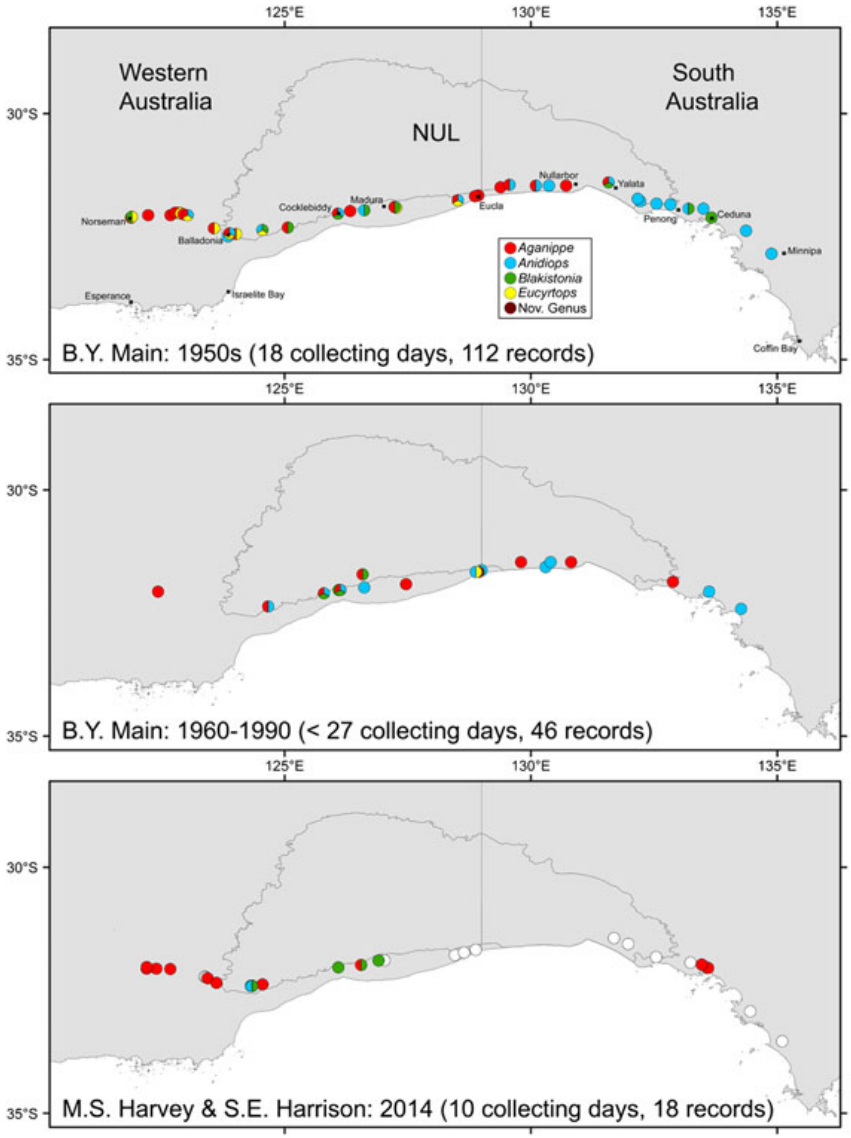

Fig. 3. Maps of southern Western Australia and southern South Australia, showing collection records of Idiopidae from the Eyre Highway section of the Nullarbor Plain (Fig. 2) from the 1950s (top), from the 1960s–1980s (middle) and from 2014 (bottom). The Interim Biogeographic Regionalisation of Australia (IBRA) Nullarbor bioregion is highlighted. Different genera are denoted by differently coloured circles; open circles from 2014 denote negative records. The number of collecting days represented by the mapped collections is shown to indicate relative survey effort; the less than symbol in panel 2 (middle) denotes a range of collecting dates for some records. Note the numerous collection records from the 1950s and the relative paucity of specimens and genera (and the low levels of sympatry) recorded at sites in 2014 (especially in south-eastern South Australia). See text for details.

assessment, given their widespread use in fields adjacent to conservation estates. For species with small population sizes, there are a series of threats that relate to the genetic viability of populations, including low standing genetic variation (Frankham 1996; Lynch & Lande 1998), inbreeding depression (e.g. Charlesworth & Charlesworth 1987) and over longer periods of time, the overriding influence of genetic drift over selection. This 'genetic load' can have the cumulative effect of lowering the fitness of populations (Kirkpatrick & Jarne 2000). Fortunately, techniques in the field of conservation genetics are now available to explore these threats, and this could be a fruitful area of research.

Finally, introduced pest species may be a threat across all landscapes, but especially within small reserves. Weeds and aggressive introduced grasses seem to choke out burrows in previously favourable areas, further reducing habitat. Rabbits have localised effects on soil stability and integrity, and it has been reported that plagues of mice become omnivorous when they run out of other food resources (M. Cowan pers. comm.); clearly, this may be detrimental to local trapdoor spiders, both by direct

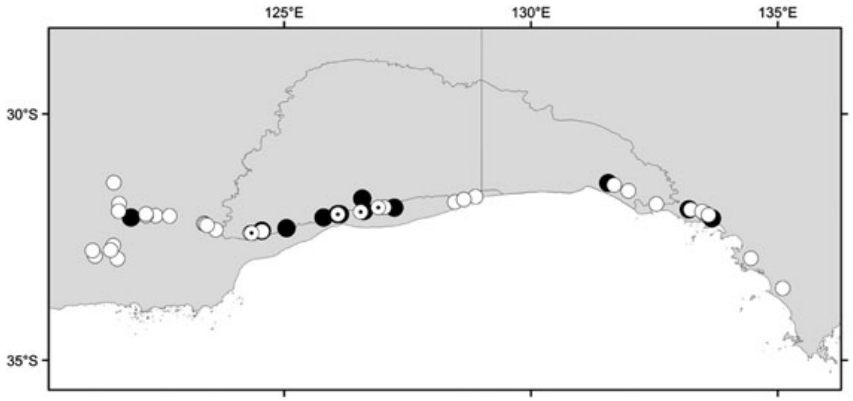

Fig. 4. Map of southern Western Australia and southern South Australia, showing collection records of *Blakistonia* from the Eyre Highway section of the Nullarbor Plain from 1950 to 1990 (large black circles) and from 2014 (small open circles with spots; Fig. 3). Other small open circles denote negative records from 2014. The Interim Biogeographic Regionalisation of Australia (IBRA) Nullarbor bioregion is highlighted. See Figure 3 (upper panel) for geographical landmarks, and see text for details.

predation and predation by mice on the spiders' invertebrate prey. It is unknown what effect foxes and feral cats might also be having on idiopid populations, but anecdotal evidence suggests that foxes dig up spiders from their burrows (N. Moore & H. Cannon pers. comm.); a detailed scat or gut content analysis would help clarify this. We also postulate that seasonal predation by foxes and/or cats on wandering male spiders (i.e. sex-biased predation), or on recent recruits that have shallow burrows, may be an overlooked but potentially significant factor in the long-term decline of populations. Demographic work has shown that for a reasonably healthy population of *A. villosus* (Fig. 1g,h) with 15–24 matriarchs, at most, only three male spiders 'run' (i.e. emerge and search for female spiders during appropriate conditions) in any one season (Main 1987). Should anything happen to this small male cohort over successive seasons, or if the number of available male spiders decreases further, recruitment may be affected. This is especially so when both sexes mature at around 8 years of age, and female spiders only reproduce at most once every two years thereafter (Main 1987). It is well documented that foxes and cats have both extraordinarily broad diets and occur in high densities in remnant habitats (Read & Bowen 2001); what effect they are having on long-term population demographics if they hunt nocturnally wandering mygalomorph spiders is at present unknown.

QUANTIFYING DECLINES AND FUTURE RESEARCH

Adequately quantifying trapdoor spider declines is essential to determining the nature and scale of the conservation problems facing different taxa and to addressing conservation priorities (where they exist) in constructive and proactive ways. Some of the most powerful approaches to understanding population dynamics are molecular, and fine-scale genetic studies on gene flow, recruitment and paternity are required, if only to provide some guiding case studies with which to inform broader management. To date, many phylogenetic studies on mygalomorph spiders have focused on deep genetic breaks, often correlating with species boundaries or at least independently evolving lineages with long histories of isolation (e.g. Satler *et al.* 2013). Finer scale genetic and geospatial studies among subpopulations are needed to test for gene flow (dispersal capacity), genetic variation (standing genetic variation and inbreeding) and/or recent extinction (e.g. Bond *et al.* 2006). These data will inform recolonisation potential and the potential for assisted reintroduction of conspecific juveniles (e.g. into habitats where a species has recently become extinct) and help clarify if male spiders can move genes between seemingly isolated habitat patches, possibly salvaging the reproductive potential of lone matriarchs. Similarly, recent developments in next-generation sequencing technology open up the potential to assess selection in non-model organisms, which could likewise inform conservation actions (Allendorf *et al.* 2010). For all genetic studies, the need to not over-collect from small populations is important (Minteer *et al.* 2014), and thus exemplar taxa should be chosen carefully for their ability to withstand representative sampling. Alternatively, silk-sampling or non-lethal tissue sampling procedures need to be developed (e.g. Smith *et al.* 2015).

Ecosystem niche modelling (Elith & Leathwick 2009) and the application of IUCN Red List assessments are two other tools useful for assessing taxa of conservation concern at different spatial scales. For example, undertaking IUCN assessments for a randomly selected taxon set provides a statistically sound and relatively unbiased method for determining the level of threat and/or the potential severity of the conservation problem facing a particular lineage or fauna (Saiz *et al.* 2015). However, importantly, these approaches first require knowledge of what the species are – the latter usually unavailable due to numerous impediments. This taxonomic issue is a critical one for Idiopidae (and other invertebrates; see Braby & Williams 2016), and another important early step in addressing trapdoor spider conservation across Australia is to facilitate taxonomic study of the fauna, the so-called 'Wallacean shortfall' (Cardoso *et al.* 2011). We now know that the Australian idiopid fauna is far more diverse than previously thought and species more difficult

to delimit accurately without a combined molecular and morphological approach. When it is known what species occur where, and therefore what species occurred in *which* remnant reserves more specifically, a foundation will exist for determining their conservation status and likely survival (or otherwise) in those same locations (e.g. Paquin *et al.* 2008). Current systematic research on Australian idiopids by the authors indicates that the majority of the Australian fauna remains undescribed. However, once taxonomic revisions and/or more rapid molecular species delimitation datasets are published, this shortfall can be addressed at an IUCN Red List assessment level (as for *I. sigillatum*; see Appendix B in the Supporting Information). For other families of trapdoor spiders, there is much to be done. Thereafter, the foundations will be in place not only for modelling, statistical and other quantitative ecological approaches but also for informing follow-up survey work over longer timeframes. Indeed, we envisage citizen science as playing a key role in future conservation efforts; e.g. online public submissions of geo-referenced burrow photos could be used to pinpoint new localities or track population fluctuations over time. Online platforms such as the Atlas of Living Australia's 'BioCollect' (http://www.ala.org.au/biocollect/) or iNaturalist (http://www.inaturalist.org/) could be used to this end. The sheer size of the Australian landscape means that concerned members of the public can play a vital part in this endeavour, and integrative solutions for enhancing their involvement need to be found. For example, the unlikely case of the 'horrid ground weaver' (*Nothophantes horridus* Merrett & Stevens, 1995) in the UK highlighted the potential value of a citizen science solution to an acute arachnid conservation problem (IUCN 2015).

Finally, demographic work at North Bungulla Nature Reserve and elsewhere has highlighted just how useful fundamental life history studies can be, especially those that are long-running and therefore powerful in having a historical perspective. Unfortunately, natural history is an endangered field of scientific endeavour (Tewksbury *et al.* 2014), but if there is to be any chance of ameliorating declines and mitigating against a mass extinction, then better data must be obtained on the natural history characteristics of these animals. For example, understanding how many mature male spiders emerge each year and when they disperse and mate could help enormously in determining if they routinely fall prey to feral predators or in facilitating any (admittedly drastic) assisted reproduction attempts in those most endangered populations with the lowest recruitment. For other populations, simply knowing their microhabitat preferences is crucial to effectively manage those microhabitats for posterity.

It should be noted that all of these research priorities will be most useful in the context of similar studies on trapdoor spiders elsewhere in Australia, e.g. in the arid Pilbara bioregion of northwestern Australia (Castalanelli *et al.* 2014; JAH unpubl. data). Indeed, comparative studies will allow us to determine whether population declines in southern Australia are unique or whether mygalomorph spider faunas are also threatened elsewhere in the world (e.g. Yanez & Floater 2000). Most importantly, determining which threats are the most urgent to manage (and why) has implications not just for spiders but also for mitigating against the mass extinction of poorly known invertebrate taxa across the globe.

We hope that this paper stimulates interest in the conservation of Australian mygalomorph spiders, a vigorous debate as to how populations can be preserved for future generations, and urgent research into their systematics, population genetics and natural history.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix A Collection records of pitfall-trapped Idiopidae from Durokoppin Nature Reserve from 1987–1991 and from 1997–1998. See text for details.
Appendix B IUCN Red List assessment for *Idiosoma sigillatum* (O.P.-Cambridge, 1870). See text for details.
Appendix C Collection records of Idiopidae from the Nullarbor Plain (Eyre Highway section) from 1950–1990 (B.Y.M.) and from 2014 (M.S.H., S.E.H.). See Figures 3–4 and text for details.

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