<u>PENSOFT</u>

EVOLUTIONAR SYSTEMATICS

Abba, a new monotypic genus of orb-weaving spiders (Araneae, Araneidae) from Australia

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https://zoobank.org/E51A70F7-3E38-46EA-9AA3-9376EA6C9D0C

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Academic editor: Danilo Harms Received 25 November 2022 Accepted 5 January 2023 Published 16 January 2023

Abstract

A new monotypic genus in the orb-weaving spider family Araneidae Clerck, 1757 is described from Australia: *Abba* gen. nov., with *Abba transversa* (Rainbow, 1912) comb. nov. as the type species. It differs from all other genera in the family by somatic characters, specifically a patch of approximately five long spines on the prolateral surface of the first leg in males and an abdominal colouration with a pair of two central spots dorsally on a creamy-white surface. Specimens of *A. transversa* comb. nov. have been collected in Queensland and New South Wales, where the species is largely summer-mature. We also provide a genus level summary of all Australian Araneidae, currently consisting of 230 described species and eight subspecies in 46 genera.

Key Words

Taxonomy, systematics, monotypy, araneids

Introduction

There are currently 230 described species and eight subspecies in 46 genera of araneid orb-weaving spiders known from Australia (Table 1). The genus Araneus Clerck, 1757 is the most speciose of these and includes almost double the number of species as each of the secondlargest genera, Argiope Audouin, 1826 and Dolophones Walckenaer, 1837 (Table 1). However, Araneus (or its junior synonym Epeira Walckenaer, 1805) was used by early arachnologists as a dumping ground for species that could not be placed in other genera, and a detailed examination of all available Australian type material of araneids over the last 15 years showed that true Araneus species do not occur in Australia (VWF unpublished data). It is clear that substantial taxonomic work is needed to transfer current Australian Araneus species into appropriate genera with most of them yet to be described (see Framenau 2019). This has recently been completed for

many genera of the informally termed 'backobourkiines' *sensu* Scharff et al. (2020) (e.g., Framenau and Kuntner 2022; Framenau et al. 2022a and references therein).

Australian araneid genera are generally species-poor, and *Cyrtobill* Framenau & Scharff, 2009, *Lariniophora* Framenau, 2011, and *Quokkaraneus* Castanheira & Framenau, 2022 are monotypic (Table 1). Arguably, this list should also include *Austracantha* Dahl, 1914, with its four current subspecies likely synonyms of the nominal species, as well as the enigmatic *Paraplectanoides* Keyserling, 1886, where the second species in the genus, *P. kochi* (O. Pickard-Cambridge, 1877), is more likely a member of the Arkyidae L. Koch, 1872 based on its original description.

Araneus transversus Rainbow, 1912 was described based on a male and female collected in the Blackall Range north of Brisbane in south-eastern Queensland (Rainbow 1912). However, the validity of this species remained controversial, specifically as Davies and

Table 1. Australian genera in the family Araneidae, number of described species in Australia and subfamily placement.

Genus	No. of species in Australia	Subfamily placement (after Scharff et al. 2020)	Comments
Acroaspis Karsch, 1878	5	backobourkiines	
Anepsion Strand, 1929	3	sister to gasteracanthines without statistical support	
Arachnura Vinson, 1863	2	argiopines	revised in Castanheira et al. (2019)
Araneus Clerck, 1758	33 (+1 subspecies)	classical Araneinae Clerck, 1757 not statistically supported	all Australian species misplaced in <i>Araneus</i> based on somatic and genitalic morphology
Argiope Audouin, 1826	17	argiopines	revised in Levi (1983); see also Abel et al. (2020)
Artifex Kallal & Hormiga, 2018	1	Phonognathinae Simon, 1894 (= Zygiellinae Wunderlich, 2004)	revised in Kallal and Hormiga (2018)
Austracantha Dahl, 1914	1 (+ 4 subspecies)	gasteracanthines	
Backobourkia Framenau, Dupérré, Blackledge & Vink, 2010	4	backobourkiines	revised in Framenau et al. (2010b)
Bijoaraneus Tanikawa, Yamasaki & Petchard, 2021	1	in unsupported clade with Eriovixia	
Carepalxis L. Koch, 1872	5	backobourkiines	
Celaenia Thorell, 1868	7	mastophorines	
Cyclosa Menge, 1866	12	in unsupported clade with <i>Leviana</i> and <i>Dolophones</i> sister to gasteracanthines + <i>Anepsion</i>	
Cyrtarachne Thorell, 1868	4 (+ 1 subspecies)	cyrtarachnines	
Cyrtobill Framenau & Scharff, 2009	1	argiopines	monotypic (Framenau and Scharff 2009)
Cyrtophora Simon, 1864	14	argiopines	inchery pre (i ramenda and Benain 2007)
Deliochus Simon, 1894	4 (+ 1 subspecies)	Phonognathinae Simon, 1894 (= Zygiellinae Wunderlich, 2004)	revised by Kallal and Hormiga (2018); 1 species and 1 subspecies likely Tetragnathidae Menge, 1866
Dolophones Walckenaer, 1837	17	in unsupported clade with <i>Leviana</i> and <i>Cyclosa</i> sister to gasteracanthines + <i>Anepsion</i>	subspecies neery returnation wenge, 1000
Eriovixia Archer, 1951	1	in unsupported clade with Bijoaraneus	
Gasteracantha Sundevall, 1833	5	gasteracanthines	
Gea C.L. Koch, 1843	2	argiopines	likely junior synonym of Argiope; revised in Levi (1983)
Herennia Thorell, 1877	1	Nephilinae Simon, 1894	revised in Kuntner (2005)
Hortophora Framenau & Castanheira, 2021	10	backobourkiines	revised in Framenau et al. (2021a)
Larinia Simon, 1874	7	paraphyletic	revised in Framenau and Scharff (2008) and Framenau and Castanheira (2022b)
Lariniophora Framenau, 2011	1	backobourkiines	monotypic (Framenau 2011b)
Leviana Framenau & Kuntner, 2022	5	in unsupported clade with Cyclosa and Dolophones sister to gasteracanthines + Anepsion	revised in Framenau and Kuntner (2022); has putative synapomorphies of backobourkiines
<i>Mangrovia</i> Framenau & Castanheira, 2022	2	not included in Scharff et al. (2020)	revised in Framenau and Castanheira (2022a)
Micropoltys Kulczyński, 1911	2	not included in Scharff et al. (2020)	revised in Smith and Levi (2010)
Nemoscolus Simon, 1895	1	argiopines	phylogenetic placement by Kallal and Hormiga (2020)
Neoscona Simon, 1864	6	in unsupported clade with NGEN04 and Agalenatea Archer, 1951	
Nephila Leach, 1815	1	Nephilinae Simon, 1894	revised in Harvey et al. (2007)
Nephilengys L. Koch, 1872	1	Nephilinae Simon, 1894	revised in Kuntner (2007)
Novakiella Court & Forster, 1993	2	backobourkiines	revised in Framenau et al. (2021b)
Novaranea Court & Forster, 1988	1	zealaraneines	species described in Framenau (2011a)
Ordgarius Keyserling, 1886	3 (+ 1 subspecies)	mastophorines	- I
Paraplectanoides Keyserling, 1886	2	sister to Nephilinae Simon, 1894	
Parawixia F.O. Pickard-Cambridge, 1904	1	backobourkiines	P. dehaani (Doleschall, 1859) misplaced in Parawixia (Scharff et al. 2020)
Phonognatha Simon, 1894	3	Phonognathinae Simon, 1894 (= Zygiellinae Wunderlich, 2004)	revised in Kallal and Hormiga (2018)
Plebs Joseph & Framenau, 2012	7	backobourkiines	revised in Joseph and Framenau (2012)
Poecilopachys Simon, 1895	3	cyrtarachnines	• • • • • • • • • • • • • • • • • • • •
Poltys C.L. Koch, 1843	8	in unsupported clade with Bijoaraneus, Eriovixa and others	revised in Smith (2006)
Quokkaraneus Castanheira & Framenau, 2022	1	basal in ARA-clade	monotypic (Castanheira and Framenau 2022); has putative synapomorphies of backobourkiines
Salsa Framenau & Castanheira, 2022	5	backobourkiines	revised in Framenau and Castanheira (2022)
Socca Framenau, Castanheira & Vink, 2022	12	backobourkiines	revised in Framenau et al. (2022a)
<i>Telaprocera</i> Harmer & Framenau, 2008	2	placement unsupported	revised in Harmer and Framenau (2008)
Thelacantha Hasselt, 1882	1	gasteracanthines	
		Nephilinae Simon, 1894	revised in Harvey et al. (2007)
Trichonephila Dahl, 1911	3		

Gallon (1986) cryptically synonymized the species with *Gea theridioides* (L. Koch, 1872) based on the syntype female, a synonymy currently not accepted in the World Spider Catalog (2022). Indeed, the male syntype has an unusual morphology for an araneid, with long spines on the first pair of legs and a distinct abdominal colouration.

Comprehensive examinations of Australian collections and key overseas institutions holding Australian spider material did not reveal any species that could be considered congeneric to the male syntype of *Araneus transversus* based on morphological characters. This species also does not display any of the synapomorphies of araneid genera currently described from Australia. Therefore, a new monotypic genus is here proposed to accommodate *A. transversus* as a phylogenetic hypothesis within the context of other genera pending further studies into the Australian Araneidae.

Materials and methods

This study is part of a comprehensive 15-year study on Australian Araneidae based on material in all major Australian museums and overseas collections where historical type material is lodged, totalling almost 12,000 records (vials).

and terminology follow Descriptions recent publications on Australian orb-weaving spiders (e.g., Framenau and Castanheira 2022c; Framenau and Kuntner 2022; Framenau et al. 2022a). We separated the characters for the genus- and species-level descriptions as done previously for Courtaraneus Framenau, Vink, McQuillan & Simpson, 2022, Lariniophora and Quokkaraneus Castanheira & Framenau, 2022 (Framenau 2011b; Castanheira and Framenau 2022; Framenau et al. 2022b), i.e., genus-level characters described here are those shown to be informative at that level by a previous morphological systematic study on the Araneidae (Scharff and Coddington 1997). The descriptions are based on recently collected specimens as the male syntype is in poor condition. Colour patterns are described based on specimens preserved in ca. 75% ethanol. The male pedipalp was expanded by alternatively submerging it for around 10 min in 10% KOH and distilled water until fully expanded. The epigyne was cleared in 10% KOH and examined embedded in lactic acid on a microscopic slide under a cover glass.

Microscope photographs were taken with two different stereo-imaging systems. At the Natural History Museum, Copenhagen (Denmark), images were taken with a Nikon D300 digital SLR camera attached via a C-mount adapter to a Leica M16A stereomicroscope. Images of different focal plains were stacked with Automontage (v. 5.02) software from Syncroscopy to increase the depth of field. At the Harry Butler Institute, Murdoch University (Australia), images were taken in different focal planes with a Leica DMC4500 digital camera mounted to a Leica M205C stereomicroscope and combined using the Leica Application Suite X, v. 3.6.0.20104. All photos were edited with Photoshop CC 2020.

All measurements are given in millimetres. They were taken with an accuracy of 0.1 mm, except for eye and labium measurements taken with an accuracy of 0.01 mm.

Maps were compiled in the software package QGis v. 3.2.6 (https://qgis.org/en/site/; accessed 14 November 2022). Geographic coordinates were extracted directly from the original labels or the registration data as provided by the museums. When no detailed geographic information was available, localities were estimated based on Google Earth v. 9.1.39.3 (https://earth.google.com/web/ accessed 14 November 2022) to the closest minute of Latitude and Longitude.

ALE	anterior lateral eyes
AME	anterior median eyes
PLE	posterior lateral eyes
PME	posterior median eyes

Collections

AM	Australian Museum, Sydney (Australia)
QM	Queensland Museum, Brisbane (Australia)
WAM	Western Australian Museum, Perth (Australia)

Taxonomy

Order Araneae Clerck, 1757 Family Araneidae Clerck, 1757

Abba gen. nov.

https://zoobank.org/0A77A238-1C08-4DA7-8A88-64E0F16EF8EE

Type species. Araneus transversus Rainbow, 1912. Designated here.

Etymology. The genus-group name honours the Swedish pop group ABBA whose songs and subsequent musicals Mamma Mia! (2008) and Mamma Mia – Here We Go again! (2018), provided hours of entertainment for the authors. The gender of the genus-group name is feminine.

Diagnosis. *Abba* gen. nov. can be diagnosed by the set of strong prolateral macrosetae on the first tibia of the males and by the distinct colouration of the abdomen in both the males and females, consisting of a pair of dark spots centrally on a uniformly creamy-white to grey dorsal surface (Figs 1A, 3, 4A).

Description. Small orb-weaving spiders, males (total length ca. 3.0–3.5) smaller than females (total length ca. 4.0-4.5). Carapace longer than wide, pear-shaped and with cephalic region comparatively narrower in males than in females; colouration yellowish-brown (green in live specimens), generally without setae (Figs 1A, 4A). Fovea transverse in males and females. Anterior median eyes largest, row of posterior eyes slightly recurved, lateral eyes almost touching; lateral eyes on joint tubercles but the row of the posterior lateral eyes slightly wider than that of the anterior lateral eyes; anterior median eyes slightly protruding from the carapace (Figs 1A, 4A). Maxillae subquadrate, yellow with anterior dark border (Figs 1B, 4B). Sternum longer than wide, yellow, with a sparse cover of setae (Figs 1B, 4B). Labium wider than long, with anterior glabrous light edge (Figs 1B, 4B). Chelicerae fangs with three promarginal teeth of similar size, and three retromarginal teeth of similar size. Legs: Leg formula I > IV > II > III; males with set of ca. five strong prolateral macrosetae on the first tibia (Figs 1A, 3). Abdomen slightly longer than wide, somewhat dorso-ventrally compressed, oval, without humeral humps, specialized

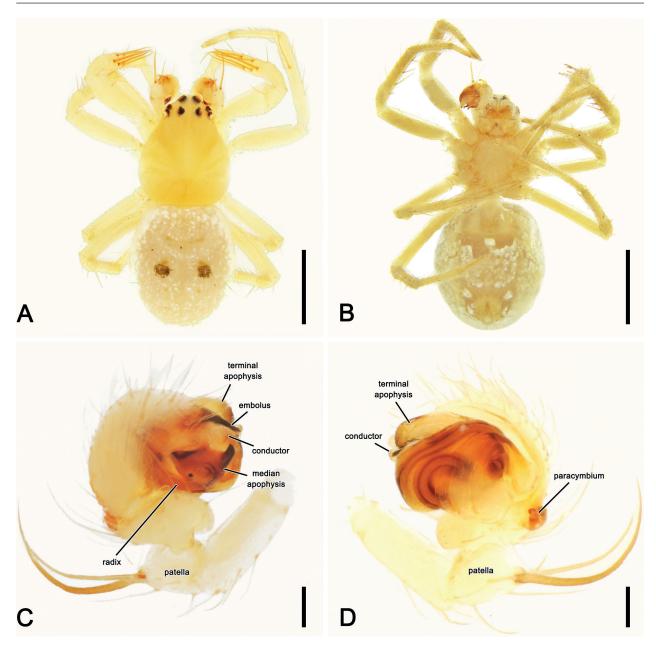


Figure 1. *Abba transversa* (Rainbow, 1912) comb. nov., male (QM S88101). A, dorsal habitus; B, ventral habitus; C, left pedipalp, ventral view; D, left pedipalp, dorsal view. Scale bars: 1 mm (A, B); 0.1 mm (C, D).

setae, sigilla, condyles or other specific structures; colour dorsally varying from beige to grey, bearing two centrally located dark spots (Figs 1A, 4A). Venter grey, sparse layer of guanine crystals (Figs 1B, 4B).

Male pedipalp patella with two macrosetae (Fig. 1C, D); paracymbium elongated and hook-like (Figs 1D, 2B); median apophysis subquadrate spatulate, with strong sclerotized finger-like tip and sclerotized base (Figs 1C, 2A, B); radix poorly developed (Figs 1C, 2A); terminal apophysis wider than long, rounded with sclerotized tip (Figs 1C, D, 2A, B); conductor elongate, membranous, apically slightly curved (Figs 1C, D, 2A, B); embolus heavily sclerotized and thick, curved basally, uncapped (Figs 1C, D, 2A, B).

Epigyne base rounded, lateral portion rounded and heavily sclerotized; atrium wide and heavily sclerotized with copulatory openings located posteriorly (Fig. 4C, D); scape approximately as long as atrium length, not exceeding posterior epigyne base, with terminal pocket (Fig. 4C); spermathecae ovoid to spherical, larger than atrium (Fig. 4C–E).

Abba transversa (Rainbow, 1912), comb. nov. Figs 1A–D, 2A–B, 3, 4A–E, 5

Araneus transversus Rainbow, 1912: 197–198, fig. 14 (male; figs 11–13 and the description of the female are a misidentification, this is *Gea theridioides*); Rainbow 1916: 101; Bonnet 1955: 614; Davies and Gallon 1986: 233.

Type material. Lectotype (designated here) of Araneus transversus Rainbow, 1912: male, Blackall Ranges,

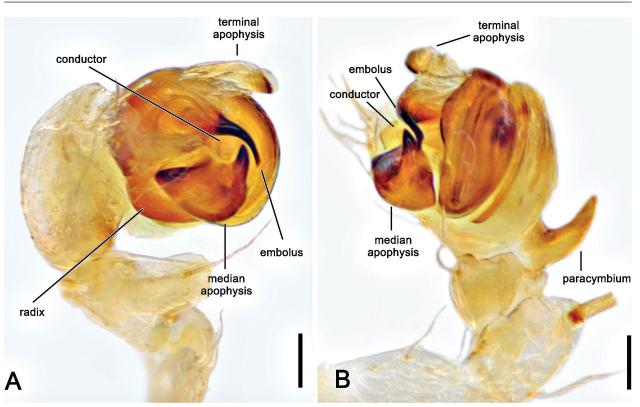


Figure 2. *Abba transversa* (Rainbow, 1912) comb. nov., male (QM S59680), left pedipalp expanded. A, ventral view; B, retrolateral view. Scale bars: 0.1 mm.

Queensland, Australia, 26°34'S, 152°52'E, C. J. Wild (QM W2123), examined. Paralectotype female, same data as lectotype (QM W2126), examined. Misidentification, this is *Gea theridioides* (Davies & Gallon, 1986; VWF pers. obs.).

Other material examined. AUSTRALIA: New South Wales: 2 males, Jamberoo Mountain, 34°40'S, 150°43'E (AM KS.54091, KS.53307). Queensland: 1 female, 5 juv., Chelsea Road Bushland Reserve, 27°28'58"S, 153°11'15"E (QM S77272); 1 male, 1 female, 1 juv., Gold Creek Reservoir, Brookfield, 27°27'53"S, 152°52'32"E (QM S88101); 1 juv., J.C. Trotter Reserve, Burbank, 27°33'08"S, 153°10'31"E (WAM T84345); 1 male, Lamington National Park, 28°12'S, 153°10'E (QM S29181); 1 male, Spear Creek near Mt Molloy, 16°42'S, 145°24'E (QM S88102); 2 males, Topaz, Hughes Road, 17°26'S, 145°42'E (QM S59680).

Diagnosis. As for the genus, which is monotypic.

Redescription. Male (based on QM S8810; expanded pedipalp is QM S59680): Total length 3.1. Carapace 1.2 long, 1.1 wide, yellow (Fig. 1A). Eye diameter AME 0.13, ALE 0.09, PME 0.11, PLE 0.08; row of eyes: AME 0.31, PME 0.32, PLE 0. 60. Chelicerae light yellow, fangs orange (Fig. 1B). Labium 0.14 long, 0.25 wide, subtriangular and yellow, maxillae yellow (Fig. 1B). Sternum 0.6 long, 0.5 wide, yellow with sparse setae (Fig. 1B). Legs yellow, with first femur ventrally mottled in grey, and first tibia bearing a set of five strong and long prolateral macrosetae (Figs 1A, B, 3); length of segments (femur + patella + tibia + metatarsus + tarsus = total length): I - 1.1 + 0.5 + 1.0 + 0.8 + 0.5 = 3.9, II - 1.0 + 0.4



Figure 3. *Abba transversa* (Rainbow, 1912) comb. nov., male (QM S88101), right leg I prolateral view. Scale bar: 0.2 mm.

+ 0.6 + 0.6 + 0.5 = 3.1, III – 0.9 + 0.3 + 0.4 + 0.5 + 0.4 = 2.5, IV – 1.1 + 0.4 + 0.8 + 0.8 + 0.5 = 3.6. Abdomen 1.9 long, 1.5 wide, dorsum grey, with scattered, small white spots, and a pair of median large dark spots (Fig. 1A); laterally off-white; venter grey centrally covered by guanine crystals (Fig. 1B). Pedipalp (Figs 1C, D, 2A, B): length of segments (femur + patella + tibia + cymbium = total length): 0.3 + 0.2 + 0.1 + 0.3 = 0.9; description as for genus.

Female (based on QM S8810): Total length 4.2. Carapace 1.6 long, 1.1 wide; yellow with dusky borders

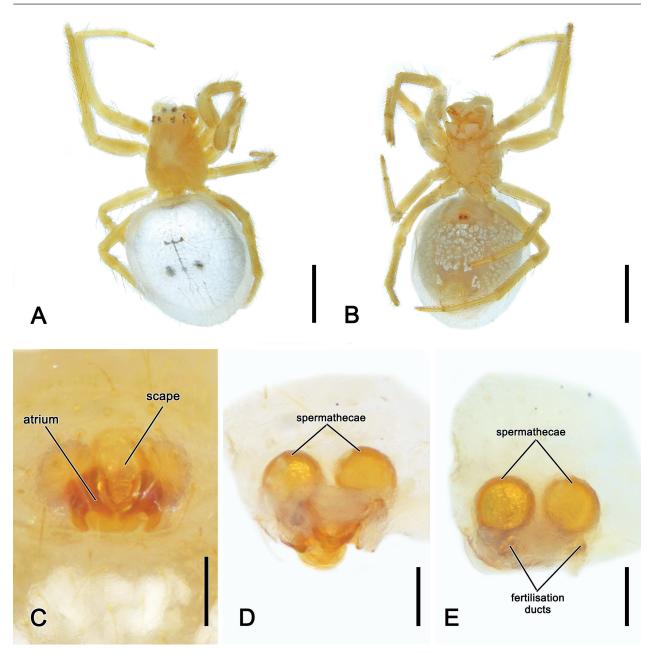


Figure 4. *Abba transversa* (Rainbow, 1912) comb. nov., female (QM S88101). A, dorsal habitus; B, ventral habitus; C, epigyne, ventral view; D, internal genitalia, ventral view; E, internal genitalia, dorsal view. Scale bars: 1 mm (A, B); 0.1 mm (C, D, E).

(Fig. 4A). Eye diameter AME 0.09, ALE 0.07, PME 0.08, PLE 0.08; row of eyes: AME 0.28, PME 0.33, PLE 0.66. Chelicerae of similar colour and dentition as male (Fig. 4B). Legs of similar colour as male, covered with thin setae (Fig. 4A, B). Pedipalp: length of segments (femur + patella + tibia + tarsus = total length): 0.3 + 0.1 + 0.2 +0.5 = 1.1. Leg formula I > IV > II > III; length of segments (femur + patella + tibia + metatarsus + tarsus = total length): I - 1.1 + 0.5 + 1.1 + 1.0 + 0.5 = 4.2, II - 1.0 + 0.4 + 1.0 + 1.0 + 0.4 = 3.8, III - 0.6 + 0.3 + 0.4 + 0.4 + 0.3 = 2.0, IV - 1.0 + 0.4 + 1.0 + 0.9 + 0.6 = 3.9. Labium 0.16 long, 0.27 wide, similar colour as male (Fig. 4B). Sternum 0.7 long, 0.6 wide, similar colour as male (Fig. 4B). Abdomen 2.6 long, 2.2 wide, dorsum off-white with a pair of two median dark spots proportionally smaller than in male (Fig. 4A); lateral and ventral parts similar to those of male (Fig. 4B). Epigyne (Fig. 4C–E) same as for genus.

Variation. Males (total length 3.0-3.3, n = 4). Live images of *Abba transversa* comb. nov. have been published online (e.g., http://www.findaspider.org.au/find/spiders/131.htm; accessed 30 October 2022). The cephalothorax, legs and ventral abdomen are green in live specimens, and the eye region is somewhat yellowish.

Remarks. Davies and Gallon (1986, p. 233) in a catalog of type specimens of the Queensland Museum firstly realized that the female syntype of *Araneus transversus* is in fact *Gea theridioides* and somewhat cryptically proposed a new synonymy ("#f = Gea theridioides (L. Koch) n. syn. – V.T.D"). This taxonomic act, however, was not accompanied by the necessary designation of the female

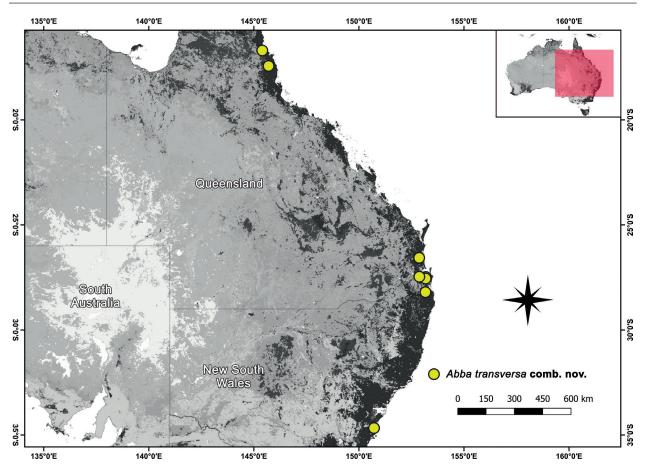


Figure 5. Distribution records of Abba transversa (Rainbow, 1912) comb. nov.

as a lectotype. Later cataloguers apparently did not accept this synonymy, and *A. transversus* is still listed as valid species (World Spider Catalog 2022). We here designate the male syntype as the lectotype of *A. transversus* to fix the species-group name of the species and thereby reject Davies and Gallon's (1986) synonymy.

Life history and habitat preferences. At the Proserpine River, Queensland, *Abba transversa* comb. nov. was found sweeping foliage and grass in an open forest (Rainbow 1916). A single label in the material examined read "coastal ironbark". Mature males and females were generally collected from November to January, except for a male, female and juvenile collected between June and July. The species appears to be largely summer-mature.

Distribution. We examined museum material from northern to south-eastern Queensland and southern New South Wales (Fig. 5). There are records from Victoria on iNaturalist (https://www.inaturalist.org/taxa/533368-Araneus-transversus; accessed 22 July 2022) that may represent this species, but without examination of genitalia an identification cannot be ascertained; these records may represent a second congeneric species.

Discussion

The erection of a monotypic genus for one of the many Australian species currently listed in *Araneus* is not taken lightly and follows extensive examinations of all available material in Australian collections over more than 15 years. Platnick (1976) and Wiley (1977) provide a philosophical discussion on monotypy, but irrespective of their opposing views, monotypic genera representing species not displaying synapomorphies of other taxa are not uncommon in spiders, including the Araneidae (Table 1). It is clear that *Abba transversa* comb. nov. does not share the synapomorphies of any currently described Australian genera. Its highly derived autapomorphies, the prolateral spines on the first leg of males and the unusual abdominal colouration, justify the erection of a new genus for this species and will improve its diagnosability in future keys of Australian araneids.

Abba transversa comb. nov. was not included in any of the recent, large-scale molecular phylogenetic analyses of the Araneidae (e.g., Kallal and Hormiga 2018; Scharff et al. 2020), and its systematic placement based on morphology within an Australian context is difficult. It does not share the putative synapomorphies of the backobourkiines, i.e., a single macroseta on the pedipalp patella of males and the median apophysis forming an arch of the radix (see Scharff et al. 2020) and is therefore unlikely part of this diverse and dominant Australian clade. The species is more likely associated with Scharff et al.'s (2020) well supported zealaraneines. Although this clade has currently no known morphological synapomorphies, most species, like *A. transversa* comb. nov., have two patellar spines on the pedipalp and the epigyne has a terminal pocket (see Court and Forster 1988). Scharff et al. (2020) identified other Australian species to be part of the zealaraneines, i.e., *Araneus albotriangulus* (Keyserling, 1887) and *Ar. talipedatus* (Keyserling, 1887), but both are very unlike *Ab. transversa* comb. nob. and deserve placement in their own new respective genera ("NGEN08" and "NGEN06" in Scharff et al. 2020, respectively).

The presence of a patch of long macrosetae on the prolateral surface of the first pair of legs in males represents one of the diagnostic characters of Abba gen. nov. Strong macrosetae on the first legs of spiders are not uncommon and occur, for example, in Arkyidae, Mimetidae Simon, 1881 and Thomisidae Sundevall, 1833 (e.g., Harms and Harvey 2009; Framenau et al. 2010a; Machado et al. 2019). However, in those families, they are present in both males and females and likely support retaining prey in these sitand-wait predators. By contrast, in Abba gen. nov., the spines on the first legs only occur in males and are therefore more likely a result of sexual selection. Unfortunately, nothing is known about the behaviour of these spiders, and it is unclear if the unusual macrosetae are used in malemale competition for mates or have a role during courtship behaviour. Sexually selected modifications of legs are very common in male orb-weaving spiders but more often relate to the second pair of legs (Framenau et al. 2021a). In many genera, including those in the Australian backobourkiines, the tibia of the second pair of legs in males is much more robust than the others and has enforced spines and spurs (e.g., Scharff and Coddington 1997; figs 1-2). In these cases, the enlarged second tibia is used to fend off females during courtship (Framenau et al. 2021a, pers. comm.).

Acknowledgements

We thank Robert Raven (retired) and Owen Seeman (both QM), Graham Milledge (retired) and Helen Smith (both AM), and Mark Harvey and Julianne Waldock (both WAM), for the loan of specimens in their care or assistance when visiting their respective institutions. Nikolaj Scharff hosted both authors at a number of occasions in Copenhagen and shared great insights into araneid phylogeny and systematics. Agnetha Fältskog, Björn Ulvaeus, Benny Andersson, and Anni-Frid Lyngstad are thanked for the many hours of musical entertainment.

We acknowledge the support of the Leibnitz Institute for the Analysis of Biodiversity Change (LIB), University of Hamburg on waiving the processing fee of this manuscript and thank Danilo Harms (editor), and the two reviewers (Robert Raven and Sarah Crews) for their valuable comments that considerably improved the quality of our manuscript.

Funding for revisions of the Australian Araneidae was provided by the Australian Biological Resources Study (ABRS) (grant no. 205-24 [2005–2008] to VWF and N. Scharff and grant number 4-EHPVRMK [2021–2023] to VWF, PSC, N. Scharff, D. Dimitrov, A. Chopra and R. Baptista).

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