

Review of the Australian and New Zealand orb-weaving spider genus *Novakiella* (Araneae, Araneidae)

Volker W. Framenau^{1,2,4}, Cor J. Vink^{3,4}, Nikolaj Scharff⁵,
Renner L. C. Baptista⁶, Pedro de S. Castanheira^{1,6}

¹ Harry Butler Institute, Murdoch University, 90 South St, Murdoch, Western Australia 6150, Australia

² Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia

³ Department of Pest-management and Conservation, PO Box 85084, Lincoln University, Lincoln 7647, Christchurch, New Zealand

⁴ Centrum für Naturkunde (CeNak), Universität Hamburg, Martin-Luther-King-Platz 3, 20146, Hamburg, Germany

⁵ Zoology Section, Research and Collections, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

⁶ Laboratório de Diversidade de Aracnídeos, Universidade do Brasil/Universidade Federal do Rio de Janeiro. Av. Carlos Chagas Filho 373, 21941-902, Ilha do Fundão, Rio de Janeiro, Brazil

<http://zoobank.org/A32F2CCD-3CB8-4570-87D1-3B38CA555E3C>

Corresponding author: Volker W. Framenau (volker.framenau@murdoch.edu.au)

Academic editor: Danilo Harms ♦ Received 23 April 2021 ♦ Accepted 17 June 2021 ♦ Published 26 July 2021

Abstract

The orb-weaving spider genus *Novakiella* Court & Forster, 1993 (family Araneidae Clerck, 1757) is reviewed to include two species, *N. trituberculosa* (Roewer, 1942) (type species, Australia and New Zealand) and *N. boletus* **sp. nov.** (Australia). *Novakiella* belongs to the informal, largely Australian ‘backobourkiine’ clade and shares with the other genera of the clade a single macroseta on the male pedipalp patella and a median apophysis of the male pedipalp that forms an arch over the radix. The proposed genus synapomorphies are the presence of a large basal conductor lobe expanding apically over the radix and the shape of the median apophysis, which extends into a basally directed, pointy projection. Males have an apico-prolateral spur on the tibia of the second leg that carries a distinct spine. Females have an epigyne with triangular base plate bearing transverse ridges and an elongate triangular scape, which is almost always broken off. The humeral humps of the abdomen are distinct. *Novakiella trituberculosa* build characteristic dome-shaped webs; however, the foraging behaviour and web-shape of *N. boletus* **sp. nov.**, currently only known from museum specimens, are not known.

Key Words

dome-shaped orb-web, new species, systematics, taxonomy

Introduction

A recent multi-gene molecular phylogenetic analysis of the orb-weaving spider family Araneidae Clerck, 1757 recovered a well-supported Australasian clade informally termed ‘backobourkiines’ (Scharff et al. 2020). This clade includes species that would previously have been considered members of the Araneinae Clerck, 1757 (see Scharff and Coddington 1997), specifically those in the genera *Acroaspis* Karsch, 1878; *Backobourkia* Framenau, Dupér-

ré, Blackledge & Vink, 2010; *Carepalxis* L. Koch, 1872; *Novakiella* Court & Forster, 1993 and *Plebs* Joseph & Framenau, 2012; but also *Singa* C. L. Koch, 1836, which has an almost global biogeographical distribution. In addition, the backobourkiines harbour Australian species apparently wrongly placed at the genus level, including some species currently listed in *Araneus* Clerck, 1757, *Eriophora* Simon, 1864 and *Parawixia* F. O. Pickard-Cambridge, 1904. All these genera were polyphyletic in Scharff et al.’s (2020) analysis, with Australian species placed in clades outside

those that included the respective type-species or assumed close relatives from the same biogeographic region.

Morphologically, the backobourkiines are still poorly circumscribed, although a single macroseta on the male pedipalp patella and the median apophysis forming an arch over the radix seem to morphologically unite all genera against many clades previously considered part of the traditional Araneinae (Scharff and Coddington 1997; Scharff et al. 2020). An ongoing revision of Australian Araneidae suggests that the backobourkiines include many more described – generally misplaced at genus level – and undescribed species.

The orb-weaving spider genus *Novakiella* was not diagnosed in detail when initially described (sub *Novakia* Court & Forster, 1988). However, the original description of the genus pointed to a peculiar genital morphology and an unusual horizontal orb-web “drawn up into a cone by threads attached to the hub” built by the type species, *N. trituberculosa* (Roewer, 1942) (Court and Forster 1988, p. 123, figs 563–566). Therefore, *Novakiella* is easily distinguished from other backobourkiine spiders by their male pedipalp morphology with a distinct enlarged conductor lobe and the curved and basally projected median apophysis (Court and Forster 1988, figs 559, 560). Female epigynes have a subtriangular base plate with transverse ridges. The scape is wrinkled, elongate triangular and extends posteriorly past the base plate (Court and Forster 1988, figs 554, 555). The genus currently comprises the type species only, originally described from New Zealand but also known from Australia (Court and Forster 1988). The recent discovery of a second species from Australia allows a more comprehensive generic diagnosis of the genus in comparison to other backobourkiines. Therefore, we herein review *Novakiella*, provide a modern diagnosis against other backobourkiine orb-weavers and (re)describe its two species.

Materials and methods

Descriptions and terminology follow recent publications on Australian orb-weaving spiders (e.g., Framenau et al. 2010; Joseph and Framenau 2012; Castanheira et al. 2019). Colour patterns are described based on specimens preserved in 75% ethanol. Male pedipalps were expanded by alternatively submerging it for 10 min in 10% KOH and distilled water until fully expanded. Female genitalia of *N. trituberculosa* were dissected and cleared with lactic acid. Measurements are given in millimetres.

Images of specimens were taken in different focal planes with a Nikon D300 digital SLR camera attached via a C-mount adapter from LM-Scope (<http://www.lmscope.com>) to a Leica M16A stereomicroscope and combined with Auto Montage (vers. 5.02) software from Syncroscopy to increase depth of field. We used 2 Nikon R1C1 wireless speedlights instead of fibre optics to illuminate the exposures. The latter were used as guide-light for focusing. Microscopic images of cleared epigynes were taken in different focal planes (ca. 20–30 images) on a Leica DMC4500 digital camera mounted to a Leica

M205C stereomicroscope and combined using the Leica Application Suite X, v. 3.6.0.20104. Images of expanded pedipalps of *N. trituberculosa* were taken with a BK Plus Laboratory System from Visionary Digital (Palmyra, PA, USA) equipped with a Canon EOS 7D camera. All photos were edited and mounted with Photoshop CC 2020.

Maps were compiled in the software package QGIS v. 2.14.0 Girona (<https://qgis.org/en/site/>; accessed 21 January 2020). Geographic coordinates were extracted directly from 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 21 January 2021).

Abbreviations

Collections

AM	Australian Museum, Sydney, Australia;
CMNZ	Canterbury Museum, Christchurch, New Zealand;
LUNZ	Lincoln University Entomology Research Collection, New Zealand;
MV	Museums Victoria, Melbourne, Australia;
NZAC	New Zealand Arthropod Collection, Auckland, New Zealand;
QM	Queensland Museum, Brisbane, Australia;
QVM	Queen Victoria Museum and Art Gallery, Launceston, Australia;
SAM	South Australian Museum, Adelaide, Australia;
WAM	Western Australian Museum, Perth, Australia;
NHMD	Natural History Museum of Denmark, Zoological Museum, University of Copenhagen, Denmark.

Morphology

Males: C, conductor; CL, conductor lobe; E, embolus; MA, median apophysis; P, paracymbium; Ra, radix; TA, terminal apophysis. Females: CO, copulatory openings; S, scape; Sp, spermatheca.

Taxonomy

Class Arachnida Cuvier, 1812

Order Araneae Clerck, 1757

Family Araneidae Clerck, 1757

Genus *Novakiella* Court & Forster, 1993, in Platnick (1993)

Novakia Court & Forster, 1988: junior homonym of *Novakia* Strobl, 1893 (Diptera) and *Novakia* Tolmachoff, 1926 (Mollusca) is another junior homonym.

Type-species. *Epeira tri-tuberculata* Urquhart, 1887.

Diagnosis. The informal clade of the backobourkiines is well supported by the molecular phylogeny of Scharff et al. (2020), but the taxonomy and systematics of the species and genera within this clade are poorly resolved. Only three genera within the clade have been revised using modern taxonomic methods: *Plebs*, *Backobourkia* and *Lariniophora* Framenau, 2011. The genera *Carepalxis* and *Acroaspis* have not been revised and their putative synapomorphies remain unknown. It is therefore difficult to diagnose *Novakiella* against these genera. Other Australian backobourkiines included in Scharff et al. (2020) represent species that have clearly been misplaced in genera they do not belong to (i.e., *Eriophora* or *Araneus*) and these represent undescribed genera (in that study listed as “NGEN01” for *Eriophora transmarina* (Keyserling, 1865), “NGEN02” for *Araneus rechenensis* Main, 1954 and “NGEN05” for *Araneus senicaudatus* Simon, 1908). Until these species have been revised and placed in new or existing genera, *Novakiella* cannot be diagnosed against them.

Novakiella distinctly differs from the revised backobourkiine genera by overall somatic morphology. The abdomen is subtriangular with strong humeral humps (Figs 1A, 3A, 4A, 6A), while it is rounded with small humerals in *Backobourkia* (i.e., Framenau et al. 2010, fig. 5), slightly elongated in *Plebs* (e.g. Joseph and Framenau 2012, figs 6, 7, 10), and strongly elongated in *Lariniophora* (Framenau 2011, figs 2, 3). Males can be differentiated by the presence of a tibial apico-prolateral spur carrying a thick spine (or macroseta) on leg II (Figs 1E, 4C). *Verrucosa* McCook, 1888 and *Carepalxis* also have a spur on leg II, but in both genera it carries two spines (Levi 2002: p. 546; Lise et al. 2015: p. 5; VWF pers. obs.). In addition, *Verrucosa* is limited to the Neotropics and not part of the backobourkiines (Scharff et al. 2020). There are distinct differences in the male pedipalp morphology between *Novakiella* and other backobourkiines. *Novakiella* males have a stout median apophysis that is drawn out into a basally pointing acute projection (Figs 1C, 2B, 4D, E, 5); in contrast, the median apophysis has a basal flange in *Backobourkia* (Framenau et al. 2010) (absent in *Novakiella*), is elongate transverse with two apical tips in *Plebs* (Joseph & Framenau, 2012, e.g. figs 4B, 8A), and has a two-humped lobe in *Lariniophora* (Framenau, 2011, fig. 4). All backobourkiines appear to have a basal extension of the conductor (discussed in Framenau et al. 2010 and there termed paramedian apophysis), but in *Novakiella* it is very different to all other described backobourkiines and much more conspicuous; we here propose a new term, conductor lobe (CL), which extends apically well past the radix (Figs 1C, 2A, B, 4D–F, 5).

Females of *Novakiella* have an elongated triangular scape without terminal pockets, as is typical for all backobourkiines above; however, these genera lack the subtriangular base plate with its transverse and lateral wrinkles (Figs 3C, 6C; Framenau et al. 2010, e.g. figs 6D, F; Framenau 2011, fig. 6; Joseph and Framenau 2012, e.g. figs 4D, 8E).

Description. Medium-sized (TL males ca. 5–9, females 8–12) orb-weaving spiders with males on average

slightly smaller than females. Carapace longer than wide, pear-shaped; cephalic area similar in shape in both sexes (Figs 1A, 3A, 4A, 6A); fovea longer than wide in males and wider than long in females, and with a dark spot in both sexes (Figs 1A, 3A, 4A, 6A); colouration (of ethanol preserved specimens) varying from reddish-brown to yellowish-brown, with black patches along carapace borders (Figs 1A, 3A, 4A, 6A). Eyes ringed in black, anterior median eyes largest, posterior eye row slightly recurved, lateral eyes almost touching, posterior lateral eyes separated from posterior median eyes by more than their diameter and located on small tubercles at the clypeus border (Figs 1A, 3A, 4A, 6A). Chelicera paturon with dark hue, fangs reddish-brown. Labium wider than long, subtriangular, with front end bulging and beige (Figs 1B, 3B, 4B, 6B). Endites rounded, inner portion beige (Figs 1B, 3B, 4B, 6B). Sternum almost as long as wide with dark contour (Figs 1B, 3B, 4B, 6B). Legs (Figs 1A, B, E, 3A, B, 4A–C, 6A, B): Leg formula IV > I > II > III, all longer than body's length with dark spots on joints; tibia II of males with apico-prolateral spur bearing a thick macroseta or spine (less pronounced in *N. boletus* sp. nov.). Abdomen subtriangular, longer than wide, with two distinct humeral humps and posterior tip reaching beyond spinnerets (Figs 1A, 3A, 4A, 6A); folium pattern distinct; sides varying in colour from yellowish-brown to black (Figs 1A, 3A, 4A, 6A), venter light coloured, generally mottled dark (Figs 1B, 3B, 4B, 6B). Male genitalia (Figs 1C, D, 2A, B, 4D–F, 5): male pedipalp patella with a single strong macroseta; paracymbium well-developed and hook-like; cymbium longer than wide; radix thick and elongated, reaching from the base of median apophysis to near the cymbium tip; conductor lobe conspicuous and projected apically, being composed of two distinct lobes (*N. trituberculosa*) or mushroom-shaped (*N. boletus* sp. nov.); terminal apophysis wider than long, rounded and tapering terminally; conductor well-developed, subquadrate; embolus uncapped, elongated, pointed and almost straight; median apophysis stout, with an acute basally pointing tip. Female genitalia (Figs 3C–E, 6C): epigyne plate wider than long, subtriangular; scape much longer than wide and extending posteriorly beyond plate (but length not known in *N. boletus* sp. nov.), generally broken off. Spermathecae spherical and occupying most of genital area.

Composition. *Novakiella trituberculosa* (Roewer, 1942) and *N. boletus* sp. nov.

Remarks. The nomenclatural history of *Novakiella* is convoluted. *Novakiella trituberculosa* was first described as *Epeira tri-tuberculata* by Urquhart (1887), before Roewer (1942) replaced the species-group name as it is a junior primary homonym of *Epeira trituberculata* Lucas, 1846, currently listed as a junior synonym of *Cyclosa insulana* (Costa, 1834). Court and Forster (1988) described the genus *Novakia* to accommodate this species; however, this new genus-group name was also preoccupied, by *Novakia* Strobl, 1893 (Diptera) and *Novakia* Tolmachoff, 1926 (Mollusca). Court and Forster, in Platnick (1993), proposed *Novakiella* Court & Forster, 1993 as a replacement name.

Distribution. Australia and New Zealand (Figs 7, 8).

***Novakiella trituberculosa* (Roewer, 1942)**

Figs 1–3, 7, 8

Epeira tri-tuberculata Urquhart 1887: 78–79, pl. 7, fig. 2; pl. 8, fig. 1 (preoccupied by *Epeira trituberculata* Lucas, 1846; currently listed as junior synonym of *Cyclosa insulana* (Costa, 1834).

Epeira tri-tuberculata Urquhart 1888: 120–121, pl. 11, figs 7, 8.

Aranea trituberculosa Roewer 1942: 834 (replacement name).

Novakia trituberculata Court and Forster 1988: 119–124, figs 359, 553–562.

Novakiella trituberculosa Court and Forster, in Platnick 1993: 457.

Type material. Syntypes of *Epeira tri-tuberculata* Urquhart, 1887, 2 females, Karaka, New Zealand (37°06'S, 174°53'E), A.T. Urquhart (CMNZ 2005.135.112). Examined.

Other material examined. AUSTRALIA: Australian Capital Territory: 1 female, 1 juvenile, Canberra, 35°18'S, 149°08'E (SAM); 1 female, Kaleen, Canberra, 35°17'S, 149°13'E, 25.iv.1990 (SAM 31192); 1 male, 1 female, Kaleen, Canberra, 35°17'S, 149°13'E, 21.v.1988 (SAM); 1 male, Red Hill, 14 Pera Place, 35°20'S, 149°08'E, 24.ii.1982, M. S. Harvey leg. (WAM T73527); 1 male, same locality, 01.iv.1983, M. S. Harvey leg. (WAM T73571); **New South Wales:** 1 male, Beecroft, 33°45'S, 151°04'E, 25.i.1999, J. Noble leg. (AM KS58630); 1 female, Botany, 33°57'S, 151°12'E, 04.vii.1961, R. Mascord leg. (AM KS32651); 1 female, same locality, 26.vii.1966, R. Mascord leg. (AM KS32652); 1 female, Coonabarabran, 'Smokey Hole', 31°16'S, 149°17'E, 04.x.1978, E. Edmondson leg. (AM KS7545); 1 male, Dulwich Hill, 33°54'S, 151°08'E, 17.ii.1977, H. Ehmann leg. (AM KS0741); 1 male, Epping Strip, 33°46'S, 151°05'E, 10.i.1996, J. Noble leg. (AM KS49920); 1 male, Hillsdale, Sydney, 33°57'S, 151°13'E, 03.ii.1972, R. Mascord leg. (AM KS34148); 1 male, Khancobin, 26.iv.1990 (SAM); 1 female, Lord Howe Island, Erskine Valley Transect, 31°34'58"S, 159°04'45"E, pitfall traps, 01.xi.1978, T. Kingston leg. (AM KS88175); 1 male, Lord Howe Island, Goat House Cave, 31°33'54"S, 159°05'18"E, 10.ii.1971, M. Gray leg. (AM KS20999); 1 female, Mount Colah, 33°40'S, 151°07'E, M. Gray leg. (AM KS48820); 1 male, Park Beach, Coffs Harbour, 30°18'S, 153°07'E, 23–24.v.1986 (SAM), 1 male, Punchbowl, 33°56'S, 151°03'E, 02.xii.1940, Ms Levitt leg. (AM KS33550); 1 male, The Rock Nature Reserve, 30km SW Wagga Wagga, 35°16'S, 147°05'E, sweeping/beating, 13.xii.2000, C. A. Car leg. (AM KS93847); **Queensland:** 1 male, Bardon, Brisbane, 27°27'S, 152°58'E (QM); 1 female, Burleigh Heads, 28°06'S, 153°26'E (QM); 1 male, 1 juvenile, Endfield Station, 27°55'S, 149°43'E (QM); 1 female, Eurimbula, 24°11'S, 151°50'E, C. Horseman leg. (AM KS12771); 1 female, Gatton, Queensland Agricultural College, 27°34'S, 152°20'E, S. Pearce leg. (QM S66755); 1 male Hurdle Gully, 13km WSW Monto, 24°54'00"S, 150°59'55"E, 23.ix–20.ix.1997, G. Monteith leg. (QM); 1 male, Jerons St Park, 27.xi.2009, R. Whyte leg. (WAM S84676); 1 male, Jevons, 26.xii.2009, R. Whyte leg. (QM S84670); 1 female, same locality,

01.i.2010, R. Whyte leg. (QM S84672); 1 male, Masthead Island, Great Barrier Reef, 23°32'S, 151°44'E, C. Hedley leg. (AM KS32650); 1 male, Mt Gavial, 1km S, 23°36'S, 150°29'E, 17.xii.1998, D. J. Cook leg. (QM S69354); 1 male, Oakey, 27°27'S, 151°42'E (QM); 1 male, Teewah Creek, Cooloola, 26°02'S, 153°03'E (QM); 1 female, Walton Bridge Reserve, 20.xi.2009, R. Whyte leg. (QM S84666); **South Australia:** 1 male, Baird Bay, 33°09'S, 134°22'E, 12.i.1995, J. M. Waldoock & P. Payne leg. (WAM T73553); 1 male, 1 female, Beautiful Valley Caravan Park, adjacent, near Wilmington, 32°39'S, 138°06'E, 14.iv.1993 (SAM); 1 male, Belalie Creek, Jamestown, 33°12'S, 138°36'E, 10.iv.1993, D. Hirst leg. (SAM); 2 males, Cape Gantheaume, 1km N Point Tinline, Kangaroo Island, 35°59'S, 137°37'E, 10.xi.1987, D. Hirst leg. (SAM); 1 male, Caracoorte Cave Reserve, 37°05'S, 140°47'E, 25.iv.1979, D. Lee leg. (SAM); 1 female, Caroline Forest, 'Snowgum Reserve', 37°56'S, 140°56'E, 20.iv.1979, G. Grass leg. (SAM); 1 male, Coromandel Valley, Mt Lofty Ranges, 32°05'S, 138°38'E, 02.iii.1996, L. N. Nicolson leg. (SAM); 1 female, Dog Lake Road, SE Langhorne Creek, 35°17'S, 139°02'E, J. Eckert leg. (SAM); 1 female, Eucla, 77km E, 31°28'S, 129°37'E, 23.ii.1978, B. Y. Main leg. (WAM T87424); 1 female, Forestville, 34°57'S, 138°35'E (SAM); 1 male, Gluepot Reserve, 11.3km W Gluepost Homestead, 33°45'16"S, 139°59'58"E, 26.xi.–06.xii.2000 (SAM NN19454); 1 female, Kangaroo Island, 35°45'S, 137°37'E (SAM); 1 male, Kangaroo Island, Western River Wilderness Protection Area, Waterfall Creek near waterfall, 35°41'44"S, 136°54'37"E, beating, 09–10.v.2010, M. G. Rix & D. Harms leg. (WAM T102789); 1 male, Lake Gilles Conservation Park, 33°05'S, 136°39'E, 21.xi.1995 (SAM); 1 female, Langhorne Creek, 35°18'S, 139°02'E, C. Wilson leg. (SAM); 1 female, 1 juvenile, Marino Rocks to Halletts Cove, near railway line, 35°04'S, 138°30'E, 05.ix.1967, H. M. Cooper leg. (SAM); 2 females, Melrose, camping area, 32°49'S, 138°11'E, 14.iv.1987, D. Hirst leg. (SAM); 1 male, Mitcham, 34°59'S, 138°37'E, 21.i.1979, R. V. Southcott leg. (SAM); 2 females, Muston, Kangaroo Island, 35°49'S, 137°44'E, 03.vii.1967, H. M. Cooper leg. (SAM); 1 female, Nappyalla, 35°20'S, 139°07'E, J. Eckert leg. (SAM); 1 female, Port Wakefield, 34°11'S, 138°09'E, 14.iii.2004, B. S. Pavey leg. (SAM); 1 female, Port Wakefield, T-junction W, 34°11'S, 138°09'E, B. Pavey leg. (SAM); 1 male, Pyap, 34°27'S, 140°29'E, 02–09.vi.1990, L. N. Nicolson leg. (SAM); 1 female, Sellicks-Aldinga Scrub, 35°17'S, 138°27'E, 22.ix.1987, D. Hirst leg. (SAM); 1 male, Serpentine Lakes, 28°30'S, 129°00'E, 16.iv.1994, D. Hirst leg. (SAM); 1 female, St Peters, Adelaide, 33°55'S, 151°11'E, 27.i.1975, P. Walker leg. (AM KS32104); 1 male, Walkerville, Adelaide, 34°53'S, 138°37'E, 20.vi.1984, J. Thurmer & D. Hirst leg. (SAM); 1 male, Windsor Gardens, Adelaide, 34°52'S, 138°39'E, 20.vi.1988, D. Hirst leg. (SAM); 2 males, East Risdon, 42°50'S, 147°21'E, 27.iv.1961, V. V. Hickman leg. (AM KS28582); **Tasmania:** 3 males 1 juvenile, Launceston, 41°27'S, 147°10'E, 06.iv.1928, V. V. Hick-

man leg. (AM KS28538), 1 female, same locality, 03.ix.1929, V. V. Hickman leg. (AM KS28547); 1 female, Liberty Creek Track, S side Macquarie Heads, 42°12'S, 145°12'E (QM); 3 males, 2 females, 2 juveniles, New Town, 42°53'S, 147°19'E, 10.ii.1934, V. V. Hickman leg. (AM KS28699); 1 female, St. Columba Falls, 41°19'17"S, 147°55'34"E, 07.iii.2006, G. Hormiga leg. (NHMD); **Victoria:** 1 female, Balwyn, 24 Yandilla Street, 37°48'S, 145°04'E, 05.iv.1981, M. S. Harvey leg. (WAM T73551); 1 male, same locality, 31.iii.1981, M. S. Harvey leg. (WAM T73572); 1 male, same locality, 12.i.1981, M. S. Harvey leg. (WAM T73573); 1 male, same locality, 05.iv.1981, M. S. Harvey leg. (WAM T73574); 1 male, same locality, 28.xii.1982, M. S. Harvey leg. (WAM T73577); 1 male, Beaconsfield, 38°03'S, 145°15'E, 07.xi.1893 (MV K9424); 1 female, Cann River, 20km N, 37°17'S, 149°12'E, 17.vi.1987, R. J. Raven leg. (QM S13154); 1 female, Canterbury, 7 Quantock St, 37°49'S, 145°04'E, 13.vi.1981, M. S. Harvey leg. (WAM T73556); 3 females Croydon, 37°47'S, 145°16'E, 28.ii.1999, S. W. Fulton leg. (MV K10088); 1 male, 1 female, 1 juvenile, Echuca, 36°08'S, 144°45'E, 01.xi.1955 (MV K9427); 1 female, Emerald, 37°56'S, 145°27'E, 13.v.1948, C. Oke leg. (AM KS32504); 1 female, Frankston, 38°08'S, 145°08'E, 30.iv.1994 (SAM); 1 male, Nyah to Kooloonong (no exact location), B. Harvey leg. (MV K9451); **Western Australia:** 1 female, Attadale, 32°01'S, 115°48'E, 20.vii.1962, A. R. Main leg. (WAM T87192); 1 female, Bannister, 32°39'S, 116°33'E, 15.vi.1985, B. Y. Main leg. (WAM T73564); 1 female, Bannister, 32°39'S, 116°33'E, 15.vi.1985, B. Y. Main leg. (WAM T73565); 1 female (WAM T73566); 1 male, Boolathana Station, 24°24'49"S, 113°44'41"E, pitfall trap, 15.i.–31.v.1995, J. M. Waldock et al. leg. (WAM T73548); 1 female, Boya, Helena Valley, 31°54'S, 116°03'E, 06.x.1982, B. Y. Main leg. (WAM T73561); 1 female (WAM T73562); 1 female, same locality, 08.x.1982, P. Hussey leg. (WAM T73563); 1 male, Commonwealth Road, West, 32°44'13"S, 118°16'16"E, wet pitfall trap, 30.x.1997–15.v.1998, N. A. Guthrie leg. (WAM T74852); 1 female, Durokoppin Nature Reserve, 31°24'S, 117°46'E, 03.vi.1989, B. Y. Main leg. (WAM T73567); 1 female, same locality, 05.v.1987, B. Y. Main leg. (WAM T73568); 1 male, Grass Patch, Fitzg. Loc. 41, 32°13'56"S, 121°46'00"E, 29.xi.1978, A. F. Longbottom leg. (WAM T73578); 1 male, Hurlstone Nature Reserve, 32°32'32"S, 119°22'42"E, wet pitfall trap, 30.x.1997–20.v.1998, P. van Heurck et al. leg. (WAM T74854); 1 male, Jarrahdale (Alcoa) Mine area, 31°16'S, 116°06'E, K. E. C. Brennan leg. (WAM T48214); 1 female, vacuum collector, M. L. Moir leg. (WAM T48215); 1 female, N of Lake King-Norseman Road, 33°04'54"S, 119°59'53"E, wet pitfall trap, 15.x.1999–25.x.2000, N. A. Guthrie leg. (WAM T74863); 1 male, Lake Morgan, Helms Arboretum, 33°43'09"S, 121°48'29"E, wet pitfall trap, 15.x.1999–01.xi.2000, P. van Heurck et al. leg. (WAM T74853); 1 male, Mount Gibson iron-ore mine, 29°36'02"S, 117°12'25"E, pitfall trap, 15–30.iv.2005, S. Thompson leg. (WAM T67918); 1 male, Roe Plain, be-

tween Mundrabilla and Madura, 32°04'S, 126°31'E, 26.ii.1990, B. Y. Main leg. (WAM T87431); 1 female, Stirling Range National Park, Moingup Spring, 34°24'S, 118°06'E, 10.vi.1993, J. M. Waldock & A. Sampey leg. (WAM T74423); 1 female, Torbay Hill, Lot 40, 35°04'S, 117°37'E, 07.x.1983, B. Y. Main leg. (WAM T73569); 1 female, same locality, 06.x.1993, B. Y. Main leg. (WAM T73570); 1 female, Two Peoples Bay Nature Reserve, track near coast, 34°59'25"S, 118°09'35"E, 01.v.2008, M. Rix & M. S. Harvey leg. (WAM T81707). **NEW ZEALAND: North Island:** 1 male, Parau Scenic Reserve, 35°05'S 173°27'E, at night, 16.ii.2000, G. Hall leg. (NZAC 03038710); 1 male, Karaka, 37°06'S, 174°53'E, A.T. Urquhart leg. (CMNZ 2005.135.112); 1 male, Hamilton, 37°48'S 175°18'E, 2014, B.N. McQuillan leg. (LUNZ 00012963); 1 female, Hamilton, 37°48'S 175°18'E, 2014, B.N. McQuillan leg. (LUNZ 00012964); **South Island:** 1 female, Kaituna Valley, 43°44'S 172°42'E, 24.v.1975, R.R. Forster leg. (NZAC 03038712).

Diagnosis. Male *N. trituberculosa* can easily be distinguished from *N. boletus* sp. nov. by the much stronger apico-prolateral spur on tibia of leg II and the morphology of key pedipalp sclerites (Figs 1C–E, 2A, B, 4D–F, 5): median apophysis with a longer basal portion and a smaller pointed curved and acute tip in *N. trituberculosa* (projection to the tip flattened, much longer, reaching beyond the radix base and tip rounded in *N. boletus* sp. nov.), conductor lobe two-lobed in *N. trituberculosa* (mushroom-shaped in *N. boletus* sp. nov.), and embolus almost straight in *N. trituberculosa* (with tip strongly bent, thin and very acute in *N. boletus* sp. nov.). Females of *N. trituberculosa* differ from those of *N. boletus* sp. nov. by details in the epigyne plate (Figs 3C, 6C), specifically its subtriangular shape in *N. trituberculosa* (trapezoidal in *N. boletus* sp. nov.); the transverse and short wrinkles, mainly laterally visible in *N. trituberculosa* (more pronounced and crossing the plate in *N. boletus* sp. nov.); copulatory openings less conspicuous in *N. trituberculosa* (clearly visible in *N. boletus* sp. nov.); and bridge thin and longer in *N. trituberculosa* (subtriangular, much wider at posterior margin in *N. boletus* sp. nov.).

Redescription. Male (WAM T73571 [images]; WAM T73573 [measurements]): Total length: 5.3. Carapace (Fig. 1A) 2.7 long, 2.1 wide, light brown with large black bands on lateral margins and yellowish setae throughout except from fovea to pedicel; cephalic area subquadrate; fovea longer than wide and bearing a long black spot. Eyes ringed in black, lateral ones located on small tubercles (Fig. 1A). AME 0.22, ALE 0.11, PME 0.14, PLE 0.11; row of eyes: AME 0.58, PME 0.40, PLE 0.86. Chelicerae with paturon light brown and fangs reddish-brown; three promarginal teeth, central one largest, two or three retromarginal teeth, basal one largest. Legs (Fig. 1A, B, E) yellow with dark brown spots on joints; tibiae II with strong apico-prolateral spur that carries a stout spine; metatarsi and tarsi of leg II slightly curved; leg formula IV > I > II > III; length of segments (femur + patella + tibia + metatarsus + tarsus = total length): I – 3.97 + 1.30

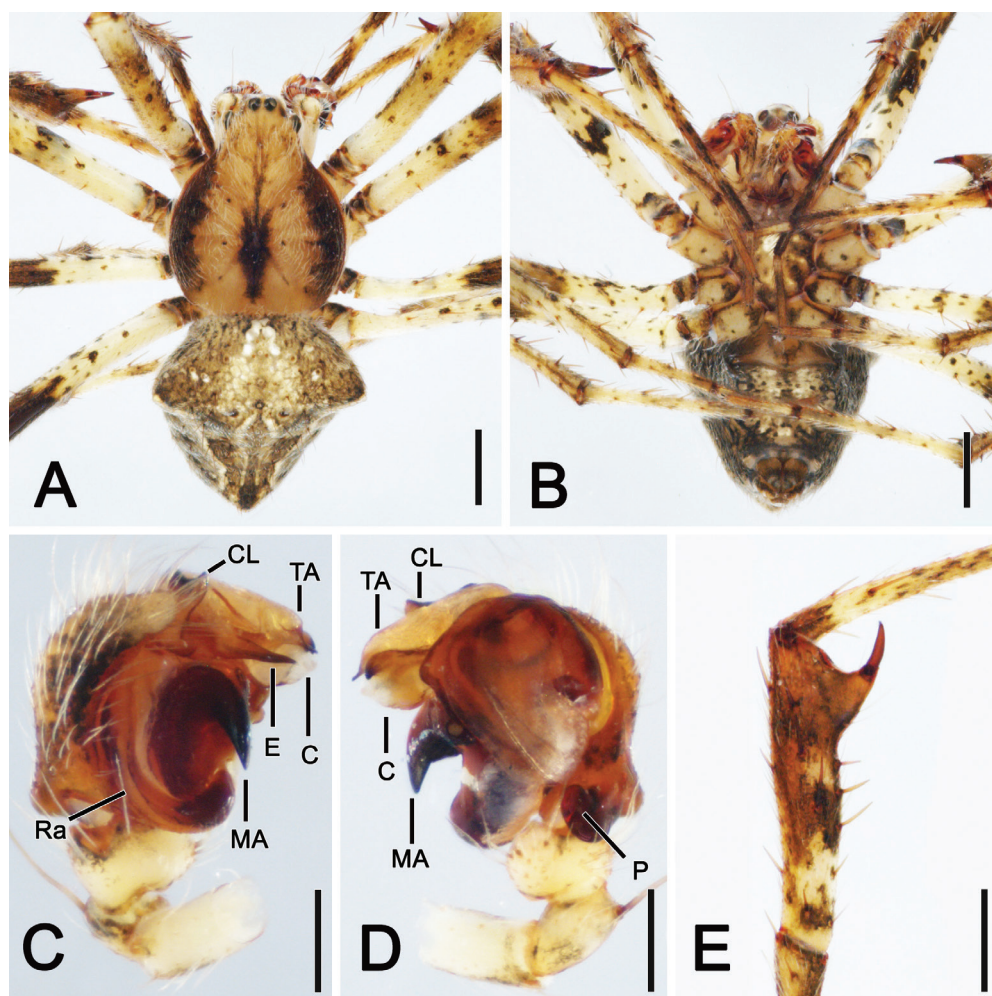


Figure 1. *Novakiella trituberculosa*, male (WAM T73571). **A.** Dorsal habitus; **B.** ventral habitus; **C.** Left pedipalp, mesal view; **D.** Left pedipalp, ventral view. Abbreviations: C, conductor; CL, conductor lobe; E, embolus; MA, median apophysis; P, paracymbium; Ra, radix; TA, terminal apophysis. Scale bars: **A, B,** 1 mm; **C, D,** 0.5 mm; **E,** 1.2 mm.

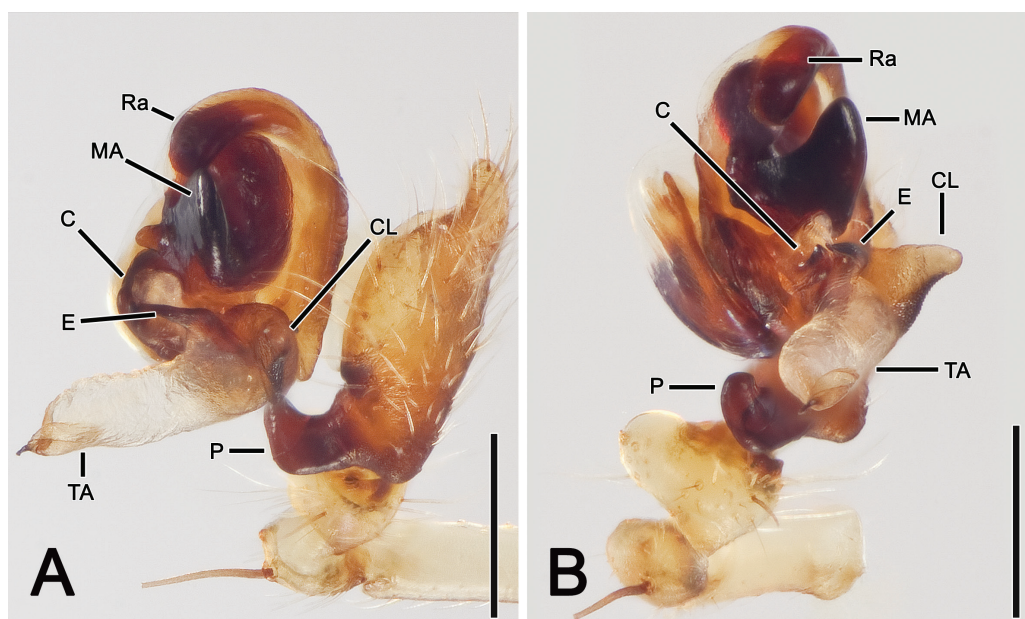


Figure 2. *Novakiella trituberculosa*, male (WAM T73571), expanded left pedipalp. **A.** Ventral view; **B.** Retrolateral view. Abbreviations: C, conductor; CL, conductor lobe; E, embolus; MA, median apophysis; P, paracymbium; Ra, radix; TA, terminal apophysis. Scale bars: 0.5 mm

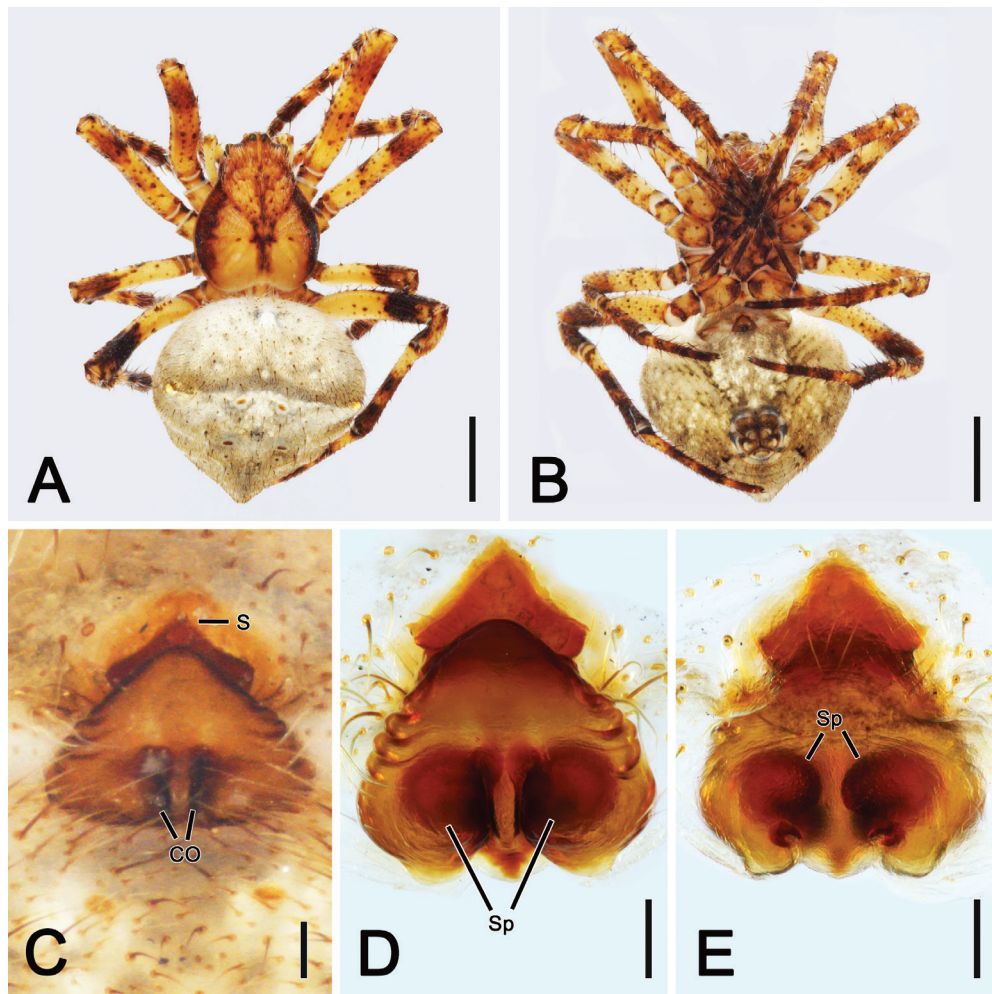


Figure 3. *Novakiella trituberculosa*, female (WAM T73556). **A.** Dorsal habitus; **B.** Ventral habitus; **C.** Epigyne, ventral view; **D.** Cleared epigyne, ventral view; **E.** Cleared epigyne, dorsal view. Abbreviations: CO, copulatory openings; S, scape; Sp, spermatheca. Scale bars: **A, B,** 2 mm; **C–E,** 0.1 mm.

+ 3.25 + 2.86 + 0.97 = 12.35, II – 2.73 + 1.17 + 2.21 + 0.90 + 0.97 = 7.98, III – 2.34 + 0.71 + 1.23 + 1.30 + 0.72 = 6.30, IV – 3.51 + 0.97 + 2.14 + 2.14 + 0.84 = 9.62. Labium wider than long, subtriangular, brown (Fig. 1B); endites rounded, light brown (Fig. 1B). Sternum slightly longer than wide, light brown, with thick black edges and large anterior guanine white spot (Fig. 1B). Abdomen (Fig. 1A, B) 3.06 long, 2.47 wide; subtriangular, longer than wide, abdominal humps strong and posterior end reaching over spinnerets; dorsum beige with posterior darker folium pattern; sparsely covered with long brown setae; sides dark olive-grey; venter beige and irregularly mottled with brown spots. Pedipalp (Figs 1C, D, 2A, B) length of segments (femur + patella + tibia + cymbium = total length): 0.58 + 0.26 + 0.26 + 0.78 = 1.88; conductor lobe bilobed, basal lobe rounded and apical lobe pointed and connected to a wide and concave lateral expansion, whose ectal border has a dense black field of scale-like structures; terminal apophysis with an inflated and membranous body, ending in curved and pointed well-sclerotised tip; embolus slightly sinuous in mesal view, tapering apically towards conductor when expanded (Fig. 2A, B);

conductor very conspicuous and subquadrate with a projected and sclerotised tip; median apophysis stout, heavily sclerotised, forming an arch over the radix, medially curved and extended into a basally pointing tip.

Female (WAM T73556): Total length: 9.0. Carapace 3.5 long, 2.8 wide, eyes, chelicerae, legs, labium, endites and sternum essentially as in male (Fig. 3A, B). Eye measurements: AME 0.18, ALE 0.09, PME 0.14, PLE 0.14; row of eyes: AME 0.63, PME 0.47, PLE 1.46. Pedipalp length of segments (femur + patella + tibia + cymbium = total length): 1.12 + 0.48 + 0.48 + 1.20 = 3.28. Leg formula IV > I > II > III; length of segments (femur + patella + tibia + metatarsus + tarsus = total length): I – 3.92 + 1.60 + 3.20 + 2.96 + 0.96 = 12.64, II – 3.68 + 1.52 + 2.88 + 0.90 + 0.88 = 9.86, III – 2.40 + 0.88 + 1.44 + 1.44 + 0.80 = 6.96, IV – 4.08 + 1.36 + 2.56 + 2.48 + 1.04 = 11.52. Abdomen (Fig. 3A, B) 5.00 long, 4.80 wide, similar to male in shape and colour, but slightly more rounded, with less projected humeral humps. Epigyne plate subtriangular, with smooth anterior portion near the basis of scape and lateral wrinkles; scape broken off (Fig. 3C–E) (as in all specimens examined by us). If present, scape

triangular with indistinct transverse wrinkles (Court and Forster 1988, figs 554, 555). Spermathecae spherical and very large, occupying most of the genital area, medially connected to copulatory openings (Fig. 3D, E).

Remarks. The study was conducted over many years and at different institutions and therefore imaging and descriptive work based on variable specimens (plural) availability at the time. This explains why the male *N. trituberculosa* is here redescribed based on two specimens; one imaged many years ago, but not measured, and the measurements added for a second specimen more recently.

Habitat preferences and life history. In Australia, mature males of *N. trituberculosa* were found between November and June, with peaks in January and April. Mature females were found all year round with the lowest numbers of records in November and December. Here, the species is mainly found in “pastoral habits” and constructs a horizontal orb-web amongst low grasses or weeds, with the centre pulled up by stabilizing threads. The webs are up to 0.1 m above ground. Additionally, habitat descriptions on specimen labels include “woodland”, “open forest”, “shrubs near ground”, “in long grass”, but the species also seems to occur in more disturbed habitats such as “among garden rubbish”, “ex toilet”, “walking on wall at night”, “inside house on wall”, “stationary on door knob”. In New Zealand it is mostly found in pastoral habitats (Court and Forster 1988), which suggests that it is introduced.

Distribution. *Novakiella trituberculosa* has been recorded from all Australian states, except Northern Territory, south of ca. 22°S Latitude (Fig. 7). In New Zealand the species is more frequently found in the North Island but it has also been found in some South Island localities (Court and Forster 1988) (Fig. 8).

Novakiella boletus sp. nov.

<http://zoobank.org/2181EC8F-7BE5-4ECD-92EC-9FB21DD4B177>

Figs 4–7

Type material. Holotype male from Maits Rest, 10 km W of Apollo Bay, Otway Ranges, Victoria, AUSTRALIA, 38°45'S, 143°34'E, 16.iii.1992, G. Milledge leg. (MV K9867).

Other material examined. **AUSTRALIA:** **New South Wales:** 1 male, Coolah Tops National Park, off Gemini Road Loop, 31°48'59"S, 150°10'31"E, beating, 12–13.iv.2010, M. G. Rix & D. Harms leg. (WAM T102788); **South Australia:** 1 female, Kelly Hill Caves camping area, Kangaroo Island, 35°59'S, 136°54'E, 09.xi.1987, D. Hirst leg. (SAM); 1 male, Loftia Recreation Park, 35°02'S, 138°42'E, pitfall traps, 20–27.iii.1990, D. Hirst leg. (SAM). **Tasmania:** 1 male, Junction Creek, Arthur Plains West, 43°5'S, 146°16'E, 08.ii.1966, A. Neboiss leg. (MV K9862); 3 females, 3.8 km SE of Beechford, 41°02'50.6"S, 146°59'20.94"E, May 2021, vehicle vibration (QVM:2021:13:0514–5, 2021:13:0517) (examination by image). **Victoria:** 1 male, Sherbrook Forest, 37°53'S, 145°21'E (MV K9864).

Etymology. The specific epithet is a Latin noun in apposition – *boletus* – meaning mushroom and it refers to the distinctly mushroom-shaped conductor lobe that is reminiscent of a chanterelle (*Cantharellus* spp.).

Diagnosis. Male *N. boletus* sp. nov. can be distinguished from *N. trituberculosa* by the weaker apico-prolateral spur on the tibia of leg II (Fig. 1E vs Fig. 5C) and the morphology of key pedipalp sclerites, specifically the mushroom-shaped conductor lobe (two-lobed in *N. trituberculosa*) (Fig. 1C vs Fig. 5F). Females of *N. boletus* sp. nov. differ from those of *N. trituberculosa* by details in the epigyne plate, specifically its transverse wrinkles that are more pronounced and mainly limited to the lateral margins in *N. trituberculosa* (Fig. 3C vs Fig. 6C).

Description. *Male* (based on holotype, MV K9867): Total length: 6.44. Carapace (Fig. 4A) 2.41 long, 2.08 wide, reddish-brown with black lateral margins, and yellowish setae mainly on the subquadrate cephalic area, fovea longer than wide, covered by a long black spot. Eyes ringed in black, lateral ones located on small tubercles (Fig. 4A). AME 0.22, ALE 0.10, PME 0.16, PLE 0.13; row of eyes: AME 0.58, PME 0.36, PLE 0.85. Chelicerae with paturon dark brown and fangs reddish brown; four promarginal teeth with the apical and third largest, three retromarginal teeth of equal size (Fig. 4B). Legs (Fig. 4A, B) yellowish-brown, mottled with chestnut brown spots; tibia of leg II with spur represented by a small apico-prolateral bulge that carries a strong macroseta; femur IV darker than other legs; leg formula IV > I > II > III; length of segments (femur + patella + tibia + metatarsus + tarsus = total length): I – 4.16 + 1.56 + 3.70 + 3.25 + 1.17 = 13.84, II – 3.38 + 1.36 + 2.92 + 0.90 + 1.11 = 9.67, III – 2.34 + 0.78 + 1.36 + 1.30 + 0.78 = 6.56, IV – 3.51 + 0.97 + 2.40 + 2.21 + 0.91 = 9.94. Labium wider than long, subtriangular and brown, with beige apical portion (Fig. 4B); endites rounded, light brown with beige edges (Fig. 4B). Sternum a little longer than wide, reddish brown, with thick darker and wavy contour and yellowish centrally placed guanine patch (Fig. 4B). Abdomen (Fig. 4A, B) 3.58 long, 2.34 wide; subtriangular, longer than wide, humeral humps conspicuous and posterior end reaching over spinnerets; dorsum yellowish-brown, with diamond-shaped patch with dark contour and a black longitudinal median line from pedicel towards posterior end, meagerly covered with long brown setae; sides beige with sparse black lines and yellow setae; venter beige irregularly covered with black spots. Pedipalps (Figs 4D–F, 5) length of segments (femur + patella + tibia + cymbium = total length): 0.78 + 0.32 + 0.26 + 1.04 = 2.40; radix thick; conductor lobe mushroom-shaped, with a projected base ending in a rounded tip and a large apical lamellar portion, which is concave at its middle portion, expanded into a wide rounded mesal projection and with its ectal border bearing a dense and dark field of scale-like structures; terminal apophysis apically projected, and longer than wide, slightly twisted and tapering to its tip; conductor rectangular and projected from behind embolus into a flat tip; embolus very thick and long, ending in a very sclerotised

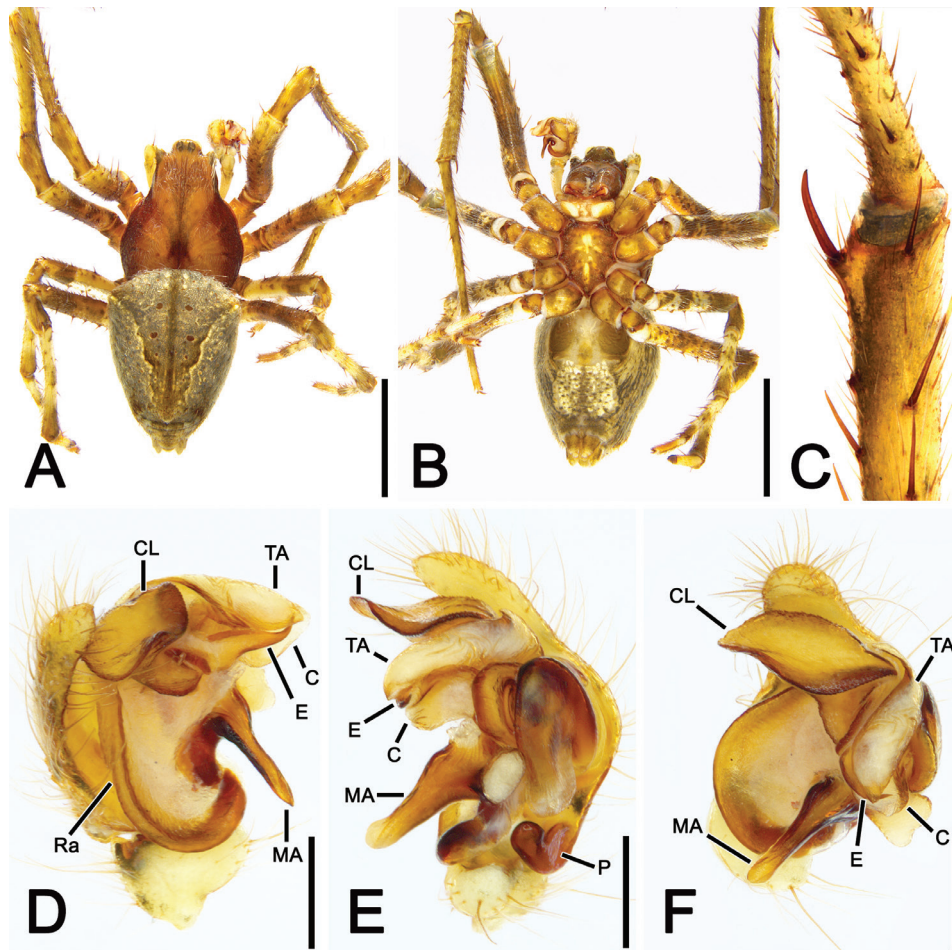


Figure 4. *Novakiella boletus* sp. nov., male holotype (MV K9867). **A.** Dorsal habitus; **B.** Ventral habitus; **C.** Left tibia, ventral view; **D.** Left pedipalp, mesal view; **E.** Left pedipalp, ventral view; **F.** Left pedipalp, apical view. Abbreviations: C, conductor; CL, conductor lobe; E, embolus; MA, median apophysis; P, paracymbium; Ra, radix; TA, terminal apophysis. Scale bars: **A, B,** 2 mm; **C,** 1 mm; **D–F,** 0.5 mm.

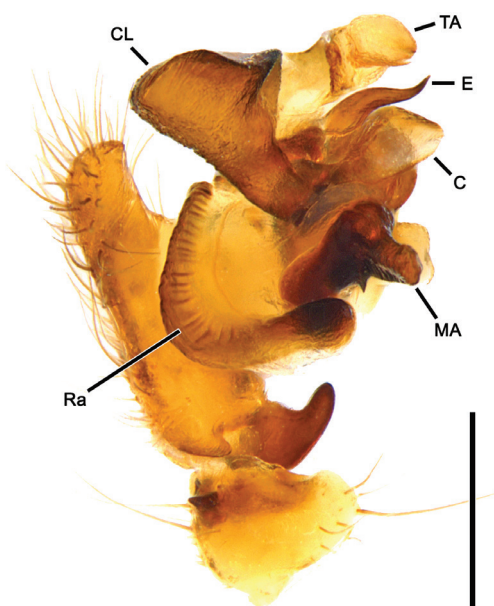


Figure 5. *Novakiella boletus* sp. nov., male holotype (MV K9867), expanded left pedipalp, mesal view. Abbreviations: C, conductor; CL, conductor lobe; E, embolus; MA, median apophysis; Ra, radix; TA, terminal apophysis. Scale bar: 0.5 mm.

distally curved tip; median apophysis stout, with a smaller basal portion and a strong median curvature, ending in a long and flattened basally pointing acute projection.

Female (SAM; from Kelly Hill Caves camping area, Kangaroo Island): Total length 8.5. Carapace (Fig. 6A) 3.7 long, 2.9 wide, as in male but with larger anterior portion. Eyes, chelicerae, legs, labium, endites and sternum generally as in male (Fig. 6A, B). Eye measurements: AME 0.2, ALE 0.11, PME 0.14, PLE 0.15; row of eyes: AME 0.68, PME 49, PLE 1.46. Pedipalp length of segments (femur + patella + tibia + cymbium = total length): $1.14 + 0.50 + 0.49 + 1.18 = 3.31$. Leg formula $IV > I > II > III$; and length of segments (femur + patella + tibia + metatarsus + tarsus = total length): I – $4.00 + 1.62 + 3.20 + 3.00 + 1.02 = 12.84$, II – $3.75 + 1.60 + 2.89 + 0.96 + 0.99 = 10.19$, III – $2.40 + 0.91 + 1.44 + 1.45 + 0.86 = 7.06$, IV – $4.12 + 1.40 + 2.58 + 2.53 + 1.05 = 11.68$. Abdomen (Fig. 6A, B) 4.5 long, 4.5 wide, with a more pronounced subtriangular shape than the male, dorsum with colour similar to male, except for the lighter folium and absent median line; venter as in male. Epigyne (Fig. 6C) plate trapezoidal with a rectangular anterior portion, crossed by long transverse wrinkles; scape broken off, but with a wide rectangular

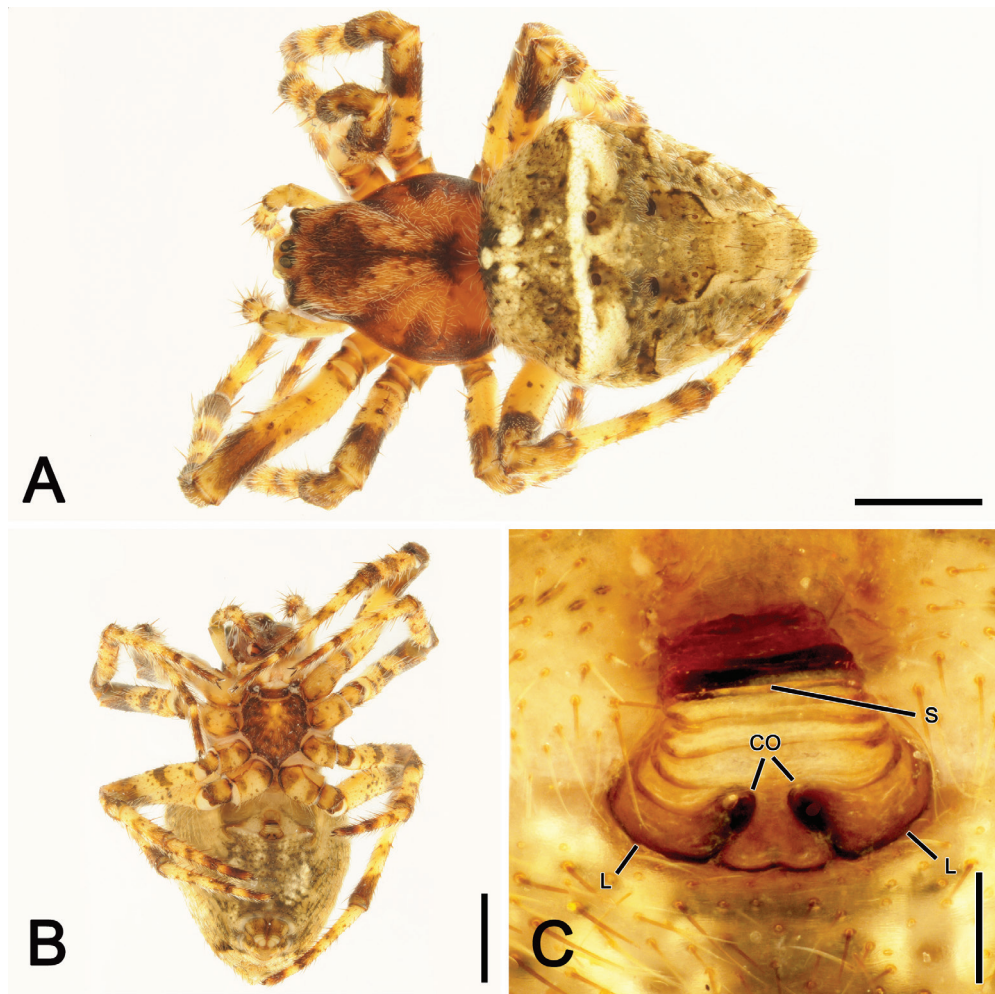


Figure 6. *Novakiella boletus* sp. nov., female (SAM). **A.** Dorsal habitus; **B.** Ventral habitus; **C.** Epigyne, ventral view. Abbreviations: CO, copulatory openings; L, lips; S, scape. Scale bars: **A, B,** 2 mm, **C,** 0.2 mm.

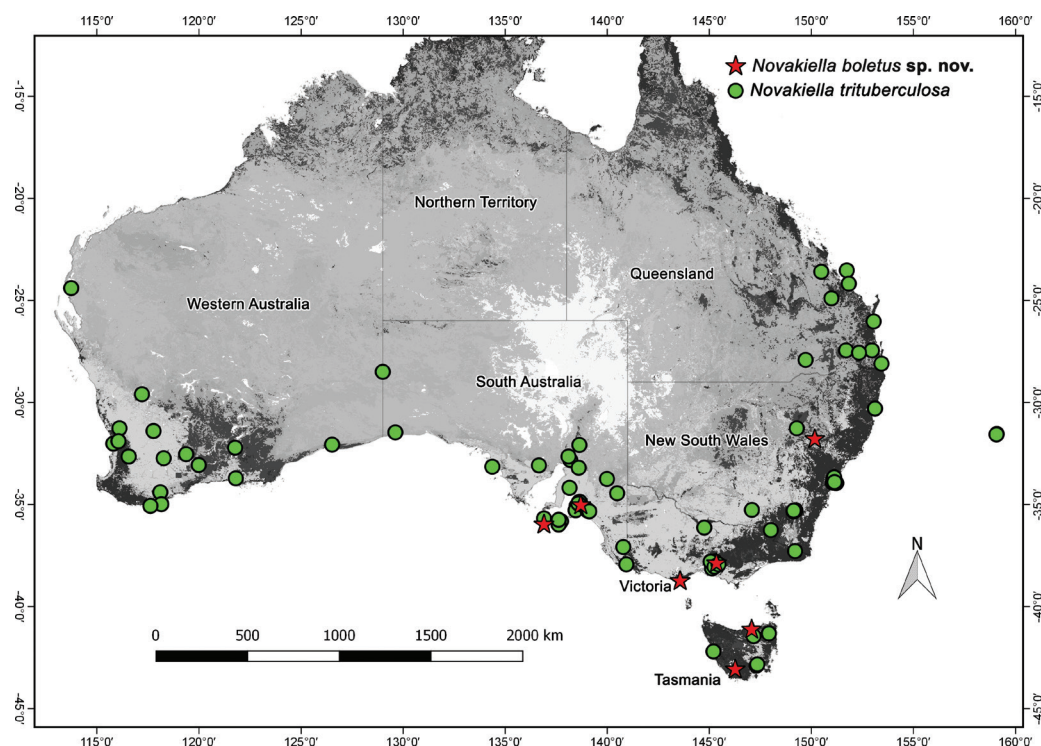


Figure 7. Distribution records of *Novakiella trituberculosa* (green circles) and *Novakiella boletus* sp. nov. (red stars) in Australia.

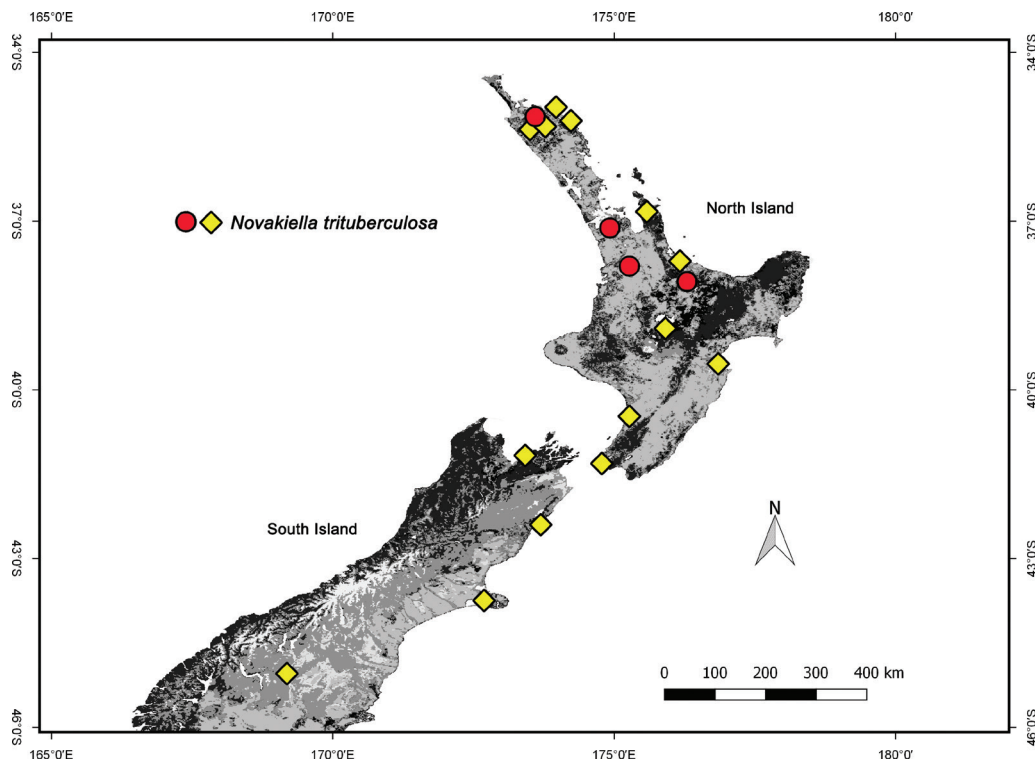


Figure 8. Distribution records of *Novakiella trituberculosa* in New Zealand; red circle points to material examined for this study and yellow diamonds point to records literature records (Court and Forster 1988).

torn basis (Fig. 6C). Spermatheca was not dissected to preserve the only available female specimen.

Habitat preferences and life history. Mature males of *N. boletus* sp. nov. were collected between February and April, females were found in May and November. Habitat descriptions include *Nothofagus cunninghamii* (Myrtle Beech) forest, *Eucalyptus amygdalina* coastal forest, and “eucalypt forest with tree fern gully”, suggesting this species occurs predominantly in temperate forests and rainforests.

Remarks. Males and female *N. boletus* sp. nov. have not been found together, but somatic features such as size range, carapace (Fig. 5A vs Fig. 6A), sternum (Fig. 5B vs Fig. 6B) and leg (Fig. 5A vs Fig. 6A) colouration match well and they are currently assumed to be the same species.

Distribution. This new species is only known from Australia, specifically New South Wales, South Australia, Victoria and Tasmania (Fig. 7).

Discussion

Araneidae are a highly diverse family with generally complex male pedipalp morphology which is traditionally used to infer phylogenetic relationships within this family as well as in other spiders (Scharff and Coddington 1997 and references therein). Developing homology hypotheses on the various pedipalp sclerites is a prerequisite to infer phylogenetic relationships using morphological data, subsequently tested by the phylogeny, but homology hypothesis based on the classical homology criteria of congruence, conjunction and similarity (Patterson 1988) is not straightforward. For example, the name paramedian apophysis

has been used for structures in the male pedipalp that are very different in shape and with different position on the male pedipalp. For instance, the lobe of the conductor seen in *Micrathena* Sundevall, 1833 (Levi 1985, figs 6–9) was considered homologous with the separate sclerite seen in *Gasteracantha* Sundevall, 1833 (Levi, 1978, figs 83, 84) and named paramedian apophysis by Levi (1978, 1985). The term paramedian apophysis was first used by Comstock (1910, pp. 179, figs 18, 19) for an extra sclerite in *Eriophora ravilla* (C.L. Koch, 1844). He writes “in this species there is an apophysis which like the median apophysis is joined by a flexible articulation to the tegulum within the cuplike cavity formed by the distal margin of the tegulum; this may be termed the paramedian apophysis”. Scharff and Coddington (1997, fig. 95) tested the homology of the paramedian apophysis (in the broad definition of Levi) on a phylogeny based on morphological characters and found that the paramedian apophysis had developed several times independently within Araneidae. The same results are obtained if the character is mapped on the new molecular phylogeny of Scharff et al. (2020). Each presence of a paramedian apophysis therefore has to be considered individually and probably represent different non-homologous structures. Interestingly, a paramedian apophysis in the form of a separate sclerite inserting on the tegulum next to the median apophysis, is a possible synapomorphy for the clade called gasteracanthines in Scharff and Coddington (1997) and Scharff et al. (2020). In other backobourkiines (i.e. *Backobourkia*; Framenau et al., 2010, figs 6A, 10A; *Plebs*, Joseph & Framenau, figs 8A, 11A), the paramedian apophysis is clearly connected basally to the conductor and thus not homologous to the one

in *Micrathena*, and could thus be better termed conductor lobe. Levi (1985) considered the paramedian apophysis as a synapomorphy that could group different genera like *Eriophora*, *Parawixia*, *Alpaida* O. Pickard-Cambridge, 1889 and *Wagneriana* F. O. Pickard-Cambridge, 1904.

In *Novakiella*, a basal conductor lobe is also present, but it is shaped very differently to that in other backbourkiines and the homology of a variety of structures in araneids in such a position remains unclear (Scharff and Coddington 1997). In *Novakiella* the conductor lobe is a very prominent structure that originates between the basis of the distal hematochoa and the stipes and fills the lateral space between the terminal apophysis and the embolus basis reaching far apically of the radix and connecting to the conductor from under the embolus. We initially thought it was a structure similar to the subterminal apophysis, which is a bubble-shaped structure that was first cited as a synapomorphy for *Eustala* Simon, 1895 and *Metazygia* F. O. Pickard-Cambridge, 1904 (Levi 1977) and then also cited for *Larinia* Simon, 1874 (Harrod et al. 1991), a member of the “Nuctenines” (sensu Scharff et al. 2020). However, it looks more related to the paramedian apophysis of *Eriophora* and *Backbourkia* cited above due to its origin at the base of the conductor and its shape. A large well-sclerotized transverse structure similar to the conductor lobe of *Novakiella* appears to be present in other “backbourkiine” genera, such as *Acroaspis* (see Framenau 2019: fig. 1B for *A. lancearia* (Keyserling, 1887). Testing homologies of the various pedipalp sclerites within the backbourkiines and to develop a generalized ground plan for this group will be a prerequisite to develop homology hypotheses to other major clades of the Araneidae as identified in Scharff et al. (2020). This can only be conducted once the apparently highly diverse backbourkiines have been taxonomically revised.

Novakiella trituberculosa was originally described from New Zealand, but Court and Forster (1988) considered the species to also occur in Australia, so the biogeographic origin of the genus remained ambiguous. The finding of a second species of *Novakiella* in Australia suggests that the genus evolved there and that *N. trituberculosa* is a natural or human-induced introduction to New Zealand. This is also consistent with *Novakiella* being part of the backbourkiines, a clade with likely Australian origin (Scharff et al. 2020). Likewise, *Eriophora pustulosa* (Walckenaer, 1841) is the only New Zealand species of a group of backbourkiines with a number of otherwise Australian representatives (VWF, PSC, CJV unpublished data).

Acknowledgements

We acknowledge the support of all museum curators and scientists who facilitated loans of specimens or visits to their respective institutions: Graham Milledge and Helen Smith (AM), Johnathon Ridden (CMNZ); Peter Lillywhite, Peter Marchant, Ken Walker and Catriona McPhee,

Joseph Schubert (MV), John Marris (LUNZ), Phil Sirvid (Museum of New Zealand Te Papa Tongarewa), Grace Hall (NZAC), Robert Raven and Owen Seeman (QM), David Hirst (retired) (SAM); and Mark Harvey and Julianne Waldock (WAM). Nikolaj Scharff acknowledges the contribution of Jonathan A. Coddington in the preparation of Fig. 2A, B and for discussions about the pedipalp sclerite homologies of *N. trituberculosa*. John Douglas (QVM) provided images of specimens that added to the distribution data of *N. boletus* sp. indet. when this paper was under review. Tamás Szűts and Lara Lopardo provided helpful comments to improve the quality of this study. This research was conducted under the Australian Biological Resources Study National Taxonomy Research Grants Program (ABRS) number 4-EHPVRMK.

References

- Castanheira P de S, Didham RK, Vink CJ, Framenau VW (2019) The scorpion-tailed orb-weaving spiders (Araneae, Araneidae, *Arachnura*) in Australia and New Zealand. *Zootaxa* 4706(1): 147–170. <https://doi.org/10.11646/zootaxa.4706.1.6>
- Comstock JH (1910) The palpi of male spiders. *Annals of the Entomological Society of America*. Vol III, No 3: 161–185. <https://doi.org/10.1093/aesa/3.3.161>
- Court DJ, Forster RR (1988) The spiders of New Zealand: Part VI. Family Araneidae. *Otago Museum Bulletin* 6: 68–124.
- Framenau VW (2011) *Lariniophora*, a new monotypic orb-weaving spider genus from Australia (Araneae: Araneidae: Araneinae). *Records of the Western Australian Museum* 26(2): 191–201. [https://doi.org/10.18195/issn.0312-3162.26\(2\).2011.191-201](https://doi.org/10.18195/issn.0312-3162.26(2).2011.191-201)
- Framenau VW, Dupérré N, Blackledge TA, Vink CJ (2010) Systematics of the new Australasian orb-weaving spider genus *Backbourkia* (Araneae: Araneidae: Araneinae). *Arthropod Systematics & Phylogeny* 68: 79–111.
- Harrod JC, Levi HW, Leibesperger LB (1991) The Neotropical orb-weavers of the genus *Larinia* (Araneae: Araneidae). *Psyche*, Cambridge 97: 241–265. <https://doi.org/10.1155/1990/25941>
- Joseph MM, Framenau VW (2012) Systematic review of a new orb-weaving spider genus (Araneae: Araneidae), with special reference to the Australasian-Pacific and South-East Asian fauna. *Zoological Journal of the Linnean Society* 166: 279–341. <https://doi.org/10.1111/j.1096-3642.2012.00845.x>
- Levi HW (1978) The American orb-weaver genera *Colphepeira*, *Micrathena* and *Gasteracantha* North of Mexico (Araneae: Araneidae). *Bulletin Museum of Comparative Zoology* 148(9): 417–442.
- Levi HW (1985) The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). *Bulletin Museum of Comparative Zoology* 150(8): 429–618.
- Levi HW (2002) Keys to the genera of araneid orbweavers (Araneae, Araneidae) of the Americas. *Journal of Arachnology* 30: 527–562. [https://doi.org/10.1636/0161-8202\(2002\)030\[0527:KTTGOA\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2002)030[0527:KTTGOA]2.0.CO;2)
- Lise AA, Kesster CC, Silva ELC da (2015) Revision of the orb-weaving spider genus *Verrucosa* McCook, 1888 (Araneae, Araneidae). *Zootaxa* 3921: 1–105. [incl. Erratum: *Zootaxa* 3956: 600] <https://doi.org/10.11646/zootaxa.3921.1.1>

- Patterson C (1982) Homology in classical and molecular biology. *Molecular Biology and Evolution* 5(6): 603–625. <https://doi.org/10.1093/oxfordjournals.molbev.a040523>
- Platnick NI (1993) *Advances in spider taxonomy 1988–1991, with synonymies and transfers 1940–1980*. The New York Entomological Society New York, 846 pp.
- Roewer CF (1942) *Katalog der Araneae von 1758 bis 1940*. 1. Band (Mesothelae, Orthognatha, Labidognatha: Dysderaeformia, Scytodiformia, Pholciformia, Zodariiformia, Hersiliaeformia, Argyropiformia). *Natura, Buchhandlung für Naturkunde und exakte Wissenschaften* Paul Budy Bremen, 1040 pp.
- Scharff N, Coddington JA (1997) A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society* 120: 355–434. <https://doi.org/10.1111/j.1096-3642.1997.tb01281.x>
- Scharff N, Coddington JA, Blackledge TA, Agnarsson I, Framenau VW, Szűts T, Hayashi CY, Dimitrov D (2020) Phylogeny of the orb-weaving spider family Araneidae (Araneae: Araneoidea). *Cladistics* 36(1): 1–21. <https://doi.org/10.1111/cla.12382>
- Urquhart AT (1887) On new species of Araneida. *Transactions of the New Zealand Institute* 19: 72–118.
- Urquhart AT (1888) On new species of Araneida. *Transactions of the New Zealand Institute* 20: 109–125.
- World Spider Catalog (2021) *World Spider Catalog Version 22.0*. Natural History Museum Bern <http://wsc.nmbe.ch/> [accessed 29 January 2021]. <https://doi.org/10.24435/2>