

**THE TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF THE
NEW ZEALAND THOMISIDAE (ARACHNIDA: ARANEAE)**

BY

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A thesis
submitted to the Victoria University of Wellington
in fulfilment of the requirements for the degree of
Doctor of Philosophy
Victoria University of Wellington

2014

ABSTRACT

The New Zealand Thomisidae (crab spiders) are represented in New Zealand by two subfamilies (Stephanopinae and Thomisinae) and were used as a model group to test two competing theories on the origins of the New Zealand spider fauna. The New Zealand thomisids are also given their first full taxonomic revision. The two origin models essentially represent species radiations following recent dispersal or ancient vicariance events. Modern distribution data suggested that the stephanopines are poor dispersers and may provide evidence demonstrating a long period of separation from Australia; while in contrast, thomisines are known to be excellent dispersers. Maximum Likelihood and Bayesian analyses of cytochrome *c* suboxidase subunit I (COI), 28S ribosomal RNA (28S), histone H3 (H3), NADH dehydrogenase 1 (ND1) data and a combined genetic dataset was undertaken. Results indicate New Zealand stephanopines and thomisines form distinct endemic groups separate from sampled Australian species and appear to have separated from them around 5-6 million years ago. Additionally, genetic data from this study showed i) colour variations are not indicative of cryptic species; ii) previously described species are genetically distinct; iii) several suspected new species are also genetically distinct; iv) the relatively recent establishment of two Australian stephanopines and the occurrence of similar COI haplotypes in disjunct locations suggest that the dispersal ability of stephanopines is greater than previously thought and that radiation following colonization from Australia is a plausible explanation for the current diversity of the New Zealand thomisid biota.

The taxonomic revision raises the number of described species from eight to eleven based on a combination of morphological and genetic data. In the stephanopines, *Bryantymella* Gen. nov. is erected to contain the type species *Bryantymella angularis* (Urquhart, 1885) comb. nov. as well as *B. angulata* (Urquhart, 1885) comb. nov., *B. thorini* sp. nov. and *B. brevirostris* sp. nov. Two Australian species, *Sidymella longipes* (Koch, 1874) and *S. trapezia* (Koch, 1874), are also recorded for New Zealand. *Sidymella benhami* (Hogg, 1910) is considered to be a junior synonym of *Bryantymella angulata*

(Urquhart, 1885). In the thomisines, all species are now included in the previously monotypic genus *Cymbachina* Bryant, 1933. The genus now encompasses the type species *C. albobrunnea* (Urquhart, 1893), *C. ambara* (Urquhart, 1885) comb. nov., *C. albolimbata* (L. Koch, 1893) comb. nov., *C. sphaeroides* (Urquhart, 1885) comb. nov. and *D. urquharti* sp. nov. *Synema suteri* Dahl, 1907 is regarded as a junior synonym of *C. ambara* (L. Koch 1893). All previously described species are redescribed to a modern standard and sexes for some species are described for the first time. Three new species are described. Photographs of adults and diagnostic genitalic characters are included, as are diagnostic keys and updated synonymic, geographic and biological information.

Overall, this study indicates that New Zealand thomisids appear to have split from their Australian relatives some 5-6 million years ago and taken in concert with the recent establishment of two Australian stephanopine species, it appears that dispersal to New Zealand by Australian colonists and subsequent radiation into endemic New Zealand forms is a plausible explanation for the current state of the fauna. Genetic and morphological data are mutually supporting and in concert have helped inform the first taxonomic revision ever undertaken for this family in New Zealand.

ACKNOWLEDGEMENTS

A thesis is rarely, if ever, conducted in isolation, and this project is by no means an exception to that rule. As the acknowledgements sections in Chapters 2 and 3 illustrate, I have had the good fortune to rely on the support and generosity of many. In addition to the many people listed there, I would like to reiterate my thanks to my supervisors, Phil Lester and Geoff Chambers. Their mix of badgering, encouragement and giving me not quite enough rope to hang myself with kept me on track. This project would not have been possible without the support of a number of managerial staff and colleagues at Te Papa. Anna Cowie and Carol Diebel both encouraged me to take on this project. It would never have started without them and Claudia Orange ensured the project continued. Simon Whittaker, my former line manager deserves special thanks and his support, particularly in the difficult early stages, is greatly appreciated. My workmates Ricardo Palma and Mike Fitzgerald provided plenty of technical advice and encouragement, as did my frequent co-author, Cor Vink of Canterbury Museum. Last, but most importantly, I would like to thank my wife Alicia and my children, Amelia and Michael, for their patience with me during this thesis. I owe them a lot of weekends and many apologies for the extremely bad language whenever my phylogenetic analyses wouldn't run.

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CHAPTER 1: INTRODUCTION, THESIS QUESTIONS AND CHAPTER OUTLINE

Note: This chapter uses species names as they were prior to the taxonomic revision of Chapter 2, reflecting the state of taxonomy and systematics at the outset of the project.

MORPHOLOGY

Spiders of the family Thomisidae are commonly known as crab spiders because of their ability to move sideways in a crab-like manner. Thomisids are diverse both in form and in number of species (Jocqué & Dippenaar-Schoeman 2006). See the *Taxonomy and Systematics* section for more detailed taxon count information.

In New Zealand, general body forms range from sleek, smooth and slender in genera such as *Diaea* to rugose and gnarled in *Sidymella* (see Fig. 1). New Zealand thomisids are not especially large and rarely exceed 1cm in body length (Pers. obs.)

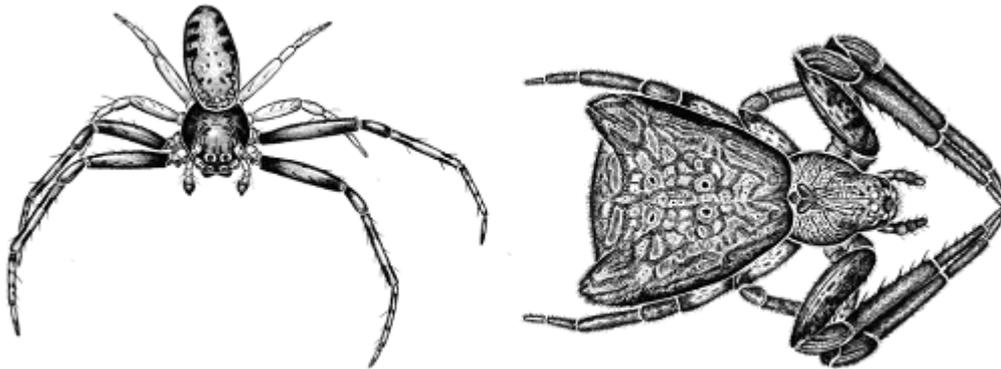


Fig. 1. *Diaea ambara* (left), *Sidymella* sp. (right). Reproduced from Forster (1967).

Despite such gross differences in general form, thomisids possess a number of morphological characters that in combination define the family. Note that terms in bold are defined in the short glossary below. Thomisids are eight-eyed spiders, with lateral (and sometimes other) eyes typically mounted on tubercles. The legs are laterigrade (i.e. point outwards), with each leg

terminating in two claws. The first two pairs of legs are typically longest and strongest and are armed with strong spines used in prey capture. The architecture of the male **palp** is broadly consistent (Fig. 2). The **tegulum** of the male palp is disk-like or ovoid and the **sperm duct** turning prolaterally and terminating distally as the **embolus**. Male palps also bear **tibial apophyses**. The female **epigynum** is **entelegyne**, often with guide pockets or a hood. General character information was compiled from Bryant's (1933) figures, Schick (1965) and Ono's (1998) thomisid revisions, Shield and Strudwick's description of a new Australian thomisid, (2000), Jocqué and Dippenaar-Schoeman's (2006) family description, the phylogenetic analysis of Benjamin *et al.* (2008) and personal observation. A more detailed presentation of anatomy including a larger glossary is given in the taxonomic revision portion of this thesis (Chapter 2, Appendix B).

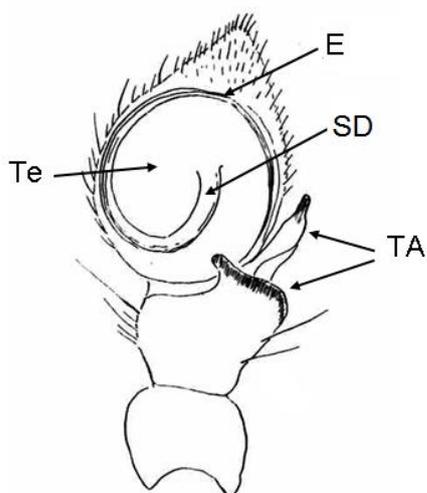


Fig. 2. A male thomisine palp. E = embolus, SD = sperm duct, Te = tegulum, TA= tibial apophyses. After Bryant (1933).

Short Glossary:

Cephalothorax; combined head/thorax region bearing eyes, legs, **palps** and mouthparts.

Embolus: terminal portion of **sperm duct**.

Entelygyne: **epigyne** with external copulatory openings.

Epigyne: ventral sclerotised plate where genital openings are located in female spiders.

Palp: small, leg-like appendage at anterior end of **cephalothorax**. Modified to form a copulatory organ in males.

Sperm duct: connection between sperm reservoir and **embolus**.

Tegulum: portion of palp bulb housing **sperm duct** giving rise to **embolus**.

Tibial apophysis: a process on the tibial segment of the male **palp**, often of high diagnostic value.

BIOLOGY AND ECOLOGY

Thomisids are widely regarded as free-living ambush spiders (Forster & Forster 1999). The capture of insect prey is as simple as flexing the first two pairs of previously outstretched legs and drawing prey in towards the chelicerae where it is bitten and killed (Jackson *et al.* 1995). As noted earlier, the first two pairs of legs bear long spines and these help prevent the prey's escape. Like other spiders, thomisids are carnivorous but nectivory is also known. Pollard *et al.* (1995) report that males of the North American thomisid *Misumenooides formosipes* (Walckenaer, 1837) have a much greater surface area to volume ratio than their larger female counterparts and use nectar in preference to water because it is an energy source in addition to countering dehydration. Taylor and Pfannenstiel (2008) found that other spiders make use of nectar and that nectivory is also quite common among female thomisids.

As ambush predators, thomisids generally do not construct a prey capture web. However, Jackson *et al.* (1995) reported occasional use of a series of criss-crossed non-sticky threads for prey capture by an unidentified New Zealand species of *Diaea*. They also cited several historical reports that suggest a number of other Australasian thomisids may possess similar capabilities. It is not known how widespread this behaviour is in thomisids in general or in New Zealand species in particular. What is certain is that thomisids do employ silk in a variety of ways including for egg-sac construction (Cutler 2003), draglines (Leonard & Morse 2006) and for ballooning in some species (Decae 1987, Greenstone *et al.* 1987, Morse 1992, Bonte *et al.* 2003). Forster & Forster (1999) also report thomisine males bind female partners prior to mating with them (Fig. 3). They note the silk is insufficient to restrain the female after mating ceases, so quite what function is served by this behaviour is not fully clear.



Fig 3. Mating in *Diaea*. The female (top right) has been tied to the leaf with silk by the male (lower left). Reproduced from Forster & Forster (1999)

New Zealand thomisids are only known to produce a single egg-sac at a time. Maternal guarding of egg-sacs has been reported in both New Zealand (Forster & Forster 1999) and overseas thomisids (Eberhard 1987). Personal observation indicates thomisids will shelter the egg-sacs inside leaves that are curled and held in place with silk, while stephanopines attach their egg-sacs to the underside of leaves (Fig. 4). Male thomisids have no known parental role beyond mating.



Fig. 4. Egg-sacs and maternal guarding in *Diaea* (left) and *Sidymella* (right). Reproduced from Forster & Forster (1999).

As part of a wider assemblage of spiders, thomisids can have an important role in the control of agricultural pests (Riechert & Lockley 1984). They are also important as food for many other organisms. Harris (1994) lists *Diaea*

ambara (Urquhart, 1885) as a host species for the endemic New Zealand sphecid wasp *Pison morosum* although there are no New Zealand records for the Pompilidae, a family of wasps that specialise in hunting spiders (Harris 1987). A dietary analysis of mouse stomachs from the Orongorongo Valley's hard beech forests by Alley *et al.* (2001) found *Sidymella angularis* (Urquhart, 1885) was the third most abundant spider species on the basis of trap data but ranked second with regard frequency of occurrence in mouse stomachs. Bishop observed entomophagous fungi fatally affecting ballooning spiders, including Thomisidae. Forster and Forster (1999) also depict a specimen of *Diaea* parasitized by a mite (see Fig. 5).



Fig. 5. *Diaea* and parasitic mite. Reproduced from Forster and Forster (1999).

Thomisids such as *Sidymella* and *Cymbachina* are known to frequent leaf-litter and lichen respectively, while *Diaea* is most commonly found on flowers and foliage (Forster & Forster 1999). Ambushing flower-visiting insects is a common method of prey capture in thomisids and some species have the ability to alter their colouration to blend in with the flower substrate (Insaust & Casas 2008). To human eyes this looks like camouflage, however, Heiling *et al.* (2003) observed a dual role for crab spider colouration. They found, that while a white-coloured *Thomisus spectabilis* Doleschall, 1859 may appear well concealed against a white daisy, under ultraviolet light the spider's colour pattern enhances the attractiveness of the flower to bees, thus increasing the odds of encountering prey. The role of colour in New Zealand's thomisids is not yet understood. Collections of multiple individuals of *Diaea* sp. from the

same shrub can yield a range of specimens of different colours including shades of red, yellow and green (Pers. obs.). However, we do not know if this represents the ability to change colour, the result of dietary influence or something else. It could represent nothing more than variation within a population as Vink (2002) observed in the New Zealand Lycosidae (wolf spiders) and Court and Forster (1988) observed in the Araneidae (orbweb spiders).

DISTRIBUTION:

Crab spiders are found worldwide (Jocqué & Dippenaar-Schoeman 2006). In Zealand they are common and occur in both native ecosystems and modified habitat such as gardens (Forster & Forster 1999). They are known from offshore islands such as Tuhua (= Mayor) Korapuki and the Three Kings group. One species (*Diaea albolimbata*) is known from the Chathams (Pers. obs), but none have been recorded from other distant island groups such as the Kermadecs or the subantarctic islands. New Zealand endemic thomisids appear to be sympatric.



Fig. 6. Chathams *Diaea albolimbata* male (left) and *Pimelia arenaria* substrate (right).

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TAXONOMY AND SYSTEMATICS

The family Thomisidae was first erected by Sundevall in 1833. With over 2150 species in 174 genera, they are the sixth most diverse of the 112 spider families recorded so far (Platnick 2013). The fossil record for Thomisidae is

limited, with no Australasian examples and the earliest specimens are around 50-60 million years old (Selden & Penney 2010).

The thomisids classically comprise seven subfamilies: Aphantochilinae, Bominae, Dietinae, Stephanopinae, Strophinae, Stiphropodinae and Thomisinae (Simon 1892, Ono 1988, Jocqué & Dippenaar-Schoeman 2006) but partial rearrangements and relimitations of thomisid taxa have also been proposed if not widely adopted. For example, Wunderlich (2004) proposed the family Borboropactidae to cover part of the Thomisidae but this was rejected by Benjamin *et al.* (2008) as they stated Borboropactidae was paraphyletic. While the monophyly of Thomisidae has been confirmed by both molecular (Benjamin *et al.* 2008) and morphological (Benjamin 2011) analyses, the same studies also indicated that thomisid subfamilies need further refinement and clearer relimitation as they are either paraphyletic or polyphyletic. This includes Stephanopinae and Thomisinae, the two subfamilies present in New Zealand. Characters previously treated as diagnostic for subfamilies such as the presence of cheliceral teeth in Stephanopinae and their absence in Thomisinae (Ono 1988) have some utility in separating New Zealand members of the two subfamilies (Pers. obs), but are not phylogenetically informative in a wider context as they are not unambiguous synapomorphies (Benjamin 2011).

At a broader level of spider systematics, thomisids have been placed in the Dionycha (Fig. 7), a grouping of several families of spiders defined by the lack of a cribellum (a specialised silk-producing organ) and the absence (or major reduction) of the third tarsal claw and its' replacement with a claw tuft (Coddington & Levi, 1991). Later work by Coddington (2005) reaffirmed the placement of Thomisidae within Dionycha. However, the monophyly of the Dionycha has yet to be tested and the correct placement of thomisids relative to other members of this group is unclear (Benjamin *et al.* 2008). Coddington & Levi (1991) also acknowledge the dionychan condition occurs in other families, albeit at lower taxonomic levels.

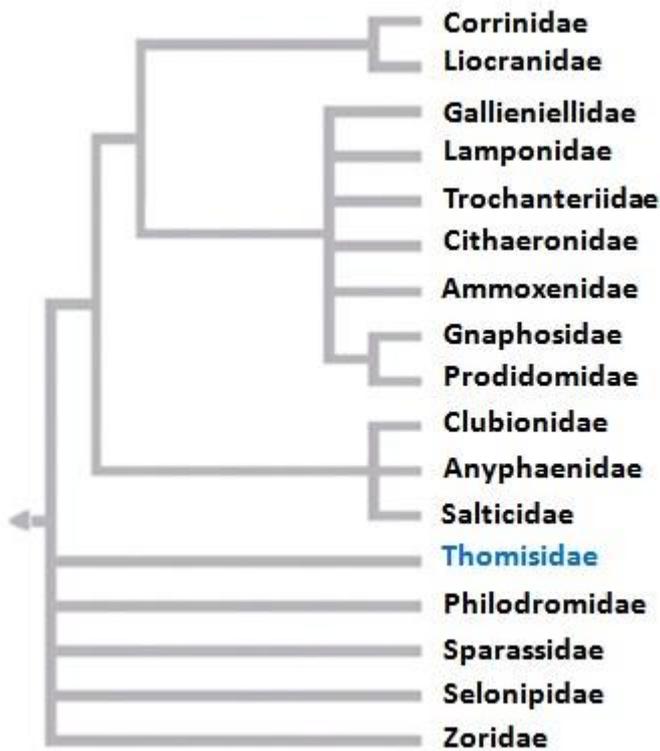


Fig. 7. The position of Thomisidae within the Dionycha of Coddington and Levi (1991).

A more recent molecular analysis (Agnarsson *et al.* 2013) of spider phylogenetics suggests Thomisidae belong in the higher Lycosoidea, the immediate sister clade to Dionycha. However, the authors note there are many contradictions between their results and Coddington's (2005) morphology-based consensus model. They suggest that available DNA data is inadequate to resolve deep level phylogeny and that the the model of Coddington *et al.* (1991) is also likely to be incorrect in some aspects.

Genus **Cymbachina** Bryant 1933

albobrunnea (Urquhart, 1893) *.....New Zealand

Xysticus albo-brunnea Urquhart, 1893: 184 (Df).

Cymbachina albobrunnea: Bryant 1933: 3 (Df).

Comment: Possibly congeneric/conspecific with Australian taxa but no possible candidates yet known.

Genus. **Diaea** Thorell 1869

albolimbata L. Koch, 1875.....New Zealand

Diaea albolimbata L. Koch, 1875a: 588, pl. 46, f. 1 (Df).

Philodromus ovatus Urquhart, 1887: 113 (Df).

Synaema albolimbata: Dahl 1907: 382, 391.

Diaea albomaculata: Bryant 1933b: 3 (lapsus).

ambara (Urquhart, 1885).....New Zealand

Philodromus ambarus Urquhart 1885: 43, pl. 10, f. 8 (Df).

Philodromus ambarus: Urquhart 1887: 112 (Dm).

Diaea ambara: Bryant 1933b: 4, pl. 1, f. 4, pl. 2, f. 14 (m).

sphaeroides (Urquhart, 1885).....New Zealand

Philodromus sphaeroides Urquhart 1885: 44 (Df).

Philodromus sphaeroides: Urquhart 1887: 111, pl. 8, f. 10 (Dm).

Diaea sphaeroides: Bryant 1933b: 4, pl. 3, f. 20 (f).

Diaea sphaeroides: Bryant 1935d: 86, pl. 10, f. 2 (m).

Comment: Unlikely that *Diaea* is the correct generic placement for New Zealand species. Also, the male of *Diaea albolimbata* is not known.

Genus **Philodromus** Thorell 1870

rubrofrontus Urquhart, 1891.....New Zealand

Philodromus rubrofrontus Urquhart, 1891: 179. *Nomen dubium*

Comment: Probabably a *Diaea*. *Philodromus* not found in NZ.

Genus **Synema** Simon 1864

mf **suteri** Dahl, 1907.....New Zealand

Synema suteri Dahl, 1907: 381, 391 (Df).

Comment: Possibly a member of the New Zealand *Diaea* as Dahl (1907) also treated *D. albolimbata* as a member of *Synema*.

Table 1: A) The thomisine thomisid fauna of New Zealand at the outset of this study. Modified from Platnick (2013). *Legend:* m=male, f=female, (Dm), (Df) or (Dmf) =description of male, female or both, *= type species for genus. Authors, publication dates and page references for associated taxonomic works are also given.

Genus ***Sidymella*** Strand 1942

f **angularis** (Urquhart, 1885).....New Zealand
Sparassus angularis Urquhart, 1885: 43, pl. 10, f. 7 (Df).
Sidyma angularis: Bryant 1933b: 5, pl. 5, f. 45 (f).

mf **angulata** (Urquhart, 1885).....New Zealand
Sparassus angulatus Urquhart, 1885: 42 (Df).
Stephanopis angulatus: Urquhart 1890c: 260, pl. 17, f. 8 (Dm).
Sidyma angulata: Dalmas 1917: 391.
Sidyma angulata: Bryant 1933b: 6, pl. 1, f. 3, pl. 4, f. 37 (mf).

f **benhami** (Hogg, 1910).....New Zealand, Stewart Is.
Stephanopis benhami Hogg, 1910: 275, f. 2 (Df).
Sidyma benhami: Dalmas 1917: 392.

Comment: Note that the transfer to *Sidymella* is by implication because the type for genus *Sidyma* was transferred there by Strand (1942). It is unlikely that *Sidymella* is the correct generic placement. Also, *Sidymella benhami* is currently unidentifiable.

Genus ***Tharpyna*** L. Koch 1874

f **munda** L. Koch 1875.....Australia, New Zealand
T. m. L. Koch 1875a: 602, pl. 47, f. 3 (Df).

Comment: Not present in New Zealand (Paquin *et al.* 2008),

Table 1. (continued): B) The stephanopine thomisid fauna of New Zealand at the outset of this study. Legend is as per Table. 1A.

At the outset of this study, knowledge of the the New Zealand thomisid fauna and how close they are to overseas relatives was limited. The taxonomic status of previously described New Zealand Thomisidae at the commencement of this study is given in Table 1 above and their taxonomic history is detailed below.

The earliest thomisid described from New Zealand was *Diaea albolimbata* Koch 1875 in his monumental work “Die Arachniden Australiens” (Koch 1875). Seven species (five *Philodromus* and two *Sparassus* species) were described by Urquhart (1885 1887 and 1893). *Synema suteri* Dahl 1907 and *Stephanopis benhami* Hogg 1910 were described in the early 20th century (Dahl 1907, Hogg 1910). There have been no new thomisids described for New Zealand since then.

Tharpyna munda Koch 1875 was erroneously recorded as being in New Zealand by Simon (1895) although the original 1875 description makes no claim to this effect. This species is not mentioned in any New Zealand publication since Koch's original description, including the faunal lists of Hutton (1904), Urquhart (1892) and Parrott (1946). The error was perpetuated in subsequent araneological catalogues (e.g. Roewer 1955) until it was corrected by Paquin *et al.* (2008).

A pioneering figure in New Zealand arachnology in the late 19th century, A.T. Urquhart named dozens of species new to science. However, his descriptions have been accurately described as "voluminous but vague" and many of his species are either unrecognisable or their names have been sunk in synonymy (Forster 1967). Urquhart's thomisid descriptions are no exception. Much of Urquhart's collection has been lost, but what remains is housed in Canterbury Museum (Nicholls *et al.* 2000). Bryant (1933, 1935a 1935b) examined and re-described much of the material, including Urquhart's extant thomisid type specimens. Of Urquhart's seven described thomisid species, Bryant had material available from six. This is the closest approximation we have to a revision of the New Zealand thomisid fauna. Bryant transferred *Xysticus albo-brunnea* Urquhart 1893 to *Cymbachina* and treated both *Sparassus angularis* Urquhart 1885 and *S. angulata* Urquhart 1885 as members of *Sidyma*. Of the four *Philodromus* species described by Urquhart, Bryant had only material from three species available to her. She synonymised *P. ovatus* Urquhart 1885 under *Diaea albolimbata* Koch (invalidly emended as *D. albomaculata*) and transferred *P. ambara* Urquhart 1885 and *P. sphaeroides* Urquhart 1885 to *Diaea*. Urquhart's remaining thomisid species, *Philodromus rubrofrontus* Urquhart 1891 was not seen by Bryant.

Note that *Philodromus* was formerly placed in the Thomisidae and is now in the related family Philodromidae (Homann 1975). Paquin *et al.* (2008) observed that while the sole description of *P. rubrofrontus* is insufficient to properly diagnose this species, it contains enough information to indicate it is

a thomisid rather than a philodromid. As a consequence of this decision, the family Philodromidae was removed from the New Zealand faunal list.

It is also important to note that those New Zealand species that are currently placed in *Diaea* are not likely to remain there given that this genus is currently ill-defined. Lehtinen (1993) describes it and several other thomisid genera as “typical ‘waste-basket’ groups, where most species are not closely related to the respective type species”. However, these spiders are correctly placed in the subfamily Thomisinae (*sensu* Ono 1988).

As noted earlier, *Xysticus albobrunnea* Urquhart was transferred to the newly created monotypic genus *Cymbachina* by Bryant (1933). While it is possible this is a truly endemic genus, other monotypic spider genera from New Zealand have sometimes later been shown to be Australian colonists. For example, New Zealand’s only lynx spider *Oxyopes gracilipes* (White 1849) was later shown to be conspecific with an Australian species, *O. mundulus* Koch 1878 (Vink & Sirvid 1998, 2000). As there are several other *Oxyopes* species in Australia, it seems more likely that *O. gracilipes* colonised New Zealand from Australia rather than the other way around (Vink & Sirvid 1998 2000). With regard to *Cymbachina* there are currently no known candidates from Australia that could be considered either congeneric or conspecific. *Cymbachina albobrunnea* is illustrated below (see Fig. 8).



Fig. 8. *Cymbachina albobrunnea*.
Reproduced from Forster and Forster
(1999).

The status of *Synema suteri* is unclear. Dahl's (1907) description is no more than a couple of lines and lacks illustrations. Furthermore, this species does not appear to have been studied since it was first published. An examination of the type material (held at the Zoologisches Museum, Humboldt Universität, Berlin) will be required before this species can be properly placed.

With respect to the stephanopine thomisids, Dalmas (1917) considered *Sparassus angulata* to be a senior synonym of *Sparassus angularis* and transferred both it and *Stephanopsis benhami* to *Sidyma*. Bryant (1933) did not refer to Dalmas (1917) and, as stated previously, maintained the distinction between *Sparassus angularis* and *Sparassus angulata*, transferring both to *Sidyma*. However, *Sidyma* is a preoccupied name, belonging to genus of arctiid moths (*Sidyma* Walker, 1856). The replacement name *Sidymella* was created by Strand (1942) for the type species of the *Sidyma* (*Stephanopsis lucida* Keyserling, 1880) and thus, by extension, all three New Zealand *Sidyma* species became species of *Sidymella*. While *Sidymella angularis* and *S. angulata* appear to be quite easily distinguished from one another on the basis of Bryant's (1933) redescriptions, *S. benhami* (Hogg) is very poorly described and at present cannot be separated from either Urquhart species. Bryant (1933) refers to a number of characteristics (e.g. cephalothoracic ridges) of the New Zealand species that do not fit *Sidyma* (= *Sidymella*). Accordingly, it is possible the New Zealand species may not remain in this genus. Regardless of final generic placement, these spiders belong in the subfamily Stephanopinae because they all have cheliceral teeth, which is a character restricted to this subfamily (Ono 1988).

There is much still to be discovered about the New Zealand Thomisidae. As noted above, questions about generic placement remain unresolved and the taxonomic status for some species remains unclear. Other than the efforts of Bryant (1933, 1935b), the New Zealand crab spiders have received little attention since they were first described in the literature. My preliminary examination of museum specimens suggests that some species such as *S. angularis* are rather variable in terms of colour and other somatic characters. Further study is needed to determine if this diversity of form is merely

intraspecific variation or if it is an indication of a species complex, and indeed, if all previously described species are still valid, monophyletic taxonomic entities. Additionally, examination of museum specimens indicates there are several thomisid species present in New Zealand that, on the basis of morphological characters, are either previously unknown endemic species or undocumented exotic colonists.

The external relationships of the New Zealand Thomisidae are poorly known because this family appears to have suffered from the same 'taxonomic neglect' across the Australian and South Pacific regions as is the case in New Zealand. There are no formal taxonomic revisions for the Thomisidae from anywhere in these regions, although there are some species records. Berland (1927; 1929a; 1929b; 1934a; 1934b) studies of collections of Pacific Island spiders noted a number of thomisids. Lehtinen (1993) indicated Indo-Pacific '*Diaea*' is distributed across the Pacific in an area spanning New Guinea, Australia and New Zealand and observed a gap in thomisid distribution for Central Polynesia. Platnick (1993) lists only one *Diaea* among the handful of thomisids known from New Caledonia. The only *Sidymella* species in the entire Austral-Pacific region appear to be confined to Australia and New Zealand (Platnick 2009). The Australian thomisid fauna contains 127 known species but is unrevised with most species described in the late 1800s (Raven *et al.* 2002). More recent work by Szymkowiak (2007) on the Australian thomisid *Diaea pulleini* suggests a definite link between Australian and New Zealand thomisids. In this paper, the author hypothesized that *D. pulleini* belongs to what could be an undescribed genus that also contains the three currently valid New Zealand *Diaea* species.

The most comprehensive and comparatively recent thomisid revision is that of Ono (1988). Ono revised the Japanese thomisids and also redefined the thomisid subfamilies as well as number of genera. This work is not without deficiencies and is at times self contradictory with respect to character descriptions. Nonetheless, Ono (1988) is still extremely useful on many levels, particularly with respect to morphological terminology.

PHYLOGENETICS

Ideally, taxonomic arrangements reflect evolutionary history. Unfortunately, this is not always the case as is evident from the great variety of species that are placed in *Diaea* that almost certainly do not belong there (Lehtinen 1993). Because the rate of change for morphological characters upon which taxonomic studies are typically based is not readily quantifiable, the value of morphological characters in elucidating evolutionary history is limited, especially in the absence of an unambiguous fossil record. Phylogenetic studies are not restricted in the same way and as Ho *et al.* (2008) state, time-scales estimated from sequence data can be used to “measure the tempo of speciation”.

Just as recent family-level taxonomic revisions are scarce for Thomisidae, so too are phylogenetic studies. Lower level phylogenetic studies exist, such as Garb (1999) and Garb and Gillespie (2006), but Benjamin *et al.* (2008) and Benjamin (2011) are thus far the only studies to approach thomisid phylogeny at a family level. As these studies point out, even the monophyly of the Thomisidae as a family has never been formally tested and our understanding of generic relationships has changed little since Simon’s (1895) day. Using three gene targets (16S ribosomal RNA (16S), cytochrome *c* oxidase subunit I (COI) and histone 3 (H3)), Benjamin *et al.* (2008) tested 25 thomisid and eleven outgroup taxa and found support for the monophyly of Thomisidae. This result should be treated cautiously given the limited taxon sampling (25 out of 174 genera). They also recovered four lineages within the family (*Borboropactus* clade, *Epidius* clade, *Stephanopsis* clade and the *Thomisus* clade) although acknowledge these groupings still await more detailed cladistic analysis (see Fig. 9 below). This study also offered support for the view expressed by some taxonomists (e.g. Lehtinen 1993, 2005) that some thomisid genera are not monophyletic. Benjamin (2011) used a cladistic approach based on morphological characters and largely corroborated the findings of Benjamin *et al.* (2008).



Fig. 9. Monophyly of the Thomisidae and four recognized clades as shown in Fig. 2 of Benjamin *et al.* (2008). One of the two most parsimonious trees (L = 3377) found under direct optimization recovers a monophyletic Thomisidae. Gap opening / gap extension cost of 2/1. Jackknife values greater than 60 are shown above the branches (caption text from Benjamin *et al.* 2008).

Returning to the other phylogenetic studies of thomisids mentioned earlier, Garb (1999) explored the radiation of Hawaiian thomisids, observing seventeen out of 21 endemic thomisid species belonged to one genus (*Misumenops*) and that there are far more species than might be expected for a landmass of the Hawaiian archipelago's current size. Combined with the

fact that molecular data indicated the endemic species appeared to be much more closely related to each other than to any other taxa Garb suggested this could be explained by a relatively recent radiation within the group although she also indicated further testing was required to better corroborate this hypothesis. Garb and Gillespie (2006) investigated the population relationships of the thomisid *Misumenops rapaensis* Berland 1934 in the Central Pacific Austral Islands and the wider origins of the Central Pacific thomisid fauna. Gressitt (1956) had previously suggested a west to east direction of colonisation for this region and while Garb and Gillespie (2006) found this pattern could explain the colonisation of the Austral Islands, colonisation of archipelagos further to the north (e.g. Society Islands, Hawaii) was linked to North America.

While molecular phylogenetic analyses of thomisids are rare, this is not true of spiders in general and there are many published studies focussed on other spider genera and families. Below are summaries of a number of such studies in chronological order.

Gillespie *et al.* (1994) examined the species radiation of Hawaiian *Tetragnatha*. These spiders are regarded as being more diverse in terms of morphology, ecology and behaviour than their mainland congeners. The authors tested whether this pattern of diversity was explained by a single or multiple colonisation events, finding evidence for the latter. In another Hawaiian centred study, Hormiga *et al.* (2003) used a combined morphological and molecular approach to study the radiation of the endemic linyphiid genus *Orsonwelles*, concluding that the pattern of speciation was a good match for the pattern of island progression that characterises the formation of the Hawaiian archipelago. In another island study, Arnedo *et al.* (2001) analysed morphological and molecular (16S and COI) sequence data to examine the radiation of the spider genus *Dysdera* in the Canary Islands and found a single origin for 84% of the 43 endemic species there, although they were not certain about how many other colonisation events were required to explain the other 16%.

In a study of a very different kind of isolated environment to an island archipelago, Heddin's (1997) phylogenetic study of an Appalachian cave-dwelling *Nesticus* species complex examined the hypothesis that observable morphological differences were consistent with recent geological events. Heddin found the genetic divergences were much deeper than would be expected if the hypothesis was true. His molecular data generally matched morphologically defined species, with variation probably due to peripatric speciation.

Moving into a global context, Garb *et al.* (2004) examined the medically important and widespread widow spider genus *Latrodectus* using COI DNA sequences. The authors drew the conclusion there are two well supported clades, *geometricus* and *mactans*, with the latter containing the bulk of *Latrodectus* species. They also found a low level of genetic divergence between specimens from Africa, Hawaii and both North and South America corroborated the idea that anthropogenic dispersal has expanded the range of *L. geometricus*. This result is unsurprising given it is a synanthropic species. In a study of New Zealand *Latrodectus*, Vink *et al.* (2008) tested whether two species (*Latrodectus katipo* Powell, 1871 and *L. atritus* Urquhart, 1890) that were separated on the basis of colour pattern and geographic range were genuinely distinct from one another or not. Using a combination of sequence data (COI and Internal transcribed spacer regions 1 and 2 (ITS1 and ITS2)), morphological characters and cross-breeding experiments, they concluded only one species (*L. katipo*) exists, with the absence of a red stripe in *L. atritus* the only notable point of difference.

Vink *et al.* (2008) is not the only New Zealand example where molecular data has been used to test whether putative species are conspecific or distinct taxonomic entities. Vink *et al.* (2011) examined four species in four genera that were all described on the basis of specimens from one sex only (female *Cambridgea reinga* Forster & Wilton, 1973, male *Nanocambridgea grandis* Blest & Vink 2000, female *Nuisiana arboris* (Marples, 1959) and male *Matachia magna* Forster, 1970). Using molecular, morphological and distributional data, they showed these four species were actually the male and

female pairs of *C. reinga* and *N. arboris*. A similar "total evidence" approach has been adopted in other New Zealand-based taxonomic studies looking at Pisauridae (Vink & Dupérré 2010), the widely distributed jumping spider *Trite planiceps* Simon, 1899 (Vink *et al.* 2011) and *Cryptachaea gigantipes* (Keyserling, 1890), a recently established colonist from Australia (Smith *et al.* 2012).

In a large scale study, Spagna and Gillespie (2008) looked at the status of the cribellum in RTA (retrolateral tibial apophysis) clade spiders (Coddington & Levi 1991), a group comprising approximately 18000 species. Using molecular data from 18S and 28S ribosomal RNA (18S and 28S), H3 and COI the authors tested the hypothesis proposed in earlier studies (e.g. Coddington & Levi 1991) that the cribellum may have been lost and regained several times across this group (Coddington & Levi 1991). Spagna and Gillespie found that the dominant pattern was of repeated loss, rather than loss and regain, of the cribellum.

If we accept both thomisids and Salticidae (jumping spiders) as part of the Dionycha as proposed by Coddington and Levi (1991), then the close relationship of these families means that molecular phylogenetic studies of the latter are of great interest. Heddin and Maddison (2001) tested the monophyly of the salticid subfamily Dendryphantinae using sequence data obtained for three mitochondrial (COI, NADH dehydrogenase subunit I (ND1) and 16S) and one nuclear gene region (28S). Overall, monophyly was confirmed but there were difficulties in reconciling the COI phylogeny with those derived from other data. These difficulties are discussed later.

A common problem in southern hemisphere taxonomy and systematics is that many species were, in the absence of better alternatives such as clearly defined local genera, placed in northern hemisphere genera when originally described. In the case of Australasian taxa, many species were described in the 19th century (e.g. Koch 1875) and have not been revised since. Confronted with such a situation for the Lycosidae (wolf spiders), Vink *et al.* (2002) tested the validity of the placement of Australasian lycosid (wolf spider)

species in Northern Hemisphere genera by testing data derived from 12S ribosomal RNA (12S) sequences taken from a number of Australasian wolf spiders as well as several Northern Hemisphere relatives and other outgroup species. They found the Australasian taxa generally formed their own grouping quite apart from Northern Hemisphere taxa. The New Zealand taxa most closely aligned with a subset of Australian genera. Vink and Patterson (2003) continued work on the New Zealand Lycosidae using both molecular (ND1 and COI) and morphological data. They found both the molecular and morphological data supported one another and that the New Zealand lycosid genus *Anoteropsis* probably radiated less than five million years ago.

While these studies use a variety of gene regions (summarised in Table 2 below) genetic data capture was accomplished through what appears to be fairly standard PCR protocols, DNA sequencing and data analysis, although the latter seems most subject to change as the increasingly more powerful algorithms appear. Data is often analysed using more than one approach in an attempt to increase certainty. For example, Spagna and Gillespie (2008) used both direct-optimization and Bayesian analyses, finding both supported their conclusions. Another common thread is that although species trees do not necessarily equate to gene trees, in the studies cited above molecular data generally supports alpha taxonomy based morphological delimitations. One potential pitfall is that occasionally the phylogenetic analyses for the widely used COI gene region are incongruent with similar analyses based on other gene regions in spider studies (e.g. Hedin & Maddison 2001, Vink & Patterson 2002). Heddin and Maddison (2001) suggested higher-level interactions such as variable selective constraints at the amino acid level might influence the dynamics of COI nucleotide evolution and hence contribute to misleading phylogenetic signals. Thus, the functional importance of the proteins encoded for by COI may be such that there are different selective constraints operating compared to other genes resulting in conflicting phylogenies when sequence data from COI and other genes are analysed.

Actin 5C – Vink & Dupérré 2010.

COI – Hedin 1997; **Garb 1999**; Arnedo *et al.* 2001; Hedin 2001; Hedin & Madison 2001; Hormiga *et al.* 2003; Vink & Paterson 2003; Garb *et al.* 2004; **Garb & Gillespie 2006**; **Benjamin et al. 2008**; Spagna & Gillespie 2008; Vink *et al.* 2008; Vink & Dupérré 2010; Vink *et al.* 2011; Smith *et al.* 2012.

ITS1-ITS2 – Vink *et al.* 2008.

ND1 – **Garb & Gillespie 2006***; Hedin 1997; Hedin & Madison 2001; Hormiga *et al.* 2003; Vink & Paterson 2003; **Garb & Gillespie 2006**.

H3 – Hormiga *et al.* 2003; **Benjamin et al. 2008**; Spagna & Gillespie 2008.

12S – Garb *et al.* 1994; Vink *et al.* 2002.

16S – Hormiga *et al.* 2003; **Garb & Gillespie 2006***; **Benjamin et al. 2008**.

18S – Spagna & Gillespie 2008.

28S – Hedin & Madison 2001; Spagna & Gillespie 2008; Vink *et al.* 2011.

*combined 16S-ND1 sequences

Table 2: Genes used to generate molecular sequences in cited studies. Thomisid studies are highlighted in **bold**.

Overall though, studies like this serve to show that molecular data can be used to answer questions that are difficult to solve with morphological analysis alone. For example, while morphological data might indicate a group has undergone radiation, it is difficult to pinpoint precisely when this might have occurred because rates of morphological change are not inherently measurable in the same way molecular sequence data is.

BIOGEOGRAPHY AND THE NEW ZEALAND SPIDER FAUNA

Much of New Zealand's flora and fauna have historically been characterised as 'Gondwanan' (Brownsey & Baker 1983), with the endemic biodiversity reflecting the long isolation of the New Zealand land mass. This view has long been the dominant model for the New Zealand spider fauna (Forster 1975; Forster & Forster 1999; Griswold 2001), with a late Mesozoic origin and speciation *in situ* after the breakup of Gondwana postulated for the spider

fauna as we know it today (Forster 1975; Zabka *et al.* 2002). More recent studies have begun to challenge this position, both in a general sense (e.g. Chambers *et al.* 2001) and for spiders in particular (Vink & Paterson 2003; Griffiths *et al.* 2005). These studies indicate that some endemic elements have speciated from ancestral stock that arrived here far more recently, possibly through ballooning or rafting. Sirvid (2008) suggested dispersal via these means was a plausible explanation for the origin of the current endemic Chatham Islands spider fauna.

The Gondwanan (= vicariance) paradigm as a general model to explain the formation of the New Zealand biota has been subject to vigorous debate in recent times. Are we really the 'Moa's Ark' of Bellamy *et al.* (1990) with New Zealand slowly drifting away from other Gondwanan remnants with the bulk of our plants and animals evolving in splendid isolation? Or are we, as McGlone (2005) puts it, the 'flypaper of the Pacific', with our biota descended from sundry stragglers that happen to have somehow dispersed here? It has been suggested that New Zealand may even have been completely submerged during the Oligocene and early Miocene some 25-22 million years ago (Landis *et al.* 2008). If true, then it would mean that the entire biota that had persisted and subsequently developed since New Zealand split from Gondwana would have been wiped out. Thus, every extant endemic organism could only be derived from ancestors that have colonised New Zealand at some point during the last 22 million years as New Zealand went from Moa's Ark to 'Moa's Submarine' (as I term it). The debate over the drowning of New Zealand is essentially one centred on the degree to which the Oligocene marine transgression inundated the New Zealand landmass. Was New Zealand entirely submerged (Landis *et al.* 2008) or was the New Zealand landmass greatly reduced in both area and relief but nonetheless still available to terrestrial organisms (Cooper & Cooper 1995)? In either case, the New Zealand biota would have been drastically (possibly completely) reduced.

Goldberg *et al.* (2008) state current distributional data in isolation is not proof of historical process. As an example, they cite a number of studies on penguins. These birds have a southern distribution (South America, Australia,

New Zealand, southern Africa and Antarctica) fitting the traditional idea of a Gondwanan distribution. Fossils (Slack *et al.* 2006) and molecular evidence (Baker *et al.* 2002) suggest penguins have been around for at least 62 million years and probably originated in Gondwana. However, penguins as we know them today may have originated in the early Oligocene with New Zealand colonised later (Baker *et al.* 2002) and there is some evidence to suggest the Australian and New Zealand populations of *Eudyptula* penguins may have had recent contact with each other (Banks *et al.* 2006). Thus, while the modern range for penguins seems to reflect a classic Gondwanan distribution, analysis of fossil and molecular data shows that a vicariance based model does not explain how it arose.

As Australia was and is New Zealand's most significant neighbouring landmass post-Oligocene, it is also the most likely source of colonists for any newly emergent New Zealand landmass. The 22 million year period between the theorised end of New Zealand's inundation and now is more than enough time to develop a distinct biota, as appears to be the case with cicadas (Arensberger *et al.* 2004). If that biota is descended from Australian colonists, any taxa that later speciate into New Zealand endemic taxa might give the illusion of an older relationship with Australia than is really the case.

Although the evidence for a continuous New Zealand presence for some taxa traditionally regarded as Gondwanan (e.g. frogs, galaxiid fishes) has been questioned (Waters & Craw 2005) there is some evidence to suggest that archaic and iconic species such as tuatara may have been here all along. Jones *et al.*, (2009) report a tuatara-like bone from Miocene deposits at St Bathans in Otago that has been dated at three million years after the end of Oligocene inundation. While this may seem like ample time for colonisation from elsewhere to occur, the authors point out that the distance involved combined with the limited swimming ability of sphenodont reptiles and the lack of any evidence for a contemporaneous presence of these reptiles in Australia make a post-Oligocene colonisation of New Zealand unlikely. This combination of circumstantial evidence and educated supposition lies behind much of the reasoning for the persistence of at least some old vicariant

elements (or their descendents) in the New Zealand biota. While Goldberg *et al.* (2008) point out that so far molecular evidence does not unequivocally support this view, a recent study on parrots suggests otherwise. Wright *et al.* (2008) propose an Australasian origin for the parrots in the Cretaceous and place the New Zealand genera *Strigops* and *Nestor* as sisters to all other parrots. Without evidence for the persistence of members of the *Strigops/Nestor* group elsewhere through to post Oligocene times, a complete submergence of the New Zealand landmass becomes problematic as a viable hypothesis. Work on the Cyphthothalmi, or mite-like harvestmen (e.g. Boyer & Giribet 2009) suggests a Gondwanan origin for these animals.

Overall, the debate about whether New Zealand was completely or only partially drowned is stimulating and has caused us to review many past assumptions. As Didham (2005) points out, New Zealand can no longer be seen only as a museum of ancient Gondwanan relics and Goldberg *et al.* (2008) describe New Zealand as a dynamic and relatively young evolutionary system. However, while the New Zealand biota may not have the complexity and completeness that might be expected if it had evolved in total isolation in a large and diverse environment over the last 80 million years (Goldberg *et al.* 2008), there are still many taxa for which anything other than a vicariance-based origin seems implausible and have yet to be properly tested. For example, the spider family Hexathelidae has a fossil record in excess of 200 million years old (Selden & Penney 2010) and has a number of species in present day Australia and New Zealand. Furthermore, Sharma and Wheeler (2013) have suggested that the evolutionary histories of lineages that survive mass extinctions are difficult to distinguish from scenarios of rapid radiation.

Anapidae	Platnick & Forster 1989
Cyatholipidae	Griswold 2001
Holarchaeidae	Forster & Platnick 1984
Gradungulidae	Forster, Platnick & Gray 1987
Mecysmaucheniidae	Forster & Platnick 1984
Orsolobidae	Forster & Platnick 1985
Pararcheidae	Forster & Platnick 1984
Synotaxidae	Forster, Platnick & Coddington 1990

Table 3: “Gondwanan” spider monographs including New Zealand taxa.

Where do spiders fit into this debate? The New Zealand spider fauna is rich and diverse, with an estimated 2000 (Paquin *et al.* 2010) to 3600 (Platnick 1992) species. It is also characterised by a high degree of endemism with 95% of the over 1100 named species being unique to New Zealand (Sirvid *et al.* 2011). Some families present in New Zealand have wider distributions that include areas such as Australia, Chile and southern Africa, leading to the New Zealand spider fauna being described as Gondwanan (Forster 1975, Forster & Forster 1999, Griswold 2001) and a number of family level monographs concentrate primarily on spiders from areas that were once part of Gondwana (see Table 3).

None of these monographs employ molecular methods and all are open to the criticism that the 'Gondwanan' tag is assumed rather than proven. However, such assumptions may not necessarily be unreasonable as members of these families are regarded as primitive and/or poor dispersers. Although an untested hypothesis, speciation after vicariance seems to be a more parsimonious explanation for these distributional patterns than dispersal over long distances. However, dispersal is not impossible to rule out. For example, Forster & Platnick's (1985) monograph on the Orsolobidae (a family found only in Australia, New Zealand and South America) shows New Zealand's orsolobid fauna comprises twenty species. The vast majority occur in mainland New Zealand, but the Chatham Islands, some 850 km from mainland New Zealand and perhaps as young as four million years old, is home to an endemic species, as are the subantarctic Auckland Islands. At the very least, the existence of these monographs with well defined morphological species described to a modern standard can still form the basis for further explorations of historical relationships through molecular analyses.

More recent studies of the New Zealand spider fauna have begun to use molecular techniques. Vink and Patterson (2003) examined the endemic New Zealand wolf spider (Lycosidae) genus *Anoteropsis*. This genus contains twenty of New Zealand's 27 known lycosid species and, as stated previously,

Vink and Paterson's data indicated the genus radiated no more than five million years ago. Griffiths *et al.* (2005) observed the genetic distance between the Australian redback (*Latrodectus hasseltii* Thorell, 1870) and the New Zealand katipo (*L. katipo*) is extremely close and that katipo is a relatively recent arrival to New Zealand. The closeness of the relationship was further demonstrated by a report of a redback introgression in a katipo sample from near Gisborne (Vink *et al.* 2008). The assumption is the redback ancestor in this case eluded border quarantine as the only known established redback populations are in central Otago (Forster & Forster 1999). Note that while redbacks and katipo can hybridise, interspecific mating is only possible in one direction. The courtship overtures of male katipo spiders are always rejected by female redbacks, whereas both katipo and redback males can mate with female katipo (Forster 1995).

Despite the richness of New Zealand's endemic spider fauna, molecular studies of New Zealand taxa with a view to elucidating phylogenetic relationships are still few in number. Family level revisions for New Zealand Pisauridae (Vink & Dupérré 2010) and Perigopidae (Vink *et al.* 2013) have concentrated on the New Zealand species and have not attempted to explore relationships with related species from elsewhere.

With respect to Thomisidae, the stephanopine species currently placed in *Sidymella* may prove to be of particular interest given the genus occurs in South America but does not appear to be known in the South Pacific outside of Australia and New Zealand. *Diaea* may have a wider range (Lehtinen 1993) but Szymkowiak's (2007) suggestion that the currently recognised New Zealand species may belong in a new genus shared with Australia is intriguing. These current distributions make the New Zealand Thomisidae an excellent candidate for the exploration of biogeographic questions. While thomisines might be widely distributed across the Austral-Pacific region and are known to be good dispersers, so far the stephanopines appear confined to large landmasses such as New Zealand and Australia but not New Caledonia. On the surface at least, they appear to fit the profile of a Gondwanan group *sensu* Forster. For the New Zealand Thomisidae, it is not inconceivable that

we may see evidence of both dispersal and vicariance at work and split on subfamilial lines.

THESIS QUESTIONS

It is clear that little is known about the New Zealand Thomisidae and the origins of the New Zealand spider fauna in general. This thesis addresses these gaps in our knowledge and uses a 'total evidence' approach that combines molecular and morphological data to explore two main areas of investigation.

1) *What is the composition of the New Zealand Thomisidae? More specifically, how many species are there and what is their taxonomic status?*

New Zealand thomisids are common and widespread yet have had little scientific attention. They have never been formally revised as a group and there have been no species described since 1910. In world terms, the state of knowledge is not much better with several authorities recognizing that many genera are in need of revision (Lehtinen 1993, 2005; Benjamin *et al.* 2008). This lack of knowledge may seem problematic but it is not an insurmountable obstacle as Vink (2002) demonstrated with his monograph on New Zealand lycosid spiders. Ultimately, a species description is a refutable hypothesis that may be falsified by later workers (e.g. through synonymy). At the heart of this question is one of identity for each species taxon and how they are placed within the Thomisidae.

2) *Does the modern New Zealand thomisid fauna support the Gondwanan vicariance model, or alternatively, are their origins better explained by more recent colonization and subsequent radiation events? If the latter, can it be estimated when such events may have occurred?*

New Zealand has a rich spider fauna with a high degree of endemism. Workers such as Forster (1975) have taken this to mean the New Zealand spiders have evolved in isolation since New Zealand began to drift away from Australia. However, others have suggested that modern distributions are not necessarily proof of historical process (e.g. Goldberg *et al.* 2008). The 'Oligocene drowning' debate also challenges traditional 'Gondwanan' (= vicariance based) assumptions about the origin of the New Zealand biota. If New Zealand really was completely inundated then our unique flora and fauna must have been descended from colonisers that arrived during the 22 million year period since the end of the inundation. Molecular phylogenetic studies on thomisids (e.g. Benjamin, *et al.* 2008) are rare, but in concert with other studies on (or including) other New Zealand taxa (e.g. cicadas (Arensburger *et al.* 2004) and parrots (Wright *et al.* 2008)) they offer methodological and analytical models that may help in better clarifying the relationships of the New Zealand thomisid fauna and exploring the timing of the evolutionary processes that shaped it.

CHAPTER OUTLINES

Chapter 2 is a full taxonomic revision of the New Zealand Thomisidae. Using morphological data supported by molecular data from Chapter 3, I will document all species known from New Zealand and discuss the following topics:

- Species previously unrecorded for New Zealand are documented and described.
- Redescribes previously known species to a modern standard and both sexes for all species are described for the first time.
- Attempts to resolve other taxonomic issues such as questions of possible synonymy and revises generic placements.
- Provides new information on the biology, distribution and taxonomy of all species.

Note that this chapter is presented in the style of a taxonomic monograph. As it forms the basis of a proposed publication draft, some of the information presented above is repeated as necessary background information. Any differences between the two versions reflect the fact that the information above represents the state of knowledge at the outset of this project whereas the version presented in Chapter 2 incorporates information uncovered in the course of this thesis. Particular attention should be paid to changes in taxon names as most species are transferred to other genera. These changes are documented in Table 1 of Chapter 2.

Chapter 3 deals with the origin and evolutionary history of the New Zealand Thomisidae, but also provides supporting information for Chapter 2. A multilocus molecular approach is used to explore:

1. The genetic distinctiveness of putative taxa. More specifically:
 - Do colour morphs signify intraspecific or interspecific differences?
 - Do molecular data confirm that previously described species are distinct taxonomic entities?
 - Do molecular data support an initial assessment that several morphotaxa represent new and undescribed species?
2. The relationships and evolutionary history of the New Zealand Thomisidae. In particular:
 - Does molecular data indicate an old fauna reflecting radiation following vicariance processes, or a young fauna descended from more recent colonists from elsewhere?

This chapter is presented in the form (and format) of a manuscript draft that has already been accepted for publication by *Invertebrate Systematics*. Readers should be aware that this work was submitted and subsequently accepted for publication before the taxonomic work was complete, so unrevised taxon names are used. Table 2 in Chapter 2 associates specimen codes and GenBank numbers used in Chapter 3 with the revised taxon names.

The *Invertebrate Systematics* paper is co-authored and the contributions of each co-author were as follows:

- Nicole Moore produced a number of DNA extractions and COI and 28S PCR. She produced all the H3 and ND1 sequences. She also helped draft the extraction and PCR protocol portions of the methods section.
- Geoff Chambers helped with experimental design and provided guidance on the preparation of the manuscript and the analysis and interpretation of data.
- Kelly Prendergast provided approximately a dozen DNA extractions and COI sequences used in her BSc. (Hons) project.
- I took the lead role in all aspects of this body of work. I did the great majority of the DNA extractions, PCR and sequence editing as well as depositing all sequence data on GenBank. I carried out all the phylogenetic analyses presented here and the interpretation of the results is ultimately my own. With the exception of a portion of the methods section as noted above, the text, tables and figures were all prepared by me.

Chapter 4 reviews the findings of the previous two chapters, makes suggestions for future research and gives some final remarks.

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**CHAPTER 2:
A TAXONOMIC REVISION OF THE NEW ZEALAND
CRAB SPIDERS (ARANEAE: THOMISIDAE)**

NOTES

This chapter should be treated as confidential and embargoed from public release until a publication based on the work contained herein is produced. According to chapter 3, article 8 of the *International Code of Zoological Nomenclature* (ICZN 1999), taxonomic decisions made in a thesis are not considered valid as a thesis does not constitute a published work. However, if descriptions, associated figures and records of new species from this thesis were made publically available before formal publication, the potential is there for the information to be published by another party under their own name.

Readers are also reminded of the notes on style and format, repetition of information and changes to taxon names given in the chapter outline at the end of Chapter 1. Table 1 documents the nomenclatorial changes.

Lastly, because this chapter is written in the style of a taxonomic monograph, reference to Sirvid *et al.* (in press) is made instead of reference to Chapter 3. The two are directly equivalent, but referral to a publication instead of a thesis chapter was judged to be a more appropriate format. While this paper may become available online or in print during marking, it had only reached the proofs stage as of this time of writing.

ABSTRACT

The Thomisidae (crab spiders) are represented in New Zealand by two subfamilies (Stephanopinae and Thomisinae) and are revised at a family level for the first time. The number of described species increases from eight to eleven and taxonomic decisions have been based on a combination of morphological and genetic data.

In the stephanopines, *Bryantymella* Gen. nov. is erected to contain the type species *Bryantymella angularis* (Urquhart, 1885) comb. nov. as well as *B. angulata* (Urquhart, 1885) comb. nov., *B. thorini* sp. nov. and *B. brevisrostris* sp. nov. Two Australian species, *Sidymella longipes* (Koch, 1874) and *S. trapezia* (Koch, 1874), are also recorded for New Zealand. *Sidymella benhami* (Hogg, 1910) is considered to be a junior synonym of *Bryantymella angulata* (Urquhart, 1885). A lectotype is designated for *B. angulata*. In the thomisines, the previously monotypic genus *Cymbachina* now encompasses all New Zealand species previously placed in *Diaea*. The type species is *Cymbachina albobrunnea* (Urquhart, 1893) and the other included species are *C. ambara* (Urquhart, 1885) comb. nov., *C. albolimbata* (L. Koch, 1893) comb. nov., *C. sphaeroides* (Urquhart, 1885) comb. nov. and *C. urquharti* sp. nov. *Synema suteri* Dahl, 1907 is now regarded as a junior synonym of *C. ambara* (L. Koch 1893).

All previously described species are re-described to a modern standard. The previously undescribed sexes for *B. angulata*, *S. longipes*, *C. albolimbata* and *C. albobrunnea* are documented for the first time and previous descriptions of the male of *B. angulata* are now recognised as *B. angularis*. Three new species are described. Photographs of adults and diagnostic genitalic characters are included, as are new diagnostic keys and updated synonymic, geographic and biological information.

INTRODUCTION

Thomisidae

Spiders of the family Thomisidae are commonly known as crab spiders because of their ability to move sideways in a crab-like manner. Thomisids are diverse both in form and in number of species (Jocqué & Dippenaar-Schoeman 2006), with over 2150 species known (Platnick 2013).

In New Zealand, two subfamilies, Thomisinae and Stephanopinae, are present. In thomisines, the general body form is sleek, smooth and slender (Fig. 1A), while stephanopines are more heavily built with a rugose and gnarled surface (Fig. 1B). New Zealand thomisids are not especially large and only females of *Bryantymella angularis* (Urqhart, 1885) are known to exceed 1cm in body length (Pers. obs.).



Fig. 1. New Zealand examples from thomisid subfamilies. **A)** *Cymbachina ambara* (Thomisinae), **B)** *Bryantella thorini* (Stephanopinae). Both figures reproduced from Forster (1967).

Despite the gross differences of general form between the two subfamilies, thomisids possess a number of morphological characters that in combination define the family. Thomisids are eight-eyed spiders, with lateral (and sometimes other) eyes mounted on tubercles in many species. The legs are laterigrade (i.e. point outwards), with each leg terminating in two claws. The

first two pairs of legs are typically longest and strongest and are armed with strong spines used in prey capture. (Jocqué & Dippenaar-Schoeman 2006, Paquin *et al.* 2010). Thomisid anatomy is depicted in Figs 2-5.

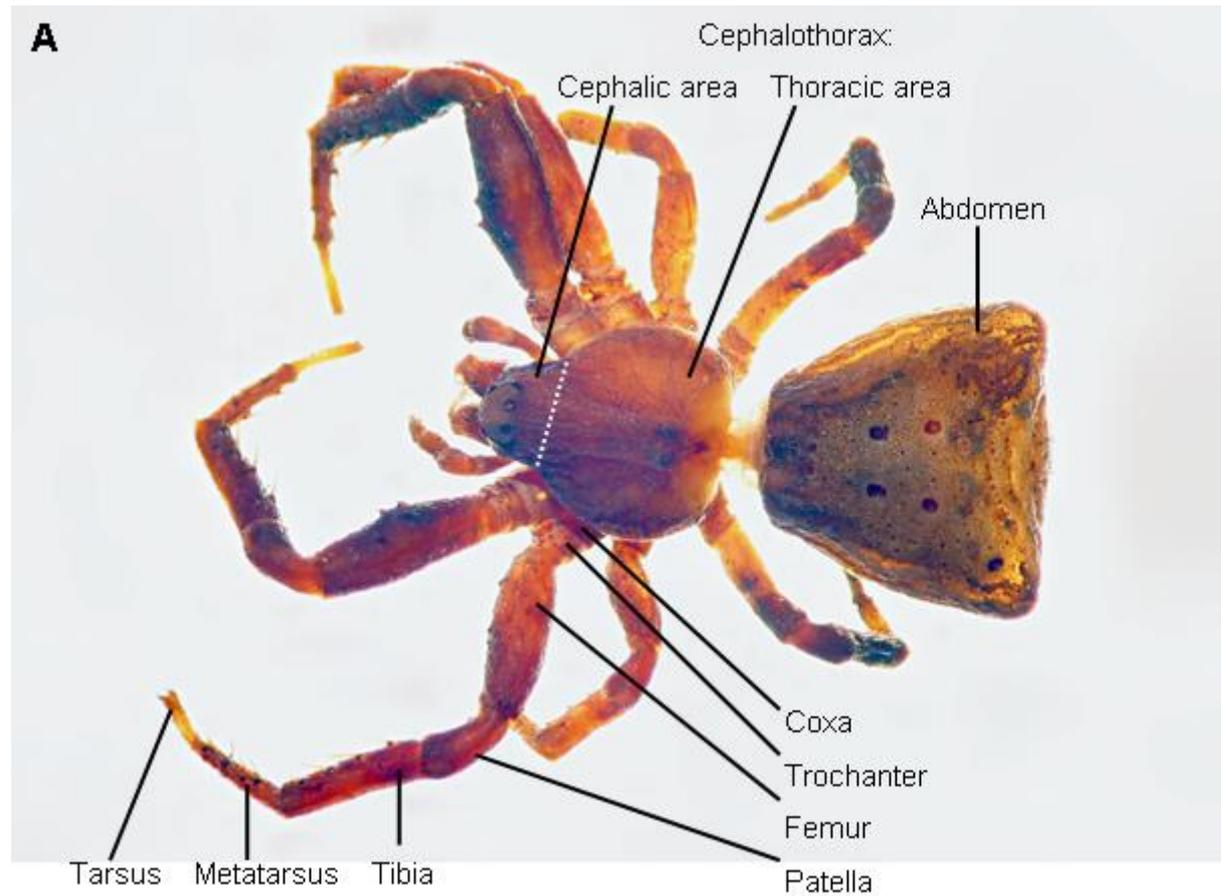


Fig 2. *Bryantymella thorini* sp. nov. female anatomy. **A)** Dorsal view

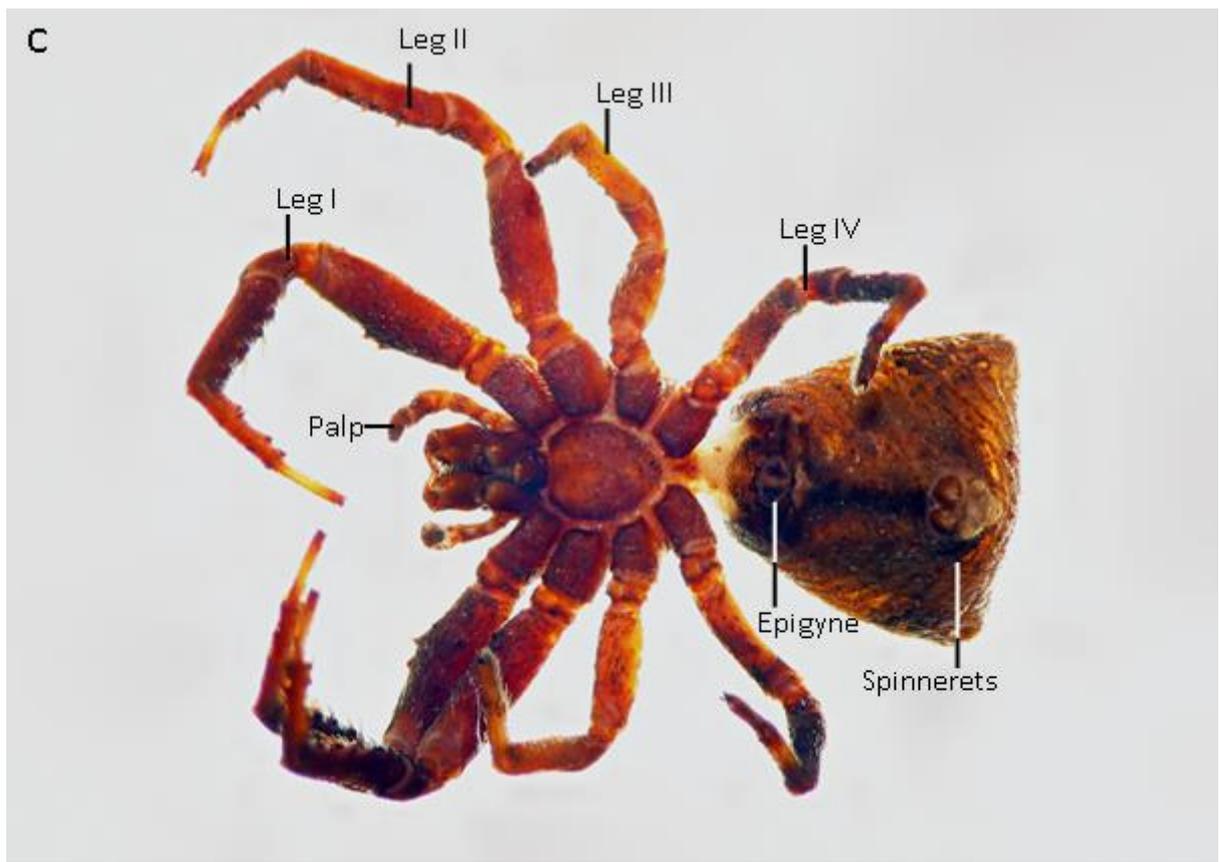
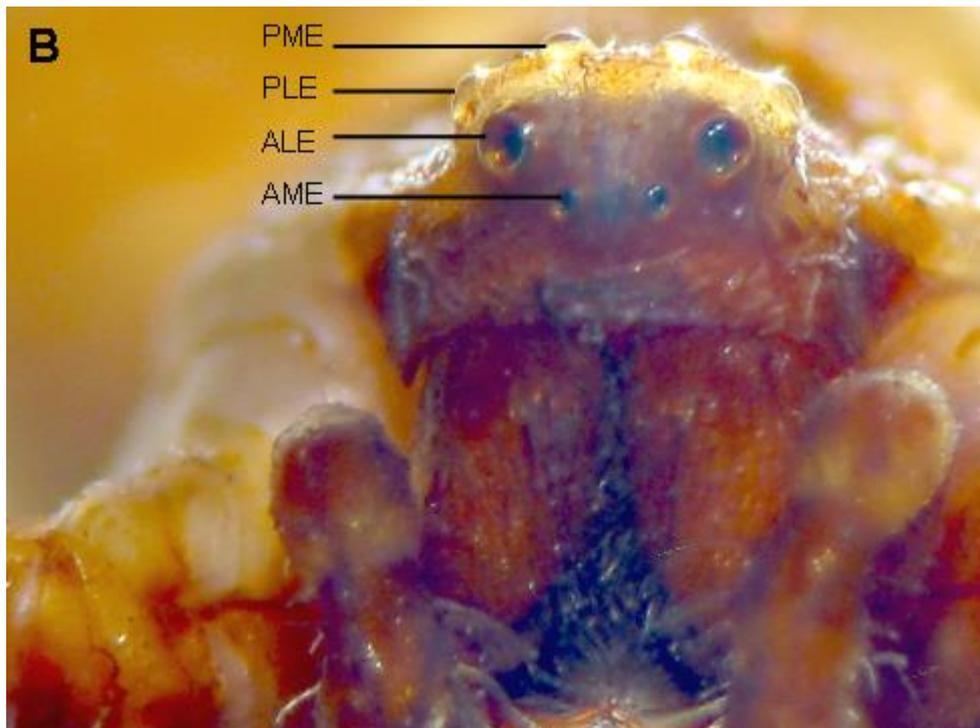


Fig 2. (cont). *Bryantymella thorini* sp. nov. female anatomy. **B)** Eye positions in anterior view (see *Methods and Conventions* for abbreviations) **C)** Ventral view.

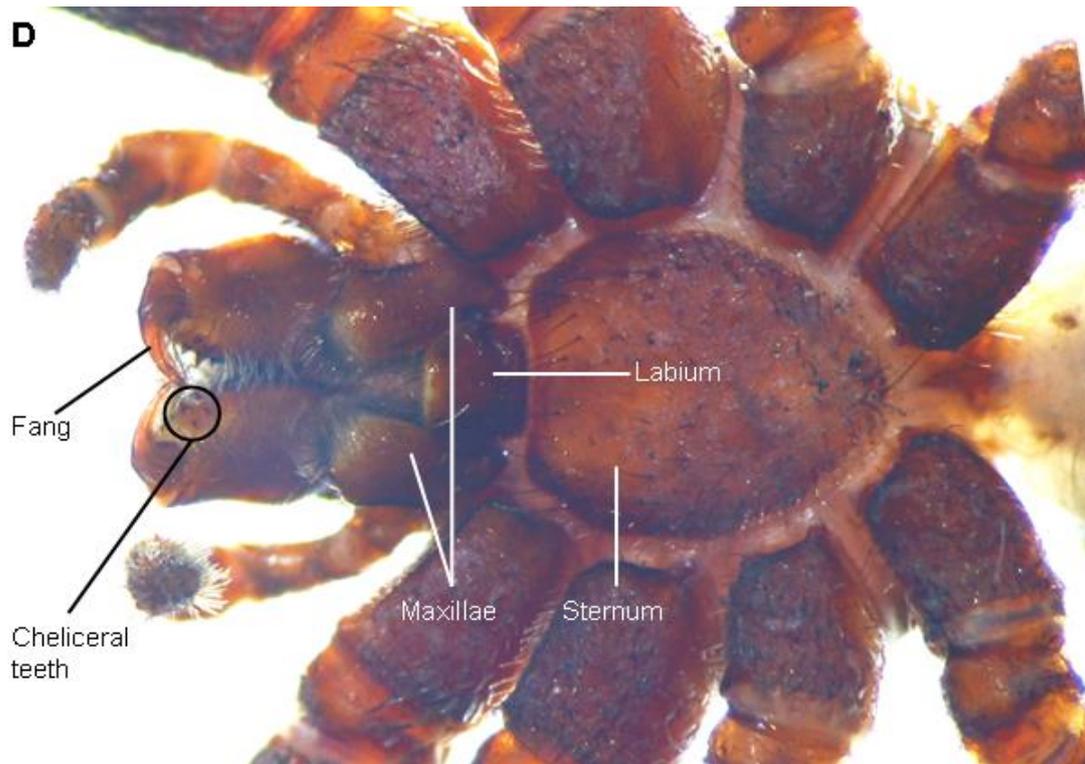


Fig. 2 (cont). *Bryantymella thorini* sp. nov. female anatomy. **D)** Anteroventral detail.

Terms in bold below (and other terms elsewhere) are defined in the *Glossary* (Appendix B) and abbreviations are given in the *Methods and Conventions* section.

The architecture of the male **palp** is broadly consistent within each subfamily (Figs 3-4). The spoon-like **cymbium** is the terminal segment of the palp and contains the **genital bulb**. In New Zealand stephanopines a **retrolateral cymbial projection** is present on the **retrolateral** margin of the cymbium and is positioned above the **retrolateral tibial apophysis** which arises from the palpal tibia. Thomisines lack a retrolateral cymbial projection but have a **ventral tibial apophysis** that is not present in stephanopines. The **tegular area** of the bulb is disk-like in thomisines and rounded but irregularly shaped in stephanopines. The **sperm duct** has a central origin in thomisines and coils around the tegular area but only a **prolateral** distal portion is visible in stephanopines. The sperm duct terminates as an **embolus**. In the stephanopines, the embolus of *Bryantymella* follows the **apical embolic bend**. This structure is lacking in *Sidymella* and the embolus terminates just

before near the distal end of the genital bulb, while in thomisines the embolus terminates just after this point but may be obscured by the sperm duct.

3

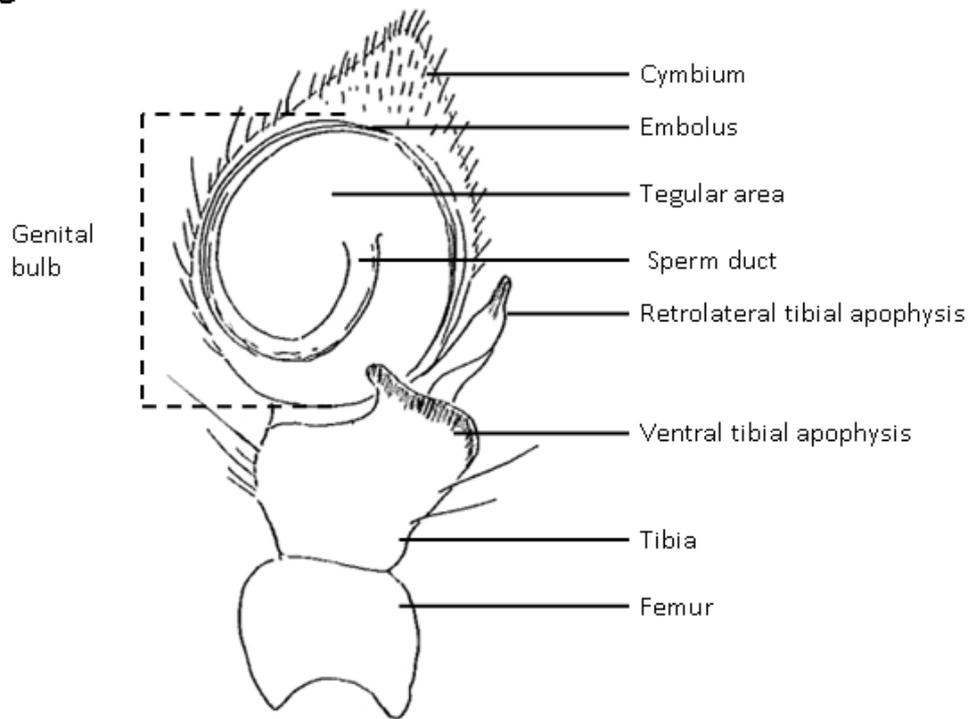


Fig. 3. *Cymbachina ambara* (Thomisinae) male palp, ventral view. After Bryant (1933).

4

A

B

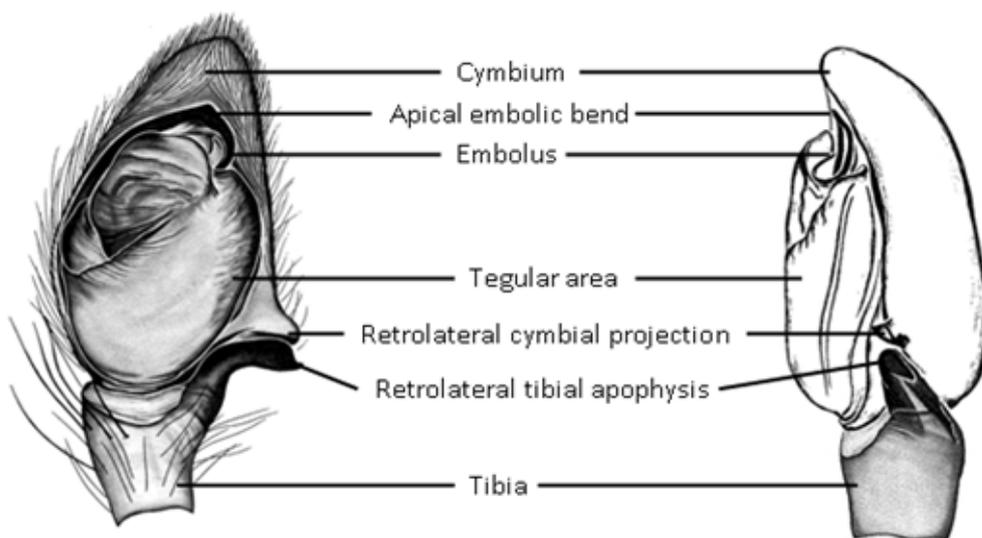


Fig. 4. Male palp of *Bryantymella angularis* (Stephanopinae). **A)** Ventral view, **B)** Retrolateral view. Both figures after Paquin *et al.* (2010).

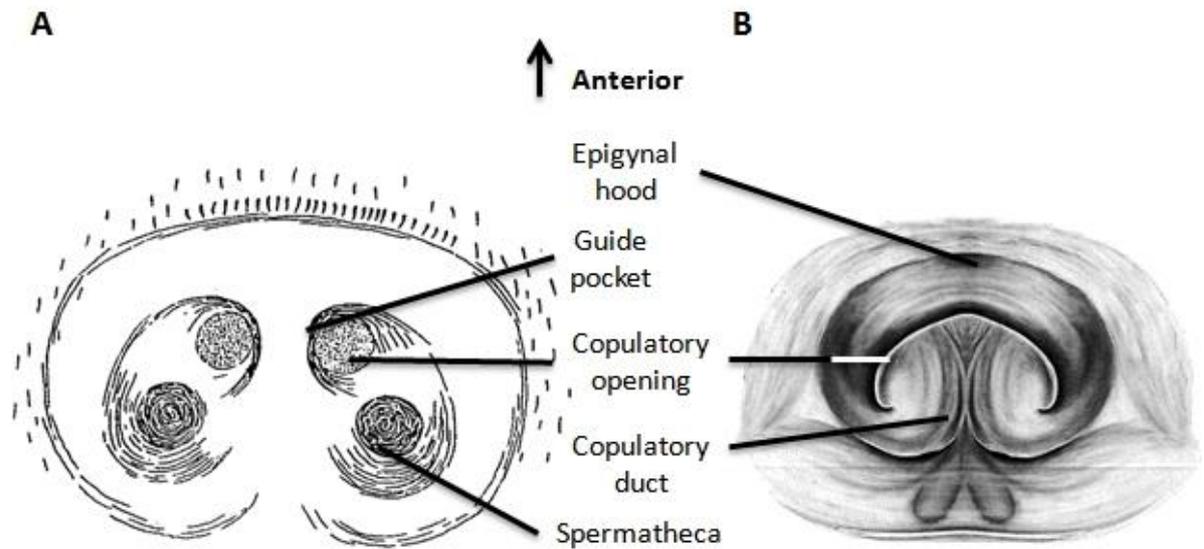


Fig. 5. External (ventral) view of female epigynes. **A)** *Bryantymella angularis* (Stephanopinae), **B)** *Cymbachina ambara* (Thomisinae). Fig. A after Bryant (1933), Fig. B. after Paquin *et al.* (2010).

The female **epigyne** (Fig. 5) is **entelegyne**, often in an **atrium** with guide pockets (stephanopines) or an anterior **epigynal hood** (thomisines). In external (ventral) view **spermathecae** and **copulatory ducts** may be visible. These structures are easier to view with excised and cleared epigynes (see *Methods and Conventions*). The number of spermathecae and form of the copulatory ducts differ between the New Zealand members of the two subfamilies. In Thomisinae, there are two globular spermathecae and the copulatory ducts form a series of demi-loops along part of their length. In Stephanopinae, the ducts are less convoluted and there are two pairs of spermathecae, one pair of which is irregularly sigmoidal in profile.

TAXONOMY AND SYSTEMATICS

The family Thomisidae was first erected by Sundevall in 1833. With over 2150 species in 174 genera, they are the sixth most diverse of the 112 spider families recorded so far (Platnick 2013).

Higher Systematics

The thomisids classically comprise seven subfamilies: Aphantochilinae, Bominae, Dietinae, Stephanopinae, Strophinae, Stiphropodinae and Thomisinae (Simon 1892, Ono 1988, Jocqué & Dippenaar-Schoeman 2006) but partial rearrangements and relimitations of thomisid taxa have also been proposed if not widely adopted. For example, Wunderlich (2004) proposed the family Borboropactidae to cover part of the Thomisidae but this was rejected by Benjamin *et al.* (2008) as they found Borboropactidae to be paraphyletic. While the monophyly of Thomisidae has been confirmed by both molecular (Benjamin *et al.* 2008) and morphological (Benjamin 2011) analyses, the same studies also indicated that thomisid subfamilies (including Stephanopinae and Thomisinae) need further refinement and clearer relimitation as they are either paraphyletic or polyphyletic. Characters previously treated as diagnostic for subfamilies such as the presence of cheliceral teeth in Stephanopinae and their absence in Thomisinae (Ono 1988) have some utility in separating New Zealand members of the two subfamilies (Pers. obs), but are not phylogenetically informative in a wider context as they are not unambiguous synapomorphies (Benjamin 2011).

At a broader level of spider systematics, thomisids have been placed in the Dionycha (Fig. 6), a grouping of several families of spiders defined by the lack of a cribellum (a specialised silk-producing organ) and the absence (or major reduction) of the third tarsal claw and its' replacement with a claw tuft (Coddington & Levi, 1991). Later work by Coddington (2005) reaffirmed the placement of Thomisidae within Dionycha. However, the monophyly of the Dionycha has yet to be tested and the correct placement of thomisids relative to other members of this group is unclear (Benjamin *et al.* 2008). Coddington and Levi (1991) also acknowledge the dionychan condition occurs in other families, albeit at lower taxonomic levels

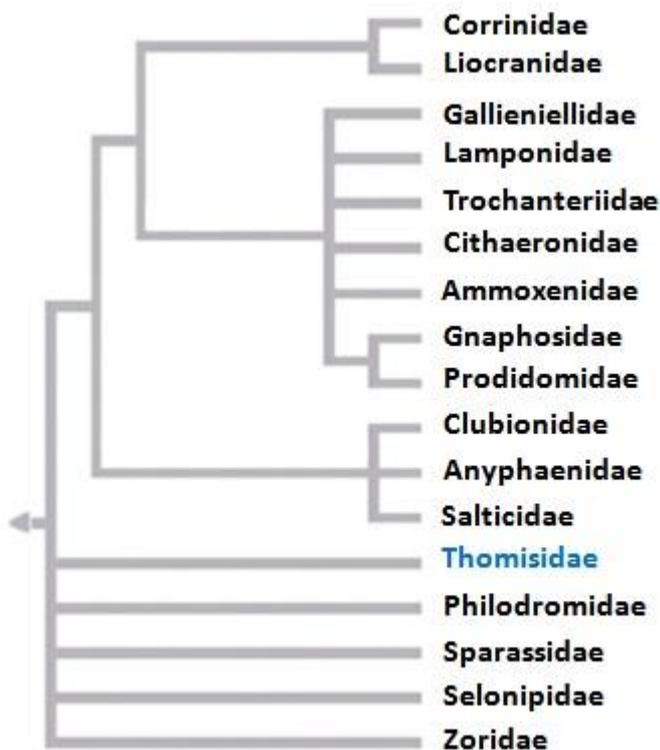


Fig. 6. The position of Thomisidae within the Dionycha of Coddington and Levi (1991).

A more recent molecular analysis (Agnarsson *et al.* 2013) of spider phylogenetics suggests Thomisidae should instead be placed in the higher Lycosoidea, the immediate sister clade to Dionycha. However, the authors note there are many contradictions between their results and Coddington's (2005) morphology-based consensus model. They suggest that available DNA data is inadequate to resolve deep level phylogeny and that the model of Coddington *et al.* (1991) is also likely to be incorrect in some aspects.

The New Zealand Thomisidae

Prior to this revision, we had a very limited knowledge of the New Zealand thomisid fauna and their relationships with overseas taxa. Table 1 lists a) the New Zealand thomisid fauna as it was known prior to this revision, b) updated names where applicable and c) new species described herein. More detailed synonymies for previously described species are provided in their descriptions.

	Previous Name	Current Name
Stephanopinae	<i>Sidymella angularis</i> (Urquhart, 1885)	<i>Bryantymella angularis</i> (Urquhart, 1885) comb. nov.
	<i>Sidymella angulata</i> (Urquhart, 1885)	<i>Bryantymella angulata</i> (Urquhart, 1885) comb. nov.
	-	<i>Bryantymella brevisrostris</i> sp. nov.
	-	<i>Bryantymella thorini</i> sp. nov.
	<i>Sidymella benhami</i> (Hogg, 1910)	<i>Bryantymella angulata</i> (Urquhart, 1885) new synonymy
	<i>Sidymella longipes</i> (L. Koch, 1874)* <i>Sidymella trapezia</i> (L. Koch, 1874)*	<i>Sidymella longipes</i> (L. Koch, 1874)* <i>Sidymella trapezia</i> (L. Koch, 1874)*
Thomisinae	<i>Cymbachina albobrunnea</i> (Urquhart, 1893) <i>Diaea albolimbata</i> L. Koch 1875	<i>Cymbachina albobrunnea</i> (Urquhart, 1893) <i>Cymbachina albolimbata</i> (L. Koch 1875) comb. nov.
	<i>Diaea ambara</i> (Urquhart, 1885)	<i>Cymbachina ambara</i> (Urquhart, 1885) comb. nov.
	<i>Diaea sphaeroides</i> (Urquhart, 1885)	<i>Cymbachina sphaeroides</i> (Urquhart, 1885) comb. nov.
	-	<i>Cymbachina urquharti</i> sp. nov.
	<i>Synema suteri</i> Dahl, 1907	<i>Cymbachina ambara</i> (Urquhart, 1885) new synonymy

Table 1. Summary of taxonomic changes to the New Zealand Thomisidae made in this revision. * denotes Australian species established in New Zealand.

The earliest thomisid described from New Zealand was *Diaea albolimbata* L. Koch, 1875 in the monumental work “Die Arachniden Australiens” (L. Koch, 1875). Seven species (five *Philodromus* and two *Sparassus* species) were described by Urquhart (1885, 1887 and 1893). *Synema suteri* Dahl, 1907 and *Stephanopsis benhami* Hogg, 1910 were described in the early 20th century. There have been no new thomisids described for New Zealand since then.

A pioneering figure in New Zealand arachnology in the late 19th century, A.T. Urquhart named dozens of species new to science. However, his descriptions have been accurately described as “voluminous but vague” and many of his species are either unrecognisable or their names have been sunk in synonymy (Forster, 1967). Much of Urquhart’s collection has been lost, but what remains is housed in Canterbury Museum (Nicholls *et al.*, 2000). Bryant examined and re-described much of the material (1933, 1935a, 1935b), including Urquhart’s extant thomisid type specimens. Of Urquhart’s seven described thomisid species, Bryant had material available from six. This is the

closest approximation we have to a revision of the NZ thomisid fauna. Bryant erected the genus *Cymbachina* for *Xysticus albo-brunnea* Urquhart, 1893 and treated both *Sparassus angularis* Urquhart, 1885 and *S. angulata* Urquhart, 1885 as members of *Sidyma* Simon, 1895. Of the four *Philodromus* species described by Urquhart, Bryant had only material from three species available to her. She synonymised *P. ovatus* Urquhart, 1885 under *Diaea albolimbata* (invalidly amending it as *albomaculata*) and transferred *P. ambara* Urquhart, 1885 and *P. sphaeroides* Urquhart, 1885 to *Diaea*. Urquhart's remaining thomisid species, *Philodromus rubrofrontus* Urquhart, 1891 was not seen by Bryant but appears to be a *nomen dubium*. See *Species Excluded From the New Zealand Fauna* for more information on this species and *Tharpyna munda* L. Koch, 1874, which appears to have erroneously been recorded for New Zealand.

It has been clear for some time that New Zealand species that are currently placed in *Diaea* were not likely to remain there. This genus is currently ill-defined, with Lehtinen (1993) describing it and several other thomisid genera as "typical 'waste-basket' groups, where most species are not closely related to the respective type species". As noted earlier, *Xysticus albobrunnea* was transferred to the newly created monotypic genus *Cymbachina* by Bryant (1933). Bryant noted differences between this genus, *Cymbacha* L. Koch, 1874 and *Xysticus* C.L. Koch, 1835, but did not do so with respect to *Diaea*. Both genera appear to be correctly placed in the subfamily Thomisinae (*sensu* Ono, 1988).

In the stephanopine thomisids Dalmas (1917) considered *Sparassus angulata* to be a senior synonym of *Sparassus angularis*, and transferred both it and *Stephanopsis benhami* to *Sidyma*. Bryant (1933) did not refer to Dalmas (1917) and, as stated previously, maintained the distinction between *Sparassus angularis* and *Sparassus angulata*, transferring both to *Sidyma*. However, *Sidyma* is a preoccupied name, belonging to genus of arctiid moths (*Sidyma* Walker, 1856). The replacement name *Sidymella* was created by Strand (1942) for the type species of the *Sidyma*, *Stephanopsis lucida* Keyserling, 1880, and thus, by extension, all three New Zealand *Sidyma*

species became *Sidymella*. Bryant (1933) refers to a number of characteristics (e.g. cephalothoracic ridges) of the New Zealand species that do not fit *Sidyra* (= *Sidymella*), suggesting they were not congeneric. These spiders are easily separated from the New Zealand thomisines on the basis of general body form and the presence of cheliceral teeth.

Previously, all New Zealand Thomisidae were considered endemic, but two species from Australia, *Sidymella longipes* L. Koch, 1874 and *S. trapezia* L. Koch, 1874 have become established in New Zealand (Sirvid *et al.* in press).

Phylogenetic Relationships and the Evolutionary History of the New Zealand Thomisidae

These topics are explored in depth in Sirvid *et al.* (in press) but in summary, genetic data from several loci (Table 2) indicates the endemic members of the two thomisid subfamilies present in New Zealand form clades distinct from sampled Australian species. They appear to have separated from their Australian relatives and subsequently began radiating into distinct New Zealand species about 5-6 million years ago, a figure close to that given for the lycosid genus *Anoteropsis* (Vink & Paterson 2003). Sirvid *et al.* (in press) also found that the thomisines consistently recovered a clade containing (as *Diaea*) *Cymbachina ambara* as sister to a subclade containing *C. albolimbata*, *C. sphaeroides* and *C. urquharti* (as an undescribed species), while in the stephanopines, two species pairs containing (as *Sidymella*) *Bryantymella angularis* and *B. thorini* (as 'dwarf *angularis*') and *B. angulata* and *B. brevirostris* (as 'snouty') respectively. That study did not include *C. albobrunnea* due to a lack of suitable specimens for DNA extraction and sequencing. However, since then a cytochrome c oxidase subunit I sequence for this species has been produced by Lara Shepherd (Museum of New Zealand Te Papa Tongarewa) and this, along with sequence data from Sirvid *et al.* (in press), was incorporated into a new Maximum Likelihood analysis of cytochrome c oxidase subunit I data for thomisid species present in New Zealand. The resulting tree is depicted in Fig. 7.

The fossil record for Thomisidae does not currently include any representatives from the Australasian subregion and the oldest fossils are 50-60 million years old (Penney & Selden 2011).

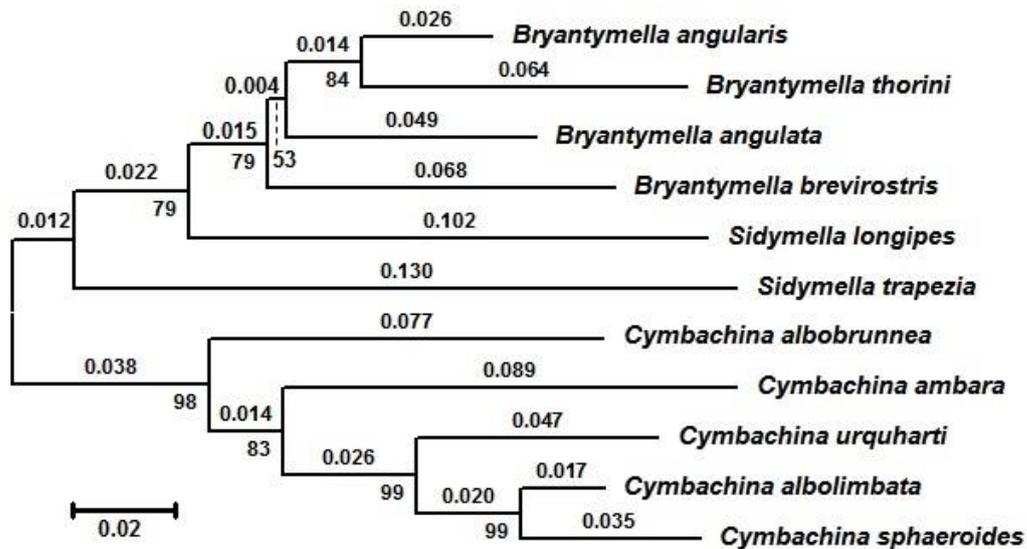


Fig. 7. Maximum Likelihood tree for the New Zealand Thomisidae based on cytochrome c oxidase subunit I data. Branch length values are given above branches, bootstrap values below. *Sidymella* species are Australian species established in New Zealand while other taxa are considered endemic.

Table 2. (following page). Molecular specimen data from Sirvid *et. al.* (in press) with updated names based on this revision. The bold italic GenBank number is the sole ITS1-ITS2 sequence from that study. The sequence for *Cymbachina albobrunnea* is new. Collection repository abbreviations are defined in the Methods and Conventions section. Specimen registration numbers are provided where available. Abbreviations for gene targets are: COI = cytochrome c oxidase subunit 1, 28S = 28S ribosomal RNA, H3 = Histone H3, ND1 = NADH dehydrogenase subunit 1, 18S ribosomal DNA (18S), ITS = internal transcribed spacer units 1 and 2.

Specimen Code	Genus	Species	GenBank Accession Number					Collection & Reg. Number	
			COI	28S	H3	ND1	18S/ITS		
SeqCymalb	Cymbachina	<i>albobrunnea</i>	KF975454	-	-	-	-	MONZ AS.004027	
7.3		<i>ambara</i>	KF669339	KF669294	-	-	-	MONZ AS.003606	
7.4		<i>ambara</i>	KF669340	KF669295	KF669314	-	-	MONZ AS.003607	
8.4		<i>ambara</i>	-	KF669296	-	-	-	MONZ AS.004055	
8.8s		<i>ambara</i>	-	KF669297	-	-	-	MONZ AS.003614	
19		<i>ambara</i>	KF669338	-	-	-	-	MONZ AS.003590	
4.3		<i>albolimbata</i>	KF669330	KF669292	-	-	-	NZAC -	
4.4		<i>albolimbata</i>	KF669331	-	-	-	-	NZAC -	
8.7		<i>albolimbata</i>	KF669332	-	-	-	-	MONZ AS.003615	
18		<i>albolimbata</i>	KF669333	KF669293	-	KF669316	-	MONZ AS.003616	
6.02		<i>urquharti</i>	KF669336	-	-	-	-	MONZ AS.003617	
6.1aa		<i>urquharti</i>	KF669337	KF669291	-	-	-	NZAC -	
115b		<i>urquharti</i>	-	KF669290	-	-	KF669329	MONZ AS.003618	
20		<i>sphaeroides</i>	KF669334	KF669288	KF669315	KF669317	KF669303	MONZ AS.003603	
27		<i>sphaeroides</i>	KF669335	KF669289	-	-	-	MONZ AS.003602	
115a		<i>sphaeroides</i>	-	KF669286	-	-	-	MONZ AS.003619	
115e		<i>sphaeroides</i>	-	KF669287	-	-	-	MONZ AS.003619	
2		Brynatymella	<i>angularis</i>	KF669363	-	-	-	-	MONZ AS.003591
3			<i>angularis</i>	KF669359	KF669268	-	-	-	MONZ AS.003592
4			<i>angularis</i>	KF669362	-	KF669305	-	-	MONZ AS.003587
6.11a	<i>angularis</i>		KF669348	-	-	-	-	MONZ AS.003621	
7.1	<i>angularis</i>		KF669354	KF669270	-	-	-	MONZ AS.001686	
7.2	<i>angularis</i>		KF669355	-	-	-	-	MONZ AS.001650	
8.2	<i>angularis</i>		KF669349	KF669272	-	-	-	MONZ AS.003622	
8.11	<i>angularis</i>		KF669360	KF669271	-	-	-	MONZ AS.003620	
9.2	<i>angularis</i>		KF669357	-	-	-	-	NZAC -	
9.13	<i>angularis</i>		KF669358	KF669273	-	KF669321	-	NZAC -	
9.14	<i>angularis</i>		KF669350	KF669274	KF669306	-	KF669300	MONZ AS.003589	
9.22	<i>angularis</i>		KF669356	-	-	-	-	MONZ AS.001651	
10	<i>angularis</i>		KF669361	-	-	-	-	MONZ AS.001447	
BMQ1	<i>angularis</i>		KF669351	KF669275	-	-	-	MONZ AS.003596	
BMQ2	<i>angularis</i>		KF669346	KF669276	-	-	-	MONZ AS.003597	
BMQ3	<i>angularis</i>		-	KF669277	-	-	-	MONZ AS.003598	
BMQ4	<i>angularis</i>		KF669347	KF669278	-	-	-	MONZ AS.003599	
BMQ5	<i>angularis</i>		KF669353	KF669279	-	-	-	MONZ AS.003600	
BMQ6	<i>angularis</i>		KF669345	KF669280	-	-	-	MONZ AS.003601	
K13	<i>angularis</i>		KF669352	KF669269	-	-	-	MONZ AS.003187	
5KOF	<i>thorini</i>		KF669364	KF669281	KF669307	KF669323	KF669302	MONZ AS.003611	
7	<i>thorini</i>		-	KF669282	-	KF669324	-	MONZ AS.003595	
9.24	<i>thorini</i>		KF669365	KF669283	-	KF669325	-	MONZ AS.003595	
6.03	<i>angulata</i>		KF669366	KF669256	-	-	-	MONZ AS.003612	
14	<i>angulata</i>		KF669369	KF669257	-	KF669320	-	MONZ AS.003613	
15	<i>angulata</i>		KF669370	KF669258	-	-	-	MONZ AS.003588	
115c	<i>angulata</i>		KF669367	KF669259	-	-	-	MONZ AS.003610	
115d	<i>angulata</i>		KF669368	KF669260	-	-	-	MONZ AS.003610	
12403	<i>angulata</i>		-	-	KF669308	KF669319	KF669301	MONZ AS.003608	
6.6	<i>brevirostris</i>		KF669372	KF669261	KF669309	KF669322	-	NZAC -	
6.9	<i>brevirostris</i>		KF669371	-	-	-	-	MONZ AS.003605	
9.3	Sidymella		<i>longipes</i>	KF669373	KF669284	KF669311	KF669326	KF669304	MONZ AS.003594
Pos9676P3			<i>longipes</i>	KF669375	-	-	-	-	MONZ AS.003609
Pos9677P3			<i>longipes</i>	KF669374	-	-	-	-	MONZ AS.003609
11593		<i>longipes</i>	KF669377	-	-	-	-	AM KS115193	
22899		<i>longipes</i>	KF669285	KF669285	-	-	-	QM 22899	
1		<i>trapezia</i>	KF669381	KF669266	-	-	-	MONZ AS.003593	
6.01		<i>trapezia</i>	-	KF669265	-	-	-	NZAC -	
6.2		<i>trapezia</i>	KF669382	KF669263	KF669310	KF669327	-	NZAC -	
9.1		<i>trapezia</i>	KF669384	KF669264	-	-	-	NZAC -	
9.6		<i>trapezia</i>	KF669383	KF669267	+	-	-	NZAC -	

Species Excluded From the New Zealand Fauna

Tharpyna munda Koch, 1874: This species was erroneously recorded as being in NZ by Simon (1895) although the original description makes no claim to this effect. This species is not mentioned in any New Zealand publication since Koch's original description, including the faunal lists of Hutton (1904), Urquhart (1892) and Parrott (1946). The error was perpetuated in subsequent araneological catalogues (e.g. Roewer, 1955) until it was corrected by Paquin *et al.* (2008).

Philodromus rubrofrontus Urquhart, 1891: The genus *Philodromus* was formerly placed in the Thomisidae and is now in the related family Philodromidae. The majority of Urquhart's described thomisines were originally placed in *Philodromus* (Urquhart 1885, 1887, 1891) and these were all subsequently transferred to the thomisid genus *Diaea* by Bryant (1933) in her review of Urquhart type specimens. Type material for *P. rubrofrontus* was not seen by Bryant (1933) and has not subsequently been found (Nicholls *et al.* 2000) so the taxonomic status of this species was not changed as *Philodromus* is still a valid genus (Platnick 2013). Paquin *et al.* (2008) observed that while the description of *P. rubrofrontus* is insufficient to properly diagnose this species, characters such as the legs, cephalothorax and colour indicate it is a thomisid rather than a philodromid. As well as lacking a clear diagnosis, Urquhart's (1891) description also lacks figures. Accordingly, this species was treated as a *nomen dubium* by Paquin *et al.* (2008). As this was the only member of Philodromidae recorded for New Zealand, the family was also removed from the New Zealand fauna.

BIOLOGY

Note that additional species-specific biological information will also be given in the Biology sections of some species descriptions.

Habitat Preferences and Dispersal:

Endemic New Zealand stephanopines (*Bryantymella* species) are recorded from leaf litter, under logs and stones and can also be beaten from foliage, including dead fern fronds. While common in native forest, the majority of species can also be found in gardens and other modified habitat. Of the established species of exotic stephanopines, *Sidymella longipes* (L. Koch, 1874) is known only from modified habitat, while *S. trapezia* (L. Koch, 1874) has been recorded from mixed coastal dune systems (A. Littek, Pers. comm.) and has also been collected from houses.

In the thomisines, one species, *Cymbachina albobrunnea* is known to frequent leaf-litter and lichen (Forster & Forster 1999). Other species are more commonly found on flowers and foliage (Forster & Forster 1999). Like New Zealand Stephanopines, they are known from both native and modified ecosystems (Pers. obs).

Thomisids are known to disperse by ballooning (Decae 1987, Greenstone *et al.* 1987, Bonte *et al.* 2003). In this behaviour, a spiderling or sufficiently small adult spider plays out a length of silk to be borne aloft on thermal updrafts and carried along on air currents. This may possibly be augmented by electrostatic forces (Goreham 2013). Ballooning has been seen in New Zealand thomisines (C.J. Vink, Pers. comm.), but not stephanopines. However, Sirvid *et al.* (in press) suggest that the presence of recently arrived species such as *Sidymella longipes* on uninhabited offshore islands such as Tuhua (Mayor) Island and the presence of similar haplotypes of the endemic *Bryantymella angularis* at disjunct locations may be evidence for ballooning in this subfamily. Sympatry occurs in all species, although some species have restricted ranges.

Colour:

The majority of New Zealand species exhibit a variety of colour forms. Collections of multiple individuals of *Cymbachina albolimbata* from the same *Pimelia arenaria* shrub can yield a range of specimens of different colours including shades of red, yellow and green (Pers. obs.). Multiple colour morphs at the same collecting site have also been observed for *Sidymella angularis* (B. McQuillan, Pers. comm.) with conspecificity confirmed by genetic data (Sirvid *et al.*, in press). While some overseas species such as *Thomisus spectabilis* have the ability to change colour (Heiling *et al.* 2003), based on observations in captivity, it seems unlikely that New Zealand species are able to do so (Pers. obs.).

In the stephanopines, colours in life are often shades of grey, yellow or brown. In conjunction with their rather rugose appearance, this seems to be a form of crypsis as these spiders usually blend in well with their surroundings (Pers. obs.). Forster and Forster (1999) note a similar effect with respect to the colouring of *Cymbachina albobrunnea* and its preference for lichen. Other thomisines are more brightly coloured (see Forster & Forster 1999: Figs 7.5-7.7). Sometimes this may aid in blending in with the flower substrate (Forster & Forster 1999: Fig. 7.5b), however, Heiling *et al.* (2003) observed a dual role for crab spider colouration. They found that while a white-coloured *Thomisus spectabilis* may appear well concealed against a white daisy, under ultraviolet light the spider's colour pattern enhances the attractiveness of the flower to bees, thus increasing the odds of encountering prey. It is not known if this occurs in New Zealand thomisines but spiders kept in captivity did not change colour (Per. obs.).

Ultimately, the role of colour in New Zealand's thomisids is not fully understood. It could represent nothing more than variation within a population as Vink (2002) observed in the New Zealand Lycosidae (wolf spiders) and Court and Forster (1988) observed in the Araneidae (orbweb spiders). It may be a by-product of dietary influence, or it could be an example of polychromatic colouration as a population level defence mechanism where distinct colour morphs may be subject to different rates of predation.

Predation and Diet:

Thomisids are widely regarded as free-living ambush spiders (Forster & Forster, 1999). The capture of insect prey is as simple as flexing the first two pairs of previously outstretched legs and drawing prey in towards the chelicerae where it is bitten and killed (Jackson *et al.*, 1995). As noted earlier, the first two pairs of legs bear long spines and these help prevent the prey's escape. Based on observations in captivity, most species appear content to wait for prey to move within reach before attacking. However, *Sidymella trapezia* appears to be a more active and aggressive species and has been observed moving quickly towards prey before striking (Pers. obs.).



Fig. 8. *Cymbachina sphaeroides* and silk. Image courtesy of Simon Pollard.

As ambush predators, thomisids generally do not construct a prey capture web. However, Jackson *et al.* (1995) reported occasional use of a series of criss-crossed non-sticky threads for prey capture by an unidentified New Zealand species of *Diaea* captured on *Muehlenbeckia complexa*. This appears to be *Cymbachina sphaeroides* based on specimens collected from *M. complexa* at a nearby locality and an additional photograph (Fig. 8) kindly provided by Simon Pollard (University of Canterbury), a co-author of the

Jackson *et al.* (1995) study. Jackson *et al.* (1995) also cited several historical reports that suggest a number of other Australasian thomisids may possess similar capabilities. It is not known how widespread this behaviour is in thomisids in general or in New Zealand species in particular.

In captivity thomisids appear to be generalist predators of insects with beetles, flies, moths and Hemiptera all proving to be palatable options provided they were of sufficiently small size to subdue (Pers. obs.). In nature, thomisines (with the exception of *Cymbachina albobrunnea*) are likely to feed primarily on flower-visiting insects.

Like other spiders, thomisids are carnivorous but nectivory is also known. Pollard *et al.* (1995) report that males of the North American thomisid *Misumenoides formosipes* (Walckenaer, 1837) have a much greater surface area to volume ratio than their larger female counterparts and use nectar in preference to water because it is an energy source in addition to countering dehydration. Taylor and Pfannenstiel (2008) found that other spiders make use of nectar and that nectivory is also quite common among female thomisids. This behaviour has not been observed in New Zealand species.

Reproductive Biology:

The etymology of the family name Thomisidae originates from the Latin word, 'thomix', meaning to bind with cord. Binding behaviour has been documented in the the genus *Xysticus* where the male ties the female down with silk before mating (Bristowe 1958). It also appears to be part of the mating behaviour of *Cymbachina sphaeroides* as described by Forster and Forster (1999). As they note, the female could almost certainly break the silk if she tried. While this may appear to be ineffectual at restraining her, it may nonetheless be an integral part of the courtship ritual, without which mating could not take place. Note that Forster and Forster's (1999) account refers to *D. ambara* but the accompanying figure (Forster & Forster 1999: Fig. 7.8) is clearly not this species. See the Biology section under the description of *C. sphaeroides* for further details as to why this is the correct identity of the species involved. The mating behaviour of other species is unknown.

Forster and Forster (1999) documented courtship and mating in an unnamed species of *Sidymella*. The male approaches the female and taps her with his front pair of legs. This appears to placate the female and the male then climbs onto her abdomen while drumming with his palps. After a momentary pause, he climbs underneath and facing forward relative to the female, inserts one palp into the epigyne. He then returns to the dorsal side of the female's abdomen and repeats the process with the other palp. This process may be repeated four or five times, taking as long as half an hour and ends abruptly with the male's departure.

New Zealand thomisids are only known to produce a single egg-sac at a time. Maternal guarding of egg-sacs has been reported in both New Zealand (Forster & Forster 1999) and overseas thomisids (Eberhard, 1987). Forster and Forster (1999: Fig. 7.10) depict *Cymbachina albolimbata* with a flattened egg-sac inside leaves that are curled and held in place with silk. In captivity *Bryantymella angularis* and *B. thorini* sp. nov., females also produce and guard single flattened egg-sacs, but these are attached to the undersides of dead leaves (Forster & Forster 1999). Male thomisids have no known parental role beyond mating.

Thomisid Pathogens, Predators and Natural Defences:

As part of a wider assemblage of spiders, thomisids can have an important role in the control of agricultural pests (Riechert & Lockley, 1984). They are also important as food for many other organisms. Harris (1994) lists *Cymbachina ambara* (as *Diaea ambara*) as a host species for the endemic New Zealand sphecid wasp *Pison morosum* Smith, 1856 although there are no New Zealand thomisid records for the Pompilidae, a family of wasps that specialise in hunting spiders (Harris, 1987). A dietary analysis of mouse stomachs from the Orongorongo Valley's hard beech forests by Alley *et al.* (2001) found *Bryantymella angularis* (as *Sidymella angularis*) was the third most abundant spider species on the basis of trap data but ranked second with regard frequency of occurrence in mouse stomachs. Bishop (1990) observed entomophagous fungi fatally affecting ballooning spiders, including

Thomisidae. Forster and Forster (1999: Fig. 7b) also depict a specimen of *Cymbachina* parasitized by a mite.

The role of colour and form in crypsis has already been discussed. *Bryantymella angularis*, *B. angulata* and *B. thorini* combine these with pulling the legs in close to the body and playing dead, sometimes for several minutes, when collected by beating or shaking vegetation. The overall effect gives the spider a resemblance to a small piece of detritus (Pers. obs) and may deceive some predators.

METHODS AND CONVENTIONS:

Morphological Abbreviations and Acronyms:

Abbreviations for morphological features are as follows:

Appendage segments:

F: Femur

Mt: Metatarsus

P: Patella

Ta: Tarsus

Ti: Tibia

Epigynal Characters

S: Spermatheca

FD: Fertilization duct

CD: Copulatory duct

Eyes:

AME: Anterior median eyes

PME: Posterior median eyes

ALE: Anterior lateral eyes

PLE: Posterior lateral eyes

Leg Surfaces:

p: Prolateral

d Dorsal

r: Retrolateral

v: Ventral

Male Palp Characters

E: Embolus

RTA: Retrolateral tibial apophysis

AEB: Apical embolic bend

VTA: Ventral tibial apophysis

RCP = retrolateral cymbial process

Collection Repositories:

Acronyms for collection repositories are as follows:

AMNZ: Auckland War Memorial Museum, Auckland, NZ

AMS: Australian Museum, Sydney, Australia

BMNH: British Museum of Natural History, London, UK

CMNZ: Canterbury Museum, Christchurch, NZ

LUNZ: Lincoln University Entomology Collection, Christchurch, NZ

MONZ: Museum of New Zealand Te Papa Tongarewa, Wellington, NZ

NZAC: New Zealand Arthropod Collection, Auckland, NZ

OMNZ, Otago Museum, Dunedin, NZ

QM: Queensland Museum, Brisbane, Australia

ZMB: Museum für Naturkunde, Berlin, Germany

Collecting and Preservation:

Thomisids can be collected by various methods. In this study, thomisines were most commonly collected by beating or sweeping vegetation, particularly flowering shrubs. Stephanopines were also collected by beating and sweeping vegetation and some species appeared to be particularly common on fresh or dead fern fronds. They were also found in litter samples and sometimes under logs and stones. Museum specimens show stephanopines have been captured in Malaise, emergence and pitfall traps. Males and juveniles of both subfamilies are known to stray indoors, particularly in spring and late summer, while thomisines are sometimes inadvertently brought in to the home on cut flowers (Pers. obs.).

Specimens captured for this study were stored in vials of 70% ethanol. Each vial included a data label listing collection details including locality, collector and date of collection. Specimens destined for molecular study were stored frozen (ideally at -20°C or lower). Using a combination of freezing and 70% ethanol means specimens

still retain enough flexibility for morphological study while DNA degradation is inhibited (Vink *et al.* 2005).

Measurements:

A full series of standard measurements were made using an eyepiece micrometer on a Zeiss Stemmi ® binocular microscope and are given in millimetres. Carapace, cephalic area, sternum and labium dimensions are given as lengths and widths separated by a solidus (/). Leg segments and eye measurements are also separated in a similar manner. Eye measurements do not include tubercles. Scale bars are also given on photographs of genitalia but are not provided for habitus images as a total length figure is available from the species descriptions.

Colour:

Colours are recorded for ethanol-preserved specimens. The value of colour as a diagnostic character is variable. Some species are recognizable by their distinct colour patterns, while other exhibit a large amount of variation and are not. Clear indications are given in where colour pattern has utility as a diagnostic character.

Spine Counts:

Only leg surfaces bearing spines are recorded. Each surface is scored by dividing it into four equal sections and counting the spines in each one. The counts are recorded for each leg segment with leg surface first followed by the spine counts running proximally to distally. Thus, Mt p0.0.0.2 means there are two spines in the distal section on the prolateral surface of the metatarsus. Surfaces on the same leg segment are separated by a solidus (/) while different segments on the same leg are separated by a semi-colon (;). Note that spine counts are indicative rather than universal for each species. For example, individuals have been observed with slightly different spine counts between the same pair of legs and common variations are given. Spines may also be broken off, although the point of attachment to the leg is usually evident as a dark spot.

Photography:

Each specimen was placed in a dish of ethanol and a series of images at different focal depths was taken with a Canon® G2 digital camera mounted on the

microscope used for measurements. Combine–ZP focus stacking software was used to merge series of photographs to produce images with an extended depth of field. To reduce the risk of movement during photography, specimens were typically held in place by KY jelly. However, male palps were usually photographed in quartz sand because the scattering of light made the RTA stand out more prominently. Epigynes were excised using a needle and cleared by soaking in 20% KOH for around 24 hours. Photoshop® CS6 was used for digital image processing such as contrast adjustment and image resizing.

Molecular Biology:

Sirvid *et al.* (in press) conducted a molecular study New Zealand thomisid phylogeny. As noted previously, that paper used tag names for three undescribed species, while most described species were included under names that are revised as a consequence of taxonomic decisions made here. GenBank accession numbers for sequences from that paper are given for each species under their new names (Table 2). One species not available for study in Sirvid *et al.* (in press) was *Cymbachina albobrunnea*, but a COI sequence for this species has since been produced and a GenBank accession number is provided. Methods for DNA sampling, PCR conditions and phylogenetic analyses are given in Sirvid *et al.* (in press).

Keys:

These are the first keys ever made for the New Zealand Thomisidae and have been constructed with non-specialists in mind. Characters were chosen to separate taxa emphasising distinctiveness and practicality in separating species over phylogenetic significance. Spider keys are usually designed for use with adult specimens, but the thomisine key works with later instar juveniles, while the stephanopine key can be used to separate *Bryantymella* juveniles.

Taxonomy and Systematics:

Under the rules of the International Commission for Zoological Nomenclature, taxonomic decisions made in a thesis have no formal standing (ICZN 1999: chapter 3, article 8). The decisions made in this chapter will be validated in a peer-reviewed

publication. Until then, this chapter should not be made publicly available in order to prevent publication of these new and updated names by other parties.

Synonymies are given for previously described species and cover the introduction of the name as well as changes to names, but not unchanged combinations repeated in other publications such as catalogues.

Material Examined:

Locality information (including latitude and longitude), collector, collection date, number of specimens, collection repository, registration number and ecological notes such as habitat where specimens were captured are given. Note that some entries may lack one or more of these fields. For example, NZAC specimens do not have registration numbers and latitude and longitude is not always determinable, particularly where a place name may be applicable to multiple localities. Examined type material is listed first, while other records are given in order of increasing latitude and end with records lacking coordinates. The level of precision of coordinates is dependent on the source data it is derived from or how the precision with which it was originally recorded. Material examined data is contained in Appendix A and is visualised in Maps 1-12.

Maps:

Maps were created from decimal latitudes and longitudes of collection localities using R software (R Development Core Team 2008).

Species concept:

A phylogenetic species concept where species are defined as the smallest aggregation of populations diagnosable by a unique combination of character states has been used in this study (Wheeler & Platnick 2000).

BIOSYSTEMATICS

Family Thomisidae

Small to medium sized spiders (3.5-11 mm in New Zealand species), Legs laterigrade; leg length order 1243, 2 claws with a claw tuft; 8 eyes in two recurved rows, mounted on tubercles in Thomisinae; Entelygne; RTA present, VTA present in Thomisinae; Ecribillate.

Key to New Zealand thomisid subfamilies

Cheliceral teeth present and cephalic region around half carapace width

Stephanopinae

Cheliceral teeth absent and cephalic region more than half carapace width

Thomisinae

Subfamily Stephanopinae

Diagnosis: Stout setae on legs and prosoma, cheliceral teeth, truncate labium and maxillae (Ono 1988). New Zealand species have subequal PME and PLE, cephalic area about half of carapace width, socketed spines on femur I, 2 pairs of spermathecae and a trapezoidal abdomen in dorsal view.

Remarks: Ono (1988) also included PME large and PME larger than PLE as diagnostic characters but for New Zealand stephanopines and PME and PLE are more accurately described as being subequal based on measurements recorded below. Benjamin (2011) also points out that the Stephanopinae as currently constituted are paraphyletic and that none of the diagnostic characters suggested by Ono (1988) are synapomorphic for this clade. However, the diagnosis given above is nonetheless sufficient to separate New Zealand stephanopines from thomisines.

Key to New Zealand Stephanopinae

- 1) Tubercle with disto-ventrally directed spine on femur I (Figs 11, 12) **2**
Femur I not as above (Figs 9, 10, 13, 14) **3**
- 2) Small protuberance between ALE and AME (Fig. 12) *Bryantymella brevirostris*
No such protuberance (Fig. 11) *Bryantymella angulata*
- 3) Two small longitudinal ridges visible on highest point of carapace (Figs 9, 10) **4**
Carapace not as above (Figs 9, 10, 13, 14) **5**
- 4) Long, thick, erect setae on postero-dorsal and posterior surface of abdomen and 2
or 3 prolateral spines on femur I (Fig. 10) *Bryantymella thorini*
Abdominal setae and femoral spines not as above (Fig. 9) *Bryantymella angularis*
- 5) RTA of male palp with bifid termination (Fig. 36), epigyne of female in excavation
(Fig. 25) *Sidymella trapezia*
RTA and epigyne not as above (Figs 24, 35) *Sidymella longipes*

***Bryantymella* Gen. nov.**

Type species: *Sparassus angularis* Urquhart, 1885

Differential diagnosis: Abdominal shape trapezoidal rather than rounded, RTA not bifid and eyes not on a prominent eminence separate *Bryantymella* from the type species for *Stephanopsis*, *St. altifrons* Pickard-Cambridge, 1869. The presence of an AEB, RCP immediately above (or nearly so) and roughly parallel to RTA on male palp and posterior eyes further forward on cephalic region separate this genus from the type species for *Sidymella*, *Si. lucida* (Keyserling, 1880). Australian species present in New Zealand currently placed in *Sidymella* have an RCP like *Bryantymella* but lack an AEB. See *Remarks* below.

Size: Small to medium sized spiders (5-11 mm long)

Carapace: Fig. 2A. Longer than wide, thoracic area highest and marked with two longitudinal ridges at apex and several fine grooves radiating from this point (n.b. these characters less pronounced in males and *B. angulata*); cephalic area approximately half thoracic width and length is approximately one quarter the length of the cephalothorax; eye region raised but not on eminence (N.B. this character more pronounced in females).

Eyes: Figs 2A-2B, 9-14. ALE>PLE>PME>AME, posterior eye row in line with coxa-trochanter joint of leg I.

Chelicerae: Fig. 2D. Two teeth on each margin, fangs short, curved and transverse.

Labium: Fig. 2D. Slightly longer than wide.

Maxillae: Fig. 2D. Narrower proximally than distally.

Legs: Fig. 2A, 2C. Length order 1243; prolateral surface of femur I armed with socketed spines; claw tufts present all legs.

Abdomen: Figs 2A, 9-14. In dorsal view trapezoidal, narrowest anteriorly with two rear lobes separated by concave posterior margin; 6 muscle spots and a crescent shaped row of indented spots near the posterior dorsal margin; rows of indented spots forming groove-like rows on lateral surfaces; postero-lateral surface bulbous and visible between rear lobes when viewed from above; hairs clavate or spatulate.

Spinnerets: Fig. 2C. Short, conical, colulus present.

Sternum: Fig. 2D. Scutiform, longer than wide, widest between coxae II and III; sparse coating of setae, mostly directed antero-medially but a denser patch of setae present at posterior end of sternum and denser patches sometimes present intercoxally.

Epigyne and internal genitalia: Fig. 5A, 20-25. Epigynal area oval or nearly circular atrium, bordered by raised hood and fringed with thick setae; two copulatory

openings, one pair of spermathecae visible in ventral view; In dorsal view, copulatory ducts translucent; Two pairs of spermathecae, one pair heavily sclerotised and irregularly or sigmoid-shaped, the other globular and less sclerotised or translucent.

Male palp: Figs 4, 31-36. Horizontal portion of RTA terminates with longer, pointed posterior margin; small retrolateral projection of the cymbial margin (RCP) immediately above and roughly parallel to RTA; embolus originates approximately halfway along and follows prolateral margin of bulb before turning sharply at the anterior apex (AEB) and coiling inwards, terminating behind tegular ridge and oriented towards prolateral margin; tegular disk irregular ovoid; patella and tibia subequal.

Etymology: Elizabeth Bryant (1933) noted that New Zealand species had characters that were not found in *Sidymella lucida*, the type species for *Sidyma* (now *Sidymella*). *Bryantymella* is named in her honour.

Remarks: New Zealand stephanopines have previously been placed in *Sparassus* Walckanaer, 1805, *Stephanopis* Pickard-Cambridge, 1869 and *Sidymella* Strand, 1942. *Sparassus* is now considered a junior synonym of *Micrommata* Latreille, 1804 (Jäger, 1999) and is in Sparassidae, not Thomisidae. Sparassids are very large, flattened-looking spiders and the only species established in New Zealand, *Delena cancerides* Walckanaer, 1837 (Sirvid *et al.* 2011), is a good example of the basic sparassid body form.

While the male palp of *St. altifrons* Pickard-Cambridge, 1869 has not been illustrated, figures of male palps for Australian species placed in *Stephanopis* by Koch (1874, 1876) and Keyserling (1890) vary greatly in form and this genus is probably polyphyletic. For example, Koch's (1874: pl. 38, fig. 2) illustration of the male palp of *Stephanopis lata* O. P.-Cambridge and his figure for the male palp of *Stephanopis cambridgei* Thorell, 1870 (Koch, 1876: pl. 65, fig. 3) differ to such a degree that they do not appear congeneric.

The two Australian *Sidymella* species in New Zealand have a projection on the retrolateral margin of the cymbium similar that of *Bryantymella*, but the embolus is

comparatively simple and short. Both characters appear to differentiate them from *Si. lucida*, and they may need to be transferred to another genus when the Australian stephanopines are fully revised. Genetic data indicates that these two species are not congeneric with *Bryantymella* (Sirvid *e al.* in press).

The endemic New Zealand stephanopines appear to be congeneric based on the form of the male palp and genetic data (Sirvid *et al.* in press). Future revisions of the Australian stephanopines may result in the transfer of several species to *Bryantymella*.

***Bryantymella angularis* (Urquhart, 1885) Comb. nov.**

Figs 4, 5A, 9, 20, 31

Map 1

Sparassus angularis Urquhart, 1885: 43, pl. 10, f. 7

Stephanopis angularis (Urquhart, 1885); Urquhart 1892: 227

Sidymanis angularis. (Urquhart, 1885); Bryant, 1933: 5

Sidymanella angularis (Urquhart, 1885); Roewer, 1955: 758

Type Data: Holotype ♀ of *Sparassus angularis* Urquhart, 1885, Tairua, Whangarei Harbour, T. Broun (CMNZ).

This specimen is in very good condition.

Paralectotype ♂ of *Sparassus angulata* Urquhart, 1885, same locality (CMNZ).
[Misidentified, see *Remarks* below and under *B. angulata*]

Differential Diagnosis: Separated from all other New Zealand *Bryantymella* by the presence of 5-6 prolateral femoral spines on femur I, larger size and genitalic form.

Colour: Fig. 9. Highly variable and of no diagnostic value. Greys and shades ranging from yellow to brown are common.

Cephalothorax: Fig. 9. Carapace clothed with fine setae; lateral eyes fringed with short spatulate setae; fringe of setae on anterior carapace margin; thoracic ridges more pronounced in female.

Abdomen: Fig. 9. Covered with small indented spots, sometimes pigmented; clothed with a mixture of posteriorly oriented clavate (thicker in female) and fine setae; medial strip of fine setae (sometimes unpigmented) running from spinnerets to pedicel and bordering epigastric furrow.

Epigyne and internal genitalia: Fig. 20. In rounded atrium fringed with thick setae; median strip separates two copulatory openings; one pair of spermathecae visible in ventral view. In dorsal view, copulatory ducts translucent, initially narrow and oriented medially and longitudinally before turning sharply outwards and broadening; two pairs of spermathecae, one pair heavily sclerotised and sigmoid-shaped, the other globular and translucent.

Male palp: Figs 4, 31. RTA strong with vertical portion at approximately 30° relative to retrolateral margin of tibia in ventral view; cymbial tip rounded; RCP strongly protuberant and rounded in ventral view.

Legs: Clothed with thick blunt-ended setae (coating denser in female) on femora and patellae and finer setae on metatarsi and tarsi; large macroseta situated between proximal spines on prolateral surface of femur I in some female specimens; 1-2 large erect macrosetae on dorsal surface of tibiae; distal trichobothria on dorsal surfaces of metatarsi and tarsi.

Female spination: Leg I F p2.2.1 (or 2).0; Ti p0.0.1.0/r0.0.1.0/v 2.2.2.2;

Mt p0.0.0.0.1/r0.1.0.0/v2.2.2.2;

Leg II F p0.1.0 (or1).0/d0.0.1.0; Ti p0.0.1.1/d0.0.1.0; v2.2.2.2;

Leg III Ti p0.0.1.0/v0.1.1.1; Mt p0.0.0.1/v0.0.0.0.2;

Leg IV Ti p0.0.1.0/v1.0.1.1; Mt p 0.0.0.2/r 0.0.0.2;

Male spination: Leg I F p 1.2.2.0; Ti p0.0.1.0/v 2.2.2.2; Mt p0.0.0.0.1/v2.2.2.2;

Leg II F /d0.1.0.0; Ti p0.0.1.0/d0.0.1.0; v2.2.2.2;

Leg III v0.1.1.1; Mt p0.0.0.2;

Leg IV Ti v0.0.0.2; Mt p 0.0.0.2

Dimensions (female): Otari-Wilton Bush, Wellington, ex pit trap, P.J. Sirvid, 23-24 Mar. 2007 (MONZ AS.003219).

Total length 8.6;

Carapace 4.9/3.30;

Cephalic Area 0.87/1.56;

Sternum 1.95/1.54;

Labium 0.66/0.59;

Leg I (F/P/Ti/Mt/Ta/Total) 5.14/2.43/4.59/3.12/1.47/16.74;

Leg II 2.57/2.02/3.67/2.66/1.28/12.20;

Leg III 2.75/1.47/2.20/1.47/1.19/9.08;

Leg IV 3.76/1.47/2.66/1.74/1.10/10.73;

Palp (F/P/Ti//Ta/Total) 1.10/0.71/0.63/0.94/3.39;

Eyes (AME/ALE/PME/PLE) 0.11/0.21/0.15/0.17;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.15
0.13/0.21/0.16/0.22

Dimensions (male): Locality data as for female.

Total length 5.23;

Carapace 2.66/2.20;

Cephalic Area 0.58/1.01;

Sternum 1.20/1.10;

Labium 0.51/0.44;

Leg I (F/P/Ti/Mt/Ta/Total) 3.58/1.47/3.67/2.48/1.06/12.25;

Leg II 3.30/1.06/2.61/2.11/0.92/10.00;

Leg III 1.56/0.73/1.47/1.01/0.64/5.41;

Leg IV 2.11/0.83/1.83/1.33/0.64/6.74;

Palp (F/P/Ti//Ta/Total) 0.94/0.55/0.39/0.79/2.68;

Eyes (AME/ALE/PME/PLE) 0.10/0.21/0.12/0.16;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.07/
0.05/0.11/0.12/0.12

Distribution: Known from throughout New Zealand including larger, well-forested offshore islands. See Appendix A and Map 1.

Biology: This species has been recorded in native forest and more modified ecosystems such as suburban gardens. It is the most commonly collected of all the New Zealand stephanopines (Pers. obs.). It has been collected in pitfall traps, litter sampling and by beating foliage and can often be found on hanging dead tree fern fronds. Eggs are laid in a flattened cocoon on the underside of dead leaves and guarded by the mother. Individuals from the same collecting site can vary markedly in colour pattern. Genetic data (Sirvid *et al.* in press) indicates these colour morphs are conspecific.

Remarks: This is the first time a description of the male of this species has been associated with the correct name. Urquhart's (1890) description of a male of *B. angulata* and Bryant's (1933) later redescription are clearly of *B. angularis*. See the *Remarks* section for *B. angulata* for further details. Dalmas (1917) incorrectly synonymised *B. angularis* under *B. angulata*, but females of both species were correctly recognized as distinct by Bryant.

***Bryantymella thorini* Sp. nov.**

Figs 2, 10, 21, 32

Map 2

Type Data: Holotype ♂, Waimea River, Nelson, NZ, C.J. Vink & S.J. Crampton, 28 Mar. 2009 (MONZ AS.003611).

Differential diagnosis: Most strongly resembles *B. angularis* but is easily distinguished by its smaller size, shorter legs relative to body size, arrangement of prolateral femoral spines on leg I and the presence of long, erect bristle-like macrosetae on the abdomen. This last character readily separates this species from all other New Zealand stephanopines.

Colour: Ranges from light tan to dark brown.

Cephalothorax: Figs 2A, 10. Carapace sparsely clothed with very short clavate setae; several long, thick forward-pointing setae in eye region.

Abdomen: Figs 2B, 2D, 10. Similar to *B. angularis*, but female abdomen broader laterally; sparsely distributed long bristle-like setae present and particularly prominent on postero-dorsal and posterior surfaces.

Epigyne and internal genitalia: Fig. 21. Superficially similar to *B. angularis* in ventral view; one pair of spermathecae visible in ventral view; internal genitalia broadly similar to *B. angularis* but both pairs of spermathecae noticeably sclerotised.

Male palp: Fig. 32. Vertical portion of RTA relatively straight in ventral view; cymbial tip acute and RCP only slightly protuberant in ventral view.

Legs: Clothed with thick blunt-ended setae (coating denser in female) on femora and patellae and finer setae on metatarsi and tarsi; large macroseta situated between proximal spines on prolateral surface of femur I in some female specimens; 1-2 large erect macrosetae on dorsal surface of tibiae; distal trichobothria on dorsal surfaces of metatarsi and tarsi.

Female spination: Leg I F p0.2 (or 3).2.0; Ti p0.1.1.0/r 0.0.1.0/v2.2.2.2; Mt p0.1.0.1/r0.0.1.0/v2.0.2.2;

Leg II Ti p0.0.1.0/Mt p0.1.0.1/v2.0.2.2;

Leg III Ti p.0.0.0.1/v0.1.1.1; Mt p0.0.0.2;

Leg IV Ti p0.0.1.0/v0.1.1.1; Mt p0.0.0.2;

Male spination: Leg I F p0.1 (or 2).1.0; Ti p 0.1.0.0/v2.2.2.2; Mt v0.2.2.2;

Leg II Ti v2.2.2.2; Mt 0.2.2.2

Dimensions (female): Raukawa Street, Stokes Valley, Wellington, NZ, B.M. Fitzgerald, 7 Dec. 2012 (MONZ AS.004046).

Total length 5.83

Carapace 2.77/2.44;

Cephalic area 1.26/0.71;

Sternum 1.29/1.17;

Labium 0.44/0.41;

Leg I (F/P/Ti/Mt/Ta/Total) 2.36/1.22/1.81/1.42/0.79/7.60;

Leg II 1.81/1.02/1.73/1.26/0.71/6.54;
Leg III 2.40/0.75/1.02/0.75/0.63/5.55;
Leg IV 67/1.34/0.87/0.71/5.39;
Palp (F/P/Ti/Ta/Total) 0.63/0.46/0.39/0.61/2.10;
Eyes (AME/ALE/PME/PLE) 0.06/0.17/0.10/0.11;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.13/
0.05/0.17/0.15/0.17

Dimensions (male): Holotype.

Total Length 3.86;
Carapace 2.05/ 1.65;
Cephalic area 0.51/0.79;
Sternum 0.87/0.85;
Labium 0.22/0.29;
Leg I (F/P/Ti/Mt/Ta/Total) 1.81/0.94/1.42/1.26/0.75/6.18;
Leg II 1.65/0.79/1.26/1.10/0.71/5.51;
Leg III 1.02/0.55/0.71/0.55/0.51/3.35;
Leg IV 1.26/0.59/0.94/0.71/0.59/4.09;
Palp (F/P/Ti/Ta/Total) 0.59/0.39/0.24/0.59/1.80;
Eyes (AME/ALE/PME/PLE) 0.07/0.15/0.12/0.11;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.07/
0.05/0.10/0.10/0.12

Distribution: Found from Northland down to Stewart Island. See Appendix A and Map 2.

Biology: Eggsacs have been recorded in late spring-early summer. They are typically attached to the undersides of dead leaves and are guarded by the mother.

Etymology: This species resembles a dwarf version of *B. angularis* and is named after one of literature's most famous dwarves, Thorin Oakenshield from J.R.R. Tolkien's "The Hobbit".

Remarks: The relatively short legs and the arrangement of femur I spines indicate Forster & Forster (1999: Figs 7.12-7.14) have depicted this species. They give an account of this species using its blunt ended posterior to right itself after falling on its back. While the holotype male and allotype female have been collected from separate localities, genetic data from specimens from these localities indicate these specimens are conspecific (Sirvid *et al.* in press).

***Bryantymella angulata* (Urquhart, 1885) Comb. nov.**

Figs 11, 22, 33

Map 3

Sparassus angulatus Urquhart, 1885: 42

Stephanopis angulatus (Urquhart, 1885); Urquhart, 1890c: 260, pl. 17, f. 8

Stephanopis angulatus (Urquhart, 1885); Urquhart, 1892: 2227

Stephanopis benhami Hogg, 1910a: 275, f. 2 **New Synonymy**

Sidyma angulata: (Urquhart, 1885); Dalmas, 1917: 391

Sidyma angulata: (Urquhart, 1885); Bryant, 1933b: 6, pl. 1, f. 3, pl. 4, f. 37

Sidyma angulata: (Urquhart, 1885); Roewer, 1955: 759

Type Data: Lectotype ♀, Whangarei Harbour, T. Broun (CMNZ).

This specimen is in pieces but is still clearly recognizable as a specimen of *B. angulata*.

Differential diagnosis: Both sexes easily separated from all other New Zealand stephanopines except *B. brevisrostris* by the presence of a large disto-ventrally oriented spine mounted on a very large tubercle on the prolateral surface of femur I. The lack of the anteriorly directed protuberance on the front of the carapace and abdomen longer than carapace distinguish this species from *B. brevisrostris*. The thoracic area is relatively low compared to other *Bryantymella* species and thoracic ridges at highest point of thorax absent, but position sometimes marked by semi-translucent patches. In females, epigyne with lateral hoods. In males, post-AEB portion of embolus much finer than in other New Zealand *Bryantymella* and RTA relatively short and lacking the strong right angle bend of other species.

Colour: Variable and of no diagnostic worth. Dark brown, red-brown and straw coloured forms common.

Cephalothorax: Fig. 11. Carapace flatter than in other *Bryantymella*; sparsely clothed with extremely short mostly clavate setae arising from small tubercles (more easily observed in darker specimens); thoracic ridges not evident, but in some specimens translucent patches in the same position can be seen.

Abdomen: Fig. 11. Venter with fine setae including a median ventral strip as in *B. angularis*; other surfaces clothed with short clavate setae; posterior portion of male abdomen protudes beyond rear lobes in dorsal view.

Epigyne and internal genitalia: Fig. 22. In atrium bordered by lateral hood, copulatory ducts visible in ventral view and curve laterally from a postero-median origin; two pairs of spermathecae also visible in ventral view; in dorsal view, one pair of spermathecae irregularly shaped, the other globular.

Male palp: Fig. 33. Portion of embolus beyond AEB often extremely fine; vertical portion of RTA at approximately 45° to retrolateral tibial margin in ventral view.

Legs: Dorsal surface of all legs clothed with short clavate setae with 1-2 larger erect seta on all tibiae; setae longer ventrally, sparse on femur but becoming finer and denser from patella onwards, disto-ventrally directed spine mounted on very large tubercle on femur I; distal trichobothria on dorsal surfaces of all metatarsi and tarsi.

Female spination: Leg I F p0.2.1.0/d0.0.1 (or 0).0; Ti p0.0.1.0/d0.0.1 (or 0).0/v2.2.2.2/Mt p0.1.0.1/r.0.1.0.1/v 2.2.2.2;

Leg II F d0.0.1 (or 0).0; Ti p0.0.1.0/v 2.2.2.2; Mt p0.1.0.0/r0.1.0.0/v2.0.2.2;

Leg III Mt p0.0.0.2;

Leg IV p Mt p0.0.0.2;

Male spination:

Leg I F p0.2.1.0/d0.0.1 (or 0).0/Ti v2.2.2.2; Mt p0.0.0.1/v2.2.2.2;

Leg II F d0.0.1 (or 0).0; Ti v2.2.2.2;Mt p0.1.0.0/v2.0.2.2;

Leg III Mt p0.0.02; Mt p0.0.02;

Leg IV Mt p 0.0.0.2/r0.0.0.1

Dimensions (female): Moutohora (Whale) I. NZ, B.M. Fitzgerald, 2-9 Feb. 1999 (MONZ AS.004048).

Total length 6.42;

Carapace 3.07/2.36;

Cephalic Area 0.67/1.18;

Sternum 1.32/1.22;

Labium 0.29/0.41;

Leg I (F/P/Ti/Mt/Ta/Total) 2.76/1.34/2.36/1.65/0.75/8.86;

Leg II 2.36/1.26/1.89/1.34/0.71/7.56;

Leg III 1.57/0.87/1.18/0.94/0.63/5.20;

Leg IV 2.28/0.83/1.50/1.18/0.59/6.38;

Palp (F/P/Ti//Ta/Total) 0.83/0.49/0.39/0.51/2.22;

Eyes (AME/ALE/PME/PLE) 0.07/0.18/0.10/0.12;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.12/
0.07/0.16/0.16/0.22

Dimensions (male): Locality data as for female.

Total length 3.54;

Carapace 1.85/1.65;

Cephalic Area 0.47/0.83;

Sternum 0.76/0.80;

Labium 0.17/0.29;

Leg I (F/P/Ti/Mt/Ta/Total) 1.73/0.91/1.65/1.26/0.55/6.10;

Leg II 1.50/0.71/1.14/0.91/0.47/4.72;

Leg III 0.83/0.47/1.06/0.51/0.39/3.27;

Leg IV 1.10/0.39/0.87/0.63/0.47/3.46;

Palp (F/P/Ti//Ta/Total) 0.63/0.27/0.24/0.46/1.61;

Eyes (AME/ALE/PME/PLE) 0.05/0.11/0.07/0.09;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.07/
0.07/0.12/0.13/0.17

Distribution: Known from throughout New Zealand including many offshore islands. See Appendix A and Map 3.

Biology: Genetic data indicates different colour morphs are conspecific (Sirvid *et al.* in press).

Remarks: The greater part of Hogg's (1910) description of *Stephanopis benhami* is applicable to other New Zealand *Bryantymella*. However, the combination of Hogg's description of setae and the figure of the epigyne indicate this species is conspecific with *B. angulata*. What remains of Hogg's primary type material is held at BMNH, but the type for this specimen is not among them (J. Beccaloni, BMNH, pers. comm.). Leg I and II dorsal femoral spines are very short and not always present, even for the same pair of legs on an individual.

This is the first time the male has been described. Urquhart (1885) described the female and recorded two localities (Whangarei Harbour and Te Karaka), thus indicating at least two specimens were seen by him. Nicholls *et al.* (2000) listed a male and a female as syntypes in the CMNZ collection although Urquhart (1885) himself did not explicitly mention having a male specimen. Examination of this male shows it is a specimen of *B. angularis* and Urquhart's (1890) later description of the male of *B. angulata* is also *B. angularis* based on characters such as the proportions of the palp (Urquhart 1890: pl. 8, Fig. 7) and femoral spination. It is probable that this was the specimen redescribed by Bryant (1933) as the male of *B. angulata*. Given two species are present in the syntypes vial, I hereby designate the female specimen as the lectotype of *B. angulata*. Benjamin's (2011: Fig. 65) depiction of the palp of *B. angulata* is also from a misidentified *B. angularis* male.

***Bryantymella brevirostris* Sp. nov.**

Figs 12, 23, 34

Map 4

Type Data: Holotype ♂, Three Kings Is, South West I., ex litter under puka forest, south west slope. A. Booth, 5 Apr. 2000 (LUNZ).

Differential diagnosis: Separated from all other New Zealand stephanopines by the presence of a small forward-pointing protuberance between the ALE and above the AME, and the abdomen is shorter than the carapace length.

Colour: Carapace red-brown with darker shading on lateral margins; abdomen yellow-brown, dorsally, dark laterally; sternum yellow-brown with a dark median stripe; lateral margins of sternum shaded in female and juveniles but shading reduced to dark intercoxal patches in male; legs brown with pale banding on legs III and IV.

Cepalothorax: Fig. 12. Longer than abdomen; clothed in fine setae arising from small tubercles (tubercles more evident in male); small median protuberance projecting between ALE and above AME; very low longitudinal thoracic ridges in female but not in male or juveniles.

Abdomen: Fig 12. Wider than long and shorter than carapace; erect setae, long, fine and arising from tubercles in male, shorter and clavate in female; ventral strip of setae between spinnerets and epigastric furrow broad with setae densest and darkest at each end of the strip.

Epigyne and internal genitalia: Fig. 23. Superficially similar to *B. angulata* but less heavily sclerotised.

Male palp: Fig. 34. Similar to *B. angulata*, but vertical portion of RTA gently sinuate in ventral view.

Legs: Clothed with setae of various lengths and thicknesses arising from small tubercles (tubercles more evident in male); thicker clavate setae on femora, finer on other segments; disto-ventrally directed spine mounted on a large tubercle on prolateral surface of femur I but spine much shorter than in *B. angulata*; two mounds bearing setae but not spines also present on this surface (more pronounced in male)

Female spination: Leg I F p.0.1.0.0/Ti v2.2.2.2/Mt v2.0.2.2;

Leg II F p.0.1.0.0/Ti v2.2.2.2/Mt v2.0.2.2;

Leg III Mt p0.0.0.2;

Leg IV Mt p0.0.0.2;

Male spination: Leg I F p0.1.0.0.0/Ti v2.2.2.0/Mt v0.2.2.2;

Leg II Ti v2.2.2.0/Mt v0.2.2.2;

Leg III Mt p0.0.0.1;

Leg IV Mt p0.0.0.1;

Dimensions (female): Kohuronaki, Te Paki, Northland, ex pit-trap, O. Ball, 14 Jul.-
14 Aug. 2006, (MONZ: AS.3605).

Total Length 8.03;

Carapace 4.80/4.02;

Cephalic area 1.25/1.73;

Sternum 1.90/1.76;

Labium 0.62/0.66;

Leg I (F/P/Ti/Mt/Ta/Total) 2.91/1.81/2.52/1.97/1.02/10.24;

Leg II 3.07/1.73/2.28/1.81/0.94/9.84;

Leg III 2.13/1.34/1.57/1.26/0.79/7.09;

Leg IV 2.44/1.26/1.65/1.57/0.71/7.64;

Palp (F/P/Ti/Ta/Total) 1.10/0.73/0.54/0.93/3.29;

Eyes (AME/ALE/PME/PLE) 0.07/0.20/0.09/0.17;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.33/0.12/0.27/0.24/0.22

Dimensions (male): Holotype.

Total Length 5.12;

Carapace 2.95/ 2.95;

Cephalic area 0.87/ 1.34;

Sternum 1.20/ 1.20;

Labium 0.34/ 0.32;

Leg I (F/P/Ti/Mt/Ta/Total) 1.81/1.02/1.50/1.02/0.71/6.06;

Leg II 1.73/0.94/1.18/0.94/0.63/5.43;

Leg III 1.30/0.63/0.87/0.63/0.51/3.94;

Leg IV 1.57/0.63/1.02/0.87/0.55/4.65;

Palp (F/P/Ti/Ta/Total) 0.68/0.41/0.29/0.51/1.90;

Eyes (AME/ALE/PME/PLE) 0.05/0.17/0.07/0.12;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE) 0.16/0.07/
0.16/0.17/0.17

Distribution: Recorded from Te Pahi (Northland) and the Three Kings Islands I. See Appendix A and Map 4.

Biology: This species appears to be most commonly collected from leaf litter, but has also been collected by beating low vegetation and by pitfall trapping. The median protuberance on the carapace is present in both sexes and in juveniles. The only two adults known have been collected in late summer.

Etymology: Named for the small median protuberance located between the anterior eye rows.

Remarks: The only adult specimens known are a male from Three Kings Is and a female from Te Pahi. Genetic data suggests specimens from these localities are conspecific (Sirvid *et al.*, in press). Juvenile specimens from both localities have abdominal setae like the female, suggesting long abdominal setae are an adult male character rather than an indication of a second species. A single juvenile specimen is known from Great Barrier Island (OM IV36775). Until adults or specimens of the Great Barrier population suitable for genetic sequencing become available, the taxonomic status of that population remains uncertain. Specimens are often encrusted in mud and debris, which can make viewing of surface details difficult. As only two adult specimens have been available for study, the diagnostic value of colour in this species remains unknown.

***Sidymella* Strand, 1942**

Sidyma Simon 1895

Sidymella Strand, 1942 [Replacement name as *Sidyma* preoccupied]

Type species: *Stephanopsis lucida* Keyserling, 1880

Differential diagnosis: Separated from *Bryantymella* by the form of the male embolus, which is much shorter and lacks an AEB and post-AEB portion. Spines on femur I are not mounted on tubercles.

Remarks: Despite some superficial resemblance to *Bryantymella*, the two Australian species present in New Zealand are quite distinct from *Bryantymella* on the basis of genitalic characters and genetic data. On the basis of genitalic form, these two species may prove to belong to separate genera and are probably not members of *Sidymella*. However, in the absence of a taxonomic revision of Australian stephanopines it seems prudent to retain their present classification. Given the level of uncertainty, a list of characters for the genus will not be given beyond the differential diagnosis and readers are referred to the species descriptions for more detailed information

***Sidymella longipes* (L. Koch, 1874)**

Figs 13, 24, 35

Map 5

Stephanopis longipes. L. Koch, 1874: 518, pl. 39, fig. 4

Sidyma longipes (L. Koch, 1874); Dalmás, 1917: 392

Sidymella longipes (L. Koch, 1874); Roewer, 1955: 759

Type Data: Holotype ♀, Rockhampton, Australia (Museum Godeffroy (Hamburg) Nr.9907). Not seen.

Differential diagnosis: Separated from *S. trapezia* (L. Koch, 1874) by the presence of a single small prolateral femoral spine on leg I in both sexes and long, overlapping spines on tibiae and metatarsae of male legs I and II. The median stripe on the sternum runs from the anterior margin rather than the posterior margin. The embolus is more curved and gradually tapering, while the RTA terminates with a longer posterior margin. The epigyne is not in an atrium.

Colour: Carapace yellow to yellow-brown with weak brown shading on lateral margins and brown median longitudinal band along length; dorsum of abdomen mottled brown with several dark spots on lateral margins; posterior and flanks cream

with a few black patches on lateral surfaces; venter cream between spinnerets and epigastric furrow in female with a yellow median stripe in males; spinnerets and area between epigastric furrow and pedicel yellow; sternum yellow with broad but weak median stripe running from anterior margin and terminating in line with coxa III; legs yellow in female; in male leg I brown, leg II femur and patella yellow with tibia to tarsus dark yellow and legs III and IV yellow; black spotting on all legs in both sexes. Note that intensity of markings is greatly reduced in some individuals.

Cephalothorax: Fig 13. Very small anteriorly-directed clavate hairs mounted on tiny tubercles, densest along median stripe along carapace, very sparsely scattered elsewhere; setae in eye region short and fine; sternal setae fine, larger and denser antero-laterally, shorter and more sparsely distributed medially.

Abdomen: Fig 13. Long, slender and relatively smooth; posterior lateral lobes more sharply pointed than other New Zealand stephanopines; posterior dorsal margin a smooth concave arc; sparsely clothed with very short posteriorly directed clavate hairs mounted on small tubercles on all surfaces except venter; venter with fine setae, densest along median running from spinnerets to pedicel.

Epigyne and internal genitalia: Fig 24. At surface, not in atrium; paired copulatory ducts and two pairs of spermathecae visible in ventral view; in dorsal view, one pair of spermathecae C-shaped and darkly sclerotised, the other small, globular and more lightly sclerotised.

Male palp: Fig 35. RTA with longer posterior margin in ventral view; visible portion of embolus gradually tapering and more curved than in *S. trapezia*; RCP projects ventrally in lateral view.

Legs: Clothed with very short setae on femora; longer, finer setae on patellae and tibiae (more evident in male).

Female spination: Leg I F p0.1.0.0; Ti v2.2.2.2; Mt v2.2.2.2;

Leg II Ti v2.2.2.2; Mt v2.2.2.2

Male spination: Leg I F p0.0.1.0/d0.1.1.0; Ti p2.2.2.2/r 2.3.2.2/ v2.2.2.2; Mt p2.0.0.0/r1.1.0.1/v.2.2.2.2;

Leg II F p 0.1.0 (or 1).0/d0.1.0.0; Ti p0.2.2.0/r0.3.1 (or 2).0/v0.2.2.2; Mt p1.1.0.1/r1.0 (or 1).0.0/v2.2.0.2;

Leg III F p0.1.0.0./d0.0.1.0;

Leg IV F d0.1.0.0

Dimensions (female): Korapuki I., B.M. Fitzgerald 2 Mar. 1998. (MONZ AS.004053)

Total Length 8.03;

Carapace 3.23/2.60;

Cephalic area 0.71/1.02;

Sternum 1.41/1.32;

Labium 0.37/0.54;

Leg I (F/P/Ti/Mt/Ta/Total) 4.17/1.42/3.94/2.60/1.02/13.15;

Leg II 3.54/1.34/3.31/2.44/0.94/11.57;

Leg III 1.89/1.10/1.61/0.94/0.71/6.2;

Leg IV 2.05/0.87/1.26/0.94/0.79/5.91;

Palp (F/P/Ti/Ta/Total) 0.80/0.51/0.41/0.68/2.41;

Eyes (AME/ALE/PME/PLE) 0.07/0.13/0.10/0.11

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)

0.12/0.07/0.12/0.15/0.17

Dimensions (male): Locality data as for female.

Total Length 5.28;

Carapace 2.20/1.77;

Cephalic area 0.55/0.75;

Sternum 1.00/0.95;

Labium 0.29/0.24;

Leg I (F/P/Ti/Mt/Ta/Total) 4.17/1.42/3.94/2.60/1.02/13.15;

Leg II 3.54/1.34/3.31/2.44/0.94/11.57;

Leg III 1.89/1.10/1.61/0.94/0.71/6.26;

Leg IV 2.05/0.87/1.26/0.94/0.79/5.91;

Palp (F/P/Ti/Ta/Total) 0.80/0.51/0.41/0.68/2.41

Eyes (AME/ALE/PME/PLE) 0.07/0.15/0.10/0.11;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)

0.10/0.05/0.07/0.10/0.15;

Distribution: Known from the upper North Island. See Appendix A and Map 5.

Biology: This species is strongly associated with modified habitat. It is most frequently captured by beating vegetation (Pers. obs.).

Remarks: The earliest record is from Waiheke Island in 1939 (MONZ AS.004031). It is not known if this species arrived in New Zealand naturally by ballooning or by anthropogenic dispersal. However, its presence on uninhabited islands suggests it may be capable of dispersal over water. The type was not seen, but Koch's description and illustration are sufficient for the identity of this species to be clear. Material identified by the late Val Davies (QM) who had seen the type is also present in the MONZ collection.

***Sidymella trapezia* (L. Koch, 1874)**

Figs 14, 25. 36

Map 6

Stephanopis trapezia L. Koch, 1874: 512, pl. 39, f. 1

Stephanopis trapezia L. Koch, 1876; L. Koch, 760, pl. 66, f. 6

Sidyma trapezia (L. Koch, 1874); Simon, 1908: 433.

Sidymella trapezia (L. Koch, 1874); Roewer, 1955: 759

Type Data: Syntypes 2 ♀, Sydney, Australia (Museum Godeffroy (Hamburg) Nr.9913). Not seen.

Differential diagnosis: Most closely resembles *S. longipes*, but the abdomen is shorter and broader relative to the carapace, the epigyne is in an atrium and legs of males have many dorsal femoral spines. The median strip on the sternum either runs the length of the sternum or starts centrally and terminates on the posterior margin. Black markings are present on the coxae, while single black spots are present on the proximal end of the pro- and retrolateral surfaces of the patellae. The visible portion

of the embolus is less curved and is also broader posteriorly. The RTA termination is bluntly bifid.

Colour: Carapace cream to yellow with dark spotting; brown or black median longitudinal stripe, abruptly tapering posteriorly and with darker edging on the thoracic portion; abdominal dorsum mottled pale brown with dark edging; other abdominal surfaces cream to yellow with dark spotting; sternum with dark longitudinal median stripe on posterior half; legs cream to yellow with black spots and blotches, including black markings on the coxae and single pro- and retrolateral spots on the proximal end of each patella.

Cephalothorax: Fig. 14. Similar to *S. longipes* but setae in eye region thicker and denser and sternal setae denser posteriorly and laterally.

Abdomen: Fig. 14. Similar to *S. longipes*, but broader and shorter relative to carapace and posterior surface more protuberant; setae also similar, but ventral setae densest in two longitudinal bands running between spinnerets and outer margins of epigastric furrow.

Epigyne and internal genitalia: Fig. 25. In atrium bordered with thickened postero-lateral lips; spermathecae and copulatory ducts visible in ventral view; in dorsal view, two pairs of heavily sclerotised and irregularly globular spermathecae.

Male palp: Fig. 36. Visible portion of the embolus broad posteriorly and with slight thickening before anterior end; RTA termination bluntly bifid in ventral view; RCP small and extends laterally.

Legs: Clothed with straight hairs; male with many dorsal spines on femora.

Female spination: Leg I F p 0 (or 1).2.0 (or 1).0; Ti p0.1.0.1/r0.0.1.1/v2.2.2.2; Mt p1.0.0.1/r1.0.0.1/v2.2.2.2;

Leg II F p0.1.0.0/d 0.1.0.0; Ti p0.1.0 (or 1).1/r 0.0.1.1/v2.2.2.2; Mt p1.0.0.1/r0.0.0.1/v2.2.2.2;

Leg III F p0.1.0.0/d0.1.0.0; Ti p 0.0.1.0/v.0.2.0.2; Mt p1.0.1.0/r 0.0.1.1/v 0.2.0.2;

Leg IV F d0.1.0.0/Ti p 0.1.0.1/v 0.1.0.1; Mt p1.0.1.1/r0.0.0.1/v0.2.0.2;

Male spination: Leg I F p2.0.2.1/r2.1.0.0/d4.2.2.1; Ti p.1.0.1.0/r0.01.1/v2.2.2.2; Mt p0.0.0.1/r0.0.0.1/v2.2.2.2;

Leg II F p1.1.0.0/r1.0.1.0/d2.0.2.1; Ti p0.1.0.1/r1.0.1.1/v2.2.2.2; Mt p1.0.0.1/r0.0.0.1/ v2.2.2.2;

Leg III F p1.1.0.0/r1.1.1.0/d1.1.1.1; Ti p0.1.1.0/0.0.1.0/v0.2.0.2; Mt p1.0.1.1/r0.1.0.1/ v0.2.0.2;

Leg IV F p0.1.1.0/d1.1.1.1; Ti r1.0.1.0/p1.0.1.0/v.0.1.0.1/Mt p0.0.0.1/r.1.1.0.1/v0.1.0.2

Dimensions (female): Lower Hutt, C. McGuiness, 19 Apr. 2003 (MONZ AS.004052).

Total Length 8.19;

Carapace 3.78/3.46;

Cephalic area 0.79/1.73;

Sternum 1.73/1.54;

Labium 0.73/0.61;

Leg I (F/P/Ti/Mt/Ta/Total) 4.02/1.97/3.62/2.68/1.22/13.50;

Leg II 3.70/1.81/3.27/2.24/1.18/12.20;

Leg III 2.52/1.26/1.89/1.18/0.87/7.72;

Leg IV 3.23/1.26/2.05/1.50/0.94/8.98;

Palp (F/P/Ti/Ta/Total) 1.10/0.66/0.66/0.95/3.37;

Eyes (AME/ALE/PME/PLE) 0.10/0.22/0.11/0.16;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.15/0.10/0.21/0.24/0.24

Dimensions (male): Raukawa St, Stokes Valley, Wellington, B.M. Fitzgerald; Mar. 2011 (MONZ AS.004051).

Total Length 4.57;

Carapace 2.28/2.13;

Cephalic area 0.51/0.98;

Sternum 1.17/0.98;

Labium 0.30/0.37;

Leg I (F/P/Ti/Mt/Ta/Total) 3.62/1.38/3.46/2.87/2.36/13.70;
Leg II 3.46/1.30/3.15/2.52/1.42/11.85;
Leg III 2.28/0.75/1.42/1.02/0.71/6.18;
Leg IV 2.44/0.79/1.73/1.18/0.71/6.85;
Palp (F/P/Ti/Ta/Total) 1.02/0.56/0.24/0.76/2.59;
Eyes (AME/ALE/PME/PLE) 0.07/0.16/0.10/0.15;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.12/0.09/ 0.15/0.18/0.17

Distribution: Known from the lower North Island. See Appendix A and Map 6.

Biology: In captivity *S. trapezia* seems to be a more active and aggressive hunter than other stephanopines found in New Zealand (Pers. obs.). The front legs are frequently held wide apart while feeding rather than being used to hold prey. This species has been recorded in houses and also in coastal ecosystems such as dune vegetation.

Remarks: This species appears to be recently established in New Zealand with the earliest record being from the Hutt Valley in 2003 (MONZ AS.4052). It has since been found in several lower North Island localities. Its' occurrence in disjunct coastal locations may indicate it dispersed here by ballooning although this has not been proven. The syntypes were not seen but the the original description (L. Koch 1874) is sufficient for the identification of this species.

Subfamily Thomisinae (flower spiders)

Diagnosis: Lateral eye tubercles present, cheliceral teeth absent, disk-shaped tegulum (Ono 1988). New Zealand species lack sockets for femur I leg spines, have a cephalic region at least two thirds width of the carapace and abdomen not trapezoidal in dorsal view.

Remarks: Benjamin (2011) notes that the presence of lateral eye tubercles and lack of cheliceral teeth are plesiomorphic and suggested that thomisid subfamilies are all

in need of relimitation. While these characters may not ultimately prove to be phylogenetically informative, they are still useful in distinguishing thomisines from stephanopines in New Zealand.

One endemic genus, *Cymbachina* Bryant 1933, consisting of five species is present in New Zealand. Four species (previously recorded in *Diaea* Thorell, 1869) can be collected by beating vegetation, particularly flowering plants, and are known to ambush pollinating insects (Jackson *et al*, 1995). The type species *Cymbachina albobrunnea* Bryant, 1933 has rather different habits and is known to frequent lichen and litter (Forster & Forster 1999).

Key to New Zealand Thomisinae

- | | |
|---|--------------------------------|
| 1) Extensive brown markings present (Figs 15, 17) | 2 |
| Not as above (Figs 16, 18, 19) | 3 |
| 2) Horse-shoe marking on carapace, long, fine legs (Fig 17) | |
| | <i>Cymbachina ambara</i> |
| Carapace lateral areas brown, legs short and thick (Fig 15) | |
| | <i>Cymbachina albobrunnea</i> |
| 3) Tarsus IV longer than metatarsus IV (Fig 18) | <i>Cymbachina sphaeroides</i> |
| Tarsus IV equal to or shorter than metatarsus IV | 4 |
| 4) Maxillae broader distally than proximally | <i>Cymbachina urquharti</i> |
| Maxillae distal and proximal widths about equal | |
| | <i>Cymbachina albolimbata.</i> |

***Cymbachina* Bryant, 1933**

Type species: *Xysticus albo-brunnea* Urquhart, 1893

Differential diagnosis: Bryant (1933) distinguishes *Cymbachina* from the predominantly Australian genus *Cymbacha* L. Koch, 1874 on the basis of the heavy

tibial and metatarsal spines and from *Xysticus* C.L Koch, 1835 because of the tuberculate eyes and sloped clypeus. Previously, most New Zealand thomisines were placed in *Diaea* Thorell, 1869 (Bryant, 1933), but members of *Cymbachina* can be distinguished from the type species *Diaea dorsata* (Fabricius, 1777) by the presence of two tibial processes on the male palp rather than three and the more extensive antero-lateral hood over the epigyne (cf: Fig. in Roberts 1995: 156).

Size: Small to medium sized spiders (3.5-8.5 mm long).

Cephalothorax: Figs 15-19. About as long as wide; high, with posterior half of thoracic portion sloping sharply towards the posterior margin; surface very finely denticulate; cephalic area at least two thirds as wide as carapace width.

Sternum: Scutiform, longer than wide, widest between coxae II and III; clothed with fine setae, mostly directed antero-medially.

Eyes: Figs 15-19. ALE>PLE>PME>AME; eyes on tubercles, with lateral eye tubercles contiguous or nearly so.

Chelicerae: No cheliceral teeth, fangs short and transverse.

Labium: Slightly longer than wide.

Legs: Length order 1243; unsocketed spines present on femur I; coxae with fringe of fine bristles; other segments clothed with fine setae; erect bristles on tarsi and metatarsi.

Abdomen: Figs 15-19. Rounded (females) or relatively elongate (males) in dorsal view; sparse coating of large setae present in some species.

Spinnerets: Short, conical.

Epigyne and internal genitalia: Figs 26-30. In atrium with antero-lateral hood; paired copulatory ducts usually visible in ventral view; in dorsal view copulatory ducts

initially directed anteriorly before turning retrolaterally and forming a series of demi-loops; one pair of spermathecae.

Male palp: Figs 37-41. In retrolateral view RTA present; VTA erect, rectangular and on retrolateral edge of tibia in ventral view; sperm duct originates centrally and coils towards posterior margin before turning postero-laterally and encircling the margin of the bulb with the embolus terminating distally.

Remarks: When Bryant (1933) erected the genus *Cymbachina* she differentiated it from *Cymbacha* and *Xysticus*, but not *Diaea*, the genus to which she had transferred several other New Zealand thomisines. Lehtinen (1993), Szymkowiak (2007) and Szymkowiak and Dymek (2012) observed that Australian *Diaea* are not closely related to the type species, exhibit much intrageneric morphological variability, and that a complete revision is needed. Szymkowiak (2007) stated that Australian *Diaea* should be transferred to other genera. It appears a similar situation exists in New Zealand and on the basis of genitalic similarity, I have transferred the New Zealand *Diaea* species to *Cymbachina*. Szymkowiak (2007) also observed that *Diaea pulleinei* Rainbow, 1915 showed some similarity to New Zealand *Diaea* species and that together they may constitute a new genus Szymkowiak (2007). However, *D. pulleinei* males have a more denticulate tegulum and the sperm duct is oriented differently, while females have a far more extensive epigynal hood.

***Cymbachina albobrunnea* (Urquhart, 1893)**

Figs 15, 26, 37

Map 7

Xysticus albo-brunnea Urquhart, 1893a: 184.

Cymbachina albobrunnea (Urquhart, 1893); Bryant, 1933b: 3

Type data: Holotype ♀, bush near Ohaupo, A.T. Urquhart. (CMNZ).

The type is in poor condition with a shrivelled abdomen and most legs are broken and detached from the body.

Differential diagnosis: The striking colour pattern of *C. albobrunnea* is sufficient to distinguish it from other New Zealand species. The VTA is the narrowest (in ventral view) of all *Cymbachina* species and the legs are relatively short compared to those of other species.

Colour: Carapace dark brown with cream lateral edging; cream median ovoid patch on thoracic region, brown patch behind eye region; eye region cream; female sternum dark laterally with dark blotching centrally and a dark mark on the central portion of the anterior edge although sternum almost completely dark in some specimens; male sternum dark with white blotching; dorsum of abdomen cream with brown irregular median stripe flanked by darker 'T' shaped markings on either side; posterior cream; laterally marked with lines of black and cream dashes; venter with median brown longitudinal band surrounded by irregular cream 'U' which in turn is surrounded by a brown 'U' shaped marking; legs mottled cream and brown, with brown annulations on distal end of femora, patellae and metatarsi.

Cephalothorax: Fig. 15. About as long as wide; high, with posterior half of thoracic portion sloping sharply towards the posterior margin; surface finely denticulate; four erect, socketed bristles in a transverse row across cream median patch; socketed bristles also in, beside and behind eye region; eye tubercles not touching; sternum clothed with fine anteriorly directed setae.

Abdomen: Fig. 15. Broad, rounded; erect bristles on dorsum; fine setae ventrolaterally.

Epigyne and internal genitalia: Fig. 26. Posterior margins of epigynal hood almost straight and converge medially; paired copulatory ducts visible in ventral view; in dorsal view, copulatory ducts thin and translucent; one pair of lightly sclerotised spermathecae.

Male palp: Fig. 37. In retrolateral view RTA broadens medially and tapers to blunt distal point; VTA narrow on retrolateral edge of tibia in ventral view;

Legs: Coxae with fringe of fine bristles; other segments clothed with fine setae; erect bristles on tarsi and metatarsi.

Female spination Leg I F p0.2.1.1./d0.0.1.0; Ti v0.2.2.2/Mt v0.2.0.2

Leg II Ti v0.2.2.2/Mt v0.2.0.2

Leg III F d0.0.1.0

Leg IV Ti v0.0.1.0; Mt v0.0.0.1

Male spination Leg I F: p0.2.2.1/d 0.1.1.1/Ti v0.2.2.2/Mt v0.2.0.2

Leg II F p0.1.01/d0.1.0.1/Ti v0.2.2.2/Mt v0.2.0.2

Leg III F d.0.0.1.0; Ti p0.0.1.0/v0.1.0.1; Mt p0.0.1.0/v0.0.1

Leg IV Ti v0.0.1.0; Mt v0.0.0.1

Dimensions (female): Pidgeon Flat Road, near Mt Cargill, R.W. Hutton & C.L. Wilton, 3 Jun. 1969 (OMNZ IV36300).

Total Length 3.86;

Carapace 1.89/1.73;

Cephalic area 0.48/1.26;

Sternum 0.88/0.80;

Labium 0.32/0.29;

Leg I (F/P/Ti/Mt/Ta/Total) 1.38/0.67/0.94/0.87/0.55/4.41;

Leg II 1.42/0.71/0.98/0.94/0.63/4.69;

Leg III 1.02/0.55/0.63/0.55/0.47/3.23;

Leg IV 1.10/0.55/0.79/0.63/0.47/3.54;

Palp (F/P/Ti/Ta/Total) 0.44/0.32/0.24/0.39/1.39;

Eyes (AME/ALE/PME/PLE) 0.06/0.11/0.07/0.09;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.27/0.15/0.29/0.29/0.24

Dimensions (male): Aniwaniwa, Waikaremoana, H.A. Oliver, 9-16 Mar 1969 (OMNZ IV36122).

Total Length 3.54;

Carapace 1.50/1.42;

Cephalic area 0.45/1.06;

Sternum 0.73/0.66;
Labium 0.28/0.24;
Leg I (F/P/Ti/Mt/Ta/Total) 1.34/0.55/1.10/0.91/0.59/4.49;
Leg II 1.34/0.63/1.02/0.87/0.63/4.49;
Leg III 0.94/0.43/0.71/0.55/0.43/3.07;
Leg IV 0.94/0.39/0.71/0.55/0.47/3.07;
Palp (F/P/Ti/Ta/Total) 0.37/0.27/0.15/0.27/1.05;
Eyes (AME/ALE/PME/PLE) 0.06/0.11/0.07/0.09;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.20/0.12/0.22/0.24/0.20

Distribution: This species rarely collected but appears to be found nationwide. See Appendix A and Map 7.

Biology: According to Forster and Forster (1999), the colour pattern of this species means it blends well against lichen, a habitat where it is often found. Museum specimen records indicate that can also be found in leaf litter. This habitat preference is markedly different from other members of this genus.

Remarks: The male of this species is described for the first time. Forster and Forster (1999) noted this species was widespread but not commonly collected. This is borne out by the paucity of specimens available for examination from museum collections.

***Cymbachina albolimbata* (L. Koch, 1875) Comb. nov.**

Figs 16, 27, 38

Maps 8-9

Diaea albolimbata L. Koch, 1875: 588, pl. 46, f. 1

Philodromus ovatus Urquhart, 1887: 113 – Synonymy by Bryant 1933b: 3

Synaema albolimbata (L. Koch, 1875); Dahl, 1907a: 382, 391

Diaea albolimbata L. Koch, 1875; Dalmas, 1917: 389

Diaea albomaculata (L. Koch, 1875); Bryant, 1933b: 3 (lapsus)

Diaea albolimbata L. Koch, 1875; Roewer, 1955: 869

Type Data: Holotype ♀ of *Diaea albolimbata* L. Koch, 1875, New Zealand, Mr Bradley. Not available.

Holotype ♀ of *Philodromus ovatus* Urquhart, 1887, Waiwera, on *Leptospermum*, A.T. Urquhart.

The holotype of *D. albolimbata* is not listed in Rack's (1961) catalogue of arachnid type material housed at the Zoologische Museum, Hamburg, Germany and is presumed lost. This is the home of Koch's collection. The Urquhart holotype of *P. ovatus* is in poor condition.

Differential diagnosis: Has the fewest spines on the prolateral surface of femur I of any *Cymbachina* species. This species most closely resembles *Diaea urquharti* but is smaller and the maxillae are approximately as wide distally as they are proximally while in *C. urquharti* the maxillae are broader distally. In males, the form of the RTA is less angulate, the retrolateral margin of the VTA in ventral view is roughly vertical and the extension of the cymbium tip beyond the bulb is the shortest of all New Zealand *Diaea*. In females, the anterior epigynal hood appears to be slightly separate from the postero-lateral hoods.

Colour: Cephalothorax and legs straw yellow to yellow-brown; eye region cream; leg I sometimes darker with additional dark shading; dorsum of abdomen with lateral cream edging running from anterior end and females with a second pair of shorter, median cream stripes; extremely variable laterally and ventrally with red-brown, cream or straw yellow markings all known.

Cephalothorax: Fig 16. Smooth, with very sparse coating of fine black setae; both eye rows weakly recurved; lateral eye tubercles contiguous; sternum clothed with very fine setae; maxillae with concave retrolateral margin and broader distally than basally.

Abdomen: Fig 16. Longer than wide; dorsum sparsely clothed with semi-recumbant, posteriorly directed fine setae; erect fine setae on anterior surface.

Epigyne and internal genitalia: Fig 27. Ventrally concave with medium septum and with both an anterior hood and weaker postero-lateral hoods; in dorsal view; copulatory ducts oriented longitudinally before following a sequence of three hemispherical loops; one pair of irregularly shaped spermathecae with short fertilization ducts linked to anterior end of copulatory ducts.

Male palp: Fig 38. VTA in ventral view with slightly concave anterior margin, horizontal lobe on prolateral margin and retrolateral margin roughly vertical; RTA curving anteroventrally with blunt, bifid termination; cymbium tip short, truncate, with dense patch of black setae.

Legs: clothed with fine hairs; tarsi with dark scopulae.

Female spination Leg I F p0.2.0.0/d0.1.0.1; Ti p 0.1.1.1/d1.0.1.0/v.0.4.4.4; Mt p0.0.1.1/v2.4.4.2

Leg II F d0.1.0.0; Ti v0.2.4.4; Mt p0.0.0.1/r0.0.0.1/v2.2.2.2

Leg III F d0.1.0.1; Pa 1.0.0.0; Ti p.0.0.1.0/d.0.1.1.0/v0.2.0.2/Mt p0.0.0.1/v0.2.0.1

Leg IV Ti 1.0.0.0/v0.1.0.2/Mt p.0.0.1.0/r.0.0.1.0/v.0.2.0.0

Male spination Leg I F p1.1.1.2/d0.1.0.1;Ti p0.0.1.1/v0.2.2.2/Mt p0.0.0.1/r0.0.0.1/v.2.2.2.2

Leg III F d0.1.0.0; Ti p0.0.01/d.0.0.1.0/v0.2.2.2; Mt p1.0.1.0/v0.2.2.2

Leg III F p.0.1.0.1/d0.1.1.1 (or 2); Ti p1.0.1.1/r 0.0.0.1/v0.2.0.0; Mt p1.0.1.0/v0.1.0.0

Leg IV F d0.1.0.0; Ti p0.0.0.1/r0.0.0.1/ d1.0.1.0/v0.1.0.0; Mt p0.1.1.0/v0.1.0.0

Dimensions (female): Chatham Island, Henga Scenic Reserve., N. Curtis & A. Paterson, 1-10 Nov, 2005 (MONZ AS.004047).

Total Length 6.54

Carapace 2.28/2.20;

Cephalic area 0.62/1.50;

Sternum 0.88/0.73;

Labium 0.44/0.41;

Leg I (F/P/Ti/Mt/Ta/Total) 2.44/1.22/2.20/1.42/0.87/8.15;
Leg II 2.36/1.10/1.81/1.50/0.79/7.56;
Leg III 1.50/0.75/0.94/0.55/0.39/4.13;
Leg IV 1.57/0.71/1.46/0.71/0.43/4.88;
Palp (F/P/Ti/Ta/Total) 0.51/0.41/0.34/0.51/1.78;
Eyes (AME/ALE/PME/PLE) 0.09/0.12/0.07/0.10;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.32/0.22/0.43/0.38/0.32

Dimensions (male): Chatham Island, Henga Scenic Reserve, P.J. Sirvid, 2-8 Feb, 2007 (MONZ AS.001014).

Total Length 4.45;
Carapace 2.01/1.81;
Cephalic area 0.56/1.34;
Sternum 0.90/0.78;
Labium 0.37/0.39
Leg I (F/P/Ti/Mt/Ta/Total) 2.60/1.10/2.36/1.73/1.50/9.29;
Leg II 2.36/1.02/2.05/1.50/0.87/7.80;
Leg III 1.42/0.55/1.10/0.63/0.55/4.25;
Leg IV 1.50/0.63/1.02/0.71/0.55/4.41;
Palp (F/P/Ti/Ta/Total) 0.63/0.32/0.24/0.63/1.83;
Eyes (AME/ALE/PME/PLE) 0.10/0.11/0.07/0.10;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.27/0.17/0.34/0.44/0.27

Distribution: Likely to occur over most of New Zealand, given the disjunct localities for available records. Localities include Waiwera, Wairarapa, Wellington and the Chatham Islands. This is the only species of thomisid known from the Chathams. See Appendix A and Maps 8-9.

Biology: *Cymbachina albolimbata* is most frequently found on flowering plants. In the Chatham Islands it is particularly common on the local species of *Pimelia*.

Remarks: This is the first time the male of *C. albolimbata* has been described.

***Cymbachina ambara* (Urquhart, 1885) Comb. nov.**

Figs 17, 28, 39

Map 10

Philodromus ambarus Urquhart, 1885: 43.

Synema suteri Dahl, 1907: 281 **new synonymy**

Diaea ambara Bryant, 1933b: 4.

Type Data: 5 immature ♀, 2 ♂ syntypes *Philodromus ambarus* Urquhart, 1885, Tairua, Whangarei Harbour, T. Broun (CMNZ).

Syntypes of *Synema suteri* Dahl, 1907, 3 ♀, 2 ♂, New Zealand [no collector or date] (ZMH 20867).

Urquhart's syntype series is in poor condition with the majority of legs detached from specimens. The distinctive colour pattern diagnostic for this species is still visible in some specimens. The syntype series for *S. suteri* is in reasonably good condition, but the colour pattern is barely visible.

Differential diagnosis: Colour pattern is a reliable way of distinguishing this species, particularly the brown horse-shoe mark and lateral brown edging on the carapace, brown longitudinal striations and squarish brown markings on the flanks and margin of the rear portion of the abdomen respectively. The RTA has a translucent distal point and the cymbium is smaller than in other New Zealand *Cymbachina* except *C. albobrunnea*, which has a much narrower VTA. Hood bordering antero-lateral portion of epigyne.

Colour: Variable, but most specimens with straw yellow to yellow-brown carapace with brown edging on the carapace (stronger posteriorly) and brown longitudinal striations on lateral surfaces of a straw yellow abdomen. Carapace with short brown stripe between PME, two brown longitudinal stripes or brown horse-shoe shape running from PLE to apex of carapace; eye tubercles cream-white, often with brown shading between them; male chelicerae brown; female chelicerae straw yellow with brown transverse bands near each end; sternum yellow; abdominal dorsum with cream-white antero-lateral edging; often with broken brown lines anteriorly and two rows longitudinal brown squarish markings postero-laterally; spinnerets ringed with

brown; venter of males often with two brown stripes between spinnerets and epigastric furrow and broad brown marking between epigastric furrow and pedicel; cream patches may be present on abdominal surfaces; legs yellow, often with brown annulations and darker ventral shading on legs I and II; male palp yellow with brown transverse band across broadest part of dorsal surface of cymbium.

Cephalothorax: Fig. 17. Smooth with a very few fine hairs; chelicerae broader basally than distally, male chelicerae longer than female with concave prolateral margins; sternal setae few, fine, located laterally; maxillae narrower basally with retrolateral margins gently concave.

Abdomen: Fig. 17. Somatic characters similar to other *Cymbachina* species.

Epigyne and internal genitalia: Fig. 28. Median notch on posterior margin of hood; in dorsal view, copulatory ducts with single hemispherical loop; spermathecae kidney-shaped with small anterior bursa.

Male palp: Fig. 39. RTA with translucent distal point; prolateral margin of VTA very weakly concave; cymbium small and with distinct colour pattern.

Legs: Clothed with fine setae; male legs III and IV similar in size.

Female spination Leg I: Fp 0.2.0.1/d0.1.0.0; Ti p0.0.0.1/r0.0.0.1/d0.1.0.1/v2.0 (or 1).2.2; Mt p0.0.1.0/r0.1.0.1/v0.2.0.2;

Leg II Fd0.1.0.0; Ti p0.0.0.1/r0.0.0.1/d0.1.0.1/v.2.0.2.2; Mt p0.1.0.1/r0.1.0.1/v0.2.0.2;

Leg III F d0.1.0.0; Ti p.0.0.0.1/d1.0.1.0/v0.1.0.0; Mt p.0.0.0.1/r0.0.0.1/v0.0.01;

Leg IV Fd0.1.0.0; Ti d0.1.1.0; Mt p.0.0.0.1/v0.1.0.0

Male spination Leg I: Fp 0 (or 1).2.0.1/r0.0.1.1/d0.1.0.1; Ti p1.0.1.1/r1.0.1.1/d0.1.0.1/v0.2.3.2; Mt p1.0.1.1/1.0.10/v0.2.0.2;

Leg II F p0.0.1.1/r0.0.0.1; Ti p1.1.0.1/r1.1.0.1/v0.2.0.2; Mt p1.0.1.0/r1.0.1.0/v0.2.0.2;

Leg III F p 0.0.0 (or 1).0 (or 1)/d0.1.0 (or 1).1; Ti p1.0.1.0/r1.0.1.0/d0.1.0.1/v0.1.0.0;Mt p1.0.0.1/r0.0.0.1/v0.2.0.0;

Leg IV Fd0.1.0.1; Pa r.0.0.0 (or 1).0; Ti p1.0.1.0/r1.0.1.0/v0.1.0.0; Mt p1.0.0.1/r0.0.1.0/v0.2.0.0

Dimensions (female): Bream Head, B.M. Fitzgerald, 16-18 Oct. 2001 (MONZ AS.004050).

Total Length 3.70;

Carapace 1.65/1.57;

Cephalic area 0.50/1.10;

Sternum 0.88/0.80;

Labium 0.29/0.29;

Leg I (F/P/Ti/Mt/Ta/Total) 1.97/0.87/1.50/1.10/0.71/6.14;

Leg II 1.81/0.79/1.42/1.02/0.71/5.75;

Leg III 1.02/0.51/0.71/0.39/0.43/3.07;

Leg IV 1.34/0.51/0.83/0.55/0.47/3.70;

Palp (F/P/Ti/Ta/Total) 1.054/0.24/0.22/0.34/1.34;

Eyes (AME/ALE/PME/PLE) 0.07/0.15/0.07/0.12;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.20/0.17/0.30/0.34/0.27;

Dimensions (male): Locality data as for female.

Total Length 3.70;

Carapace 1.50/1.42;

Cephalic area 0.43/1.02;

Sternum 0.78/0.73;

Labium 0.32/0.27;

Leg I (F/P/Ti/Mt/Ta/Total) 1.81/0.63/1.73/1.18/0.71/6.06;

Leg II 1.73/0.63/1.57/1.18/0.71/5.83;

Leg III 0.98/0.47/0.71/0.39/0.47/3.03;

Leg IV 1.02/0.39/0.71/0.43/0.47/3.03;

Palp (F/P/Ti/Ta/Total) 0.46/0.22/0.15/0.41/1.24;

Eyes (AME/ALE/PME/PLE) 0.07/0.16/0.07/0.10;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.18/0.15/0.27/0.32/0.23;

Distribution: Known nationwide. See Appendix A and Map 10.

Biology: This species is extremely common and frequently beaten from shrubs. It is present on offshore islands and this suggests a capacity for dispersal by ballooning.

Remarks: The pointed termination of the RTA is translucent and can be hard to see in retrolateral view but the extent of this structure is quite obvious when viewed ventrally. Dalmas (1917) synonymised this species under *D. albolimbata*, and depicted a male of *D. ambara* (Dalmas 1917: Figs: 55-56) but Bryant's (1933) redescription showed the distinctiveness of these species. The syntypes of *Synema suteri* Dahl, 1907 are clearly specimens of *C. ambara*. A slide mounted male and an ethanol-preserved female both bear labels indicating they are lectotypes although only one specimen may be designated as such. This designation is invalid as it has not been formalised in a publication.

***Cymbachina sphaeroides* (Urquhart, 1885) Comb. nov.**

Figs 18, 29, 40

Map 11

Philodromus sphaeroides Urquhart, 1885: 44

Philodromus sphaeroides. Urquhart, 1887: 111

Diaea sphaeroides (Urquhart, 1885) Bryant, 1933b: 4

Type Data: Holotype ♀ of *Philodromus sphaeroides* Urquhart, 1885, Lake Tekapo, Canterbury, A.T. Urquhart (CMNZ).

The type is in poor condition but still identifiable.

Differential diagnosis: The distinct hemispherical lobe on the RTA separates males of this species from other *Cymbachina* species. Tarsus as long, or longer than metatarsus in leg IV separates both sexes of this species from *C. albobrunnea*, *C. albolimbata* and *C. urquharti*. This species also lacks the extensive brown markings of *C. ambara*.

Colour: Carapace brown with pale median 'v' shaped marking and short pale stripe between PME; eye tubercles white; sternum yellow; labium and maxillae brown; legs I and II darker than other legs and often with darker ventral shading; dorsum of cymbium brown; chelicerae brown in females, darker brown in males; abdomen straw-yellow; dorsum with five muscle spots and lateral white edging; sometimes with paired white median stripes; two brown ventral stripes between epigastric furrow and spinnerets sometimes present.

Cephalothorax: Fig. 18. Smooth with a few long fine setae; lateral eye tubercles contiguous; sternum with long fine setae; maxillae similar to those of *D. urquharti* but retrolateral margin less concave; male chelicerae narrow distally, prolateral margin concave medially and lacking thick brush of setae.

Abdomen: Fig. 18. Somatic characters similar to *D. urquharti*.

Epigyne and internal genitalia: Fig. 29. In ventral view, epigynal hood antero-lateral; in dorsal view similar to *D. albolimbata* but copulatory ducts thicker and shorter.

Male palp: Fig. 40. Retrolateral margin of VTA higher than prolateral margin in ventral view; RTA with distinct distal bulge; cymbium tip short, truncate, with dense patch of black setae.

Legs: Clothed with fine setae; dense tarsal scopulae; tarsus IV longer or equal to metatarsus IV.

Male spination Leg I F p1 (or 2).3.1.0 (or 1)/d0.1.0.0; Ti v.0.1.0.2; Mt p 0.0.1.1/r0.0.0.1/v0.2.0.2;

Leg II F p0.1.01/d0.1.0.0; Ti v0.1.0.1; Mt p0.0.1.0/v0.2.0.4;

Leg III F d0.1.1.1 (or 2); Ti p 0.0.0.1; d01.0.1/v0.1.1.0/; Mt p0.0.1.0/v0.0.1.0;

Leg IV F d0.1.1.1 (or 2); Ti p0.1.1.0; r0.0.0.1/d1.0.1.0/v0.0.1.0; Mt p0.0.1.0/v0.0.1.0

Female spination Leg I F p1.2.0 (or 1).1/d0.1.0.0; Ti v0.1.0.3; Mt p.0.0.0.1/
r0.0.0.1/v.0.2.1.2;
Leg II F d0.1.0.0; Ti v0.0.1.2; Mt p 0.0.1.1/r0.0.0.1/v 0.2.0.2;
Leg III F d0.0.1.0.0; Ti d0.1.0.1.0/v0.0.1.0; Mt p0.0.01; v0.0.1.0;
Leg IV F d0.1.0.0; Ti d1.0.0.1/v0.0.1.0; Mt p.0.0.0.1/r0.0.0.1/v0.0.1.0

Dimensions (female): Kaituna Valley, Banks Peninsula, R.R.Forster, 2 Nov. 1966
(OMNZ IV36096).

Total Length 4.65;

Carapace 2.13/2.05;

Cephalic area 0.52/1.18;

Sternum 1.10/0.95;

Labium 0.39/0.41;

Leg I (F/P/Ti/Mt/Ta/Total) 2.28/1.02/1.73/1.30/0.83/7.17;

Leg II 2.20/0.98/1.73/1.26/0.79/6.97;

Leg III 1.26/0.55/0.94/0.51/0.55/3.82;

Leg IV 1.65/0.63/0.94/0.63/0.63/4.49;

Palp (F/P/Ti/Ta/Total) 0.44/0.37/0.27/0.54/1.61;

Eyes (AME/ALE/PME/PLE) 0.09/0.13/0.09/0.11;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.30/ 0.17/0.39/0.39/0.30

Dimensions (male): Locality data as for female.

Total Length 4.25;

Carapace 2.09/1.89;

Cephalic area 0.63/1.26;

Sternum 0.95/0.88;

Labium 0.32./0.34;

Leg I (F/P/Ti/Mt/Ta/Total) 2.28/1.02/1.85/1.50/0.91/7.56;

Leg II 2.17/0.94/1.73/1.34/0.83/7.01;

Leg III 1.26/0.47/0.87/0.51/0.55/3.66;

Leg IV 1.42/0.55/0.87/0.55/0.55/3.94;

Palp (F/P/Ti/Ta/Total) 0.51/0.32/0.27/0.66/1.76;

Eyes (AME/ALE/PME/PLE) 0.09/0.15/0.09/0.10;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)

0.24/ 0.20/0.34/0.34/0.26

Distribution: Found south of Taupo. See Appendix A and Map 11.

Biology: This species is highly unusual amongst Thomisidae in that it appears to use a web to assist with prey capture (Jackson *et al.*, 1995). The authors of that study did not identify the species involved and the published figures were not clear enough for a full identification to be made. Specimens in this study were collected from *Muehlenbeckia complexa* at Birdling's Flat, Kaitorete Spit, in Canterbury, and specimens collected from the same plant species elsewhere on Kaitorete Spit are *C. sphaeroides* (MONZ AS.004049). An additional photograph (Fig. 8) provided by Simon Pollard (University of Canterbury), a co-author of the Jackson *et al.* (1995) study, is of this species. Mating habits are discussed in Forster and Forster (1999) but the specimens are incorrectly identified as *Cymbachina* (as *Diaea*) *ambara* (see Remarks below).

Remarks: The words "mating sequences" are written on a vial of *C. sphaeroides* specimens from Otago Museum (IV36294). These specimens appear to be those photographed in Fig. 7.8 in Forster and Forster (1999). This photograph is not of *C. ambara* as the spiders depicted lack the characteristic markings of that species. This species was synonymised under *Diaea albolimbata* by Dalmás (1917) but its distinctiveness was recognized by Bryant (1933).

***Cymbachina urquharti* Sp. nov.**

Fig. 19, 30, 41

Map 12

Type Data: Holotype ♂, Waiwera, A.T. Urquhart [early 1886] (CMNZ)

The holotype was selected from a vial labelled as Heautosyntypes of *Diaea sphaeroides* from the Urquhart collection (CMNZ). The specimens in this vial are in generally good condition, although some appendages are detached from specimens.

Differential diagnosis: Larger overall size, highest leg spine count, broad termination of the RTA and epigyne wider than long separates this species from all other New Zealand *Cymbachina*. Separated from *C. albolimbata* by more angulate RTA, contiguous epigynal hood and maxillae broader distally than proximally. Separated from *C. sphaeroides* by metarsus IV longer than tarsus IV.

Colour: Cephalothorax straw yellow to yellow-brown with pale Y-shaped patch medially; eye region cream; maxillae and labium brown; chelicerae yellow brown with distal portion paler in males; abdomen pale straw yellow; dorsum with five dark muscle spots and cream markings, ranging from a few spots to near complete coverage; cream spotting also present in on other surfaces; legs straw-yellow basally, darker distally.

Cephalothorax: Fig 19. Smooth with a few long fine setae; lateral eye tubercles contiguous; sternum with long fine setae; maxillae distally broader than base, retrolateral margin concave; male chelicerae with thick brush of setae on prolateral margin.

Abdomen: Fig 19. Longer than wide; narrower than carapace in males; wider in females and broadest in line with posterior muscle spots on dorsum; very sparse coating of long, fine setae.

Epigyne and internal genitalia: Fig. 30. In ventral view, concave with medium septum and with both an anterior hood and weaker postero-lateral hoods; in dorsal view similar to *D. albolimbata* but with four hemispherical loops in the copulatory ducts.

Male palp: Fig. 41. Retrolateral margin of VTA curved in ventral view; RTA curving antero-ventrally with blunt, bifid termination and posterior margin angulate; cymbium tip short, truncate, with dense patch of black setae.

Legs: Sparse coating of long, fine hairs; tarsal scopulae present; distal macrosetae present on each patella.

Female spination Leg I F p1.0.1.1; Ti d1.0.1.0/v0.3.4.4; Mt p0.1.0.1/r0.0.0.1/v3.3.2.2;

Leg II F d0.1.0.0; Ti d0.1.0.1/v0.2.1.4; Mt p1.0.1.1/r0.0.0.1/v0.2.2.2;

Leg III F d0.1.0.0; Ti p0.0.0.1/d1.0.1.0; v0.1.0.0; Mt p0.1.1.0;

Leg IV F d0.1.0.0; Ti p0.0.0.1; Mt p0.1.1.0/v0.0.1.0

Male spination Leg I F p3.4.3.0/r0.1.2.1/d0.1.1.0; Ti p0.0.1.1/r0.1.0.1/v0.2.5 (or 6).4; Mt p1.1.1.0/r1.0.1.0/v3.2.2.2.;

Leg II F p1.1.1.1/ r0.0.1.0/d0.1.0 (or 1).0; Ti p1.0.1.1/r1.0.1.1/v0.2.4.4; Mt p1.0.1.0/r1.0.1.0/v2.2.2.4;

Leg III F p0.0.1.0/d0.1.1.1; Ti p1.0.1.0/r1.0.1.0/d0.1.1.0/v0.1.0.0 ;Mt p1.0.1.0/r1.0.0.0/ v0.0.1.0;

Leg IV F p0.0.1.0/d0 (or 1).1.1.1; Ti p1.0.0.1/r1.0.1.0.1/d1.0.1.0/v0.1.0.0; Mt p1.0.1.0/r1.0.1.0/v0.1.0.0

Dimensions (female): Waiwera, A.T. Urquhart [early 1886] (CMNZ).

Total Length 8.27;

Carapace 3.07/2.68;

Cephalic area 0.94/2.05;

Sternum 1.37/1.20;

Labium 0.56/0.41;

Leg I (F/P/Ti/Mt/Ta/Total) 3.23/1.34/2.52/1.73/1.02/9.84/;

Leg II 2.99/1.42/2.52/1.73/0.91/9.57/;

Leg III 1.73/0.75/1.34/0.87/0.63/5.31/;

Leg IV 2.44/1.10/1.89/1.73/0.79/7.95/;

Palp (F/P/Ti/Ta/Total) 0.61/0.46/0.49/0.68/2.24/;

Eyes (AME/ALE/PME/PLE) 0.11/0.17/0.10/0.12/;

Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.39/0.23/0.44/0.44/0.29/

Dimensions (male): Holotype.

Total Length 5.75;

Carapace 2.53/2/20;

Cephalic area 0.94/1.73;
Sternum 1.22/1.02;
Labium 0.49/0.41;
Leg I (F/P/Ti/Mt/Ta/Total) 3.23/1.34/2.76/1.97/0.98/10.28;
Leg II 3.07/1.42/2.68/1.89/0.94/10.00;
Leg III 1.85/0.79/1.26/0.87/0.67/5.43;
Leg IV 1.97/0.79/1.34/0.94/0.71/5.75;
Palp (F/P/Ti/Ta/Total) 0.78/0.37/0.27/0.80/2.22;
Eyes (AME/ALE/PME/PLE) 0.10/0.16/0.10/0.12;
Eye interdistances (AME-AME/AME-ALE/PME-PME/PME-PLE/ALE-PLE)
0.34/0.20/0.38/0.37/0.22

Distribution: Very few specimens are known but are from quite disjunct localities so this species may prove to be widely distributed, particularly as ballooning has been confirmed for this species. See Appendix A and Map 12.

Biology: An adult male has been recorded ballooning in the Mataketake Range (LUNZ 1 Jan. 2003, no registration number).

Etymology: Named after pioneering New Zealand arachnologist, A.T. Urquhart, who described the majority of New Zealand's thomisid species and was the first collector of this species.

Remarks: Records for this species are sparse. Ideally a more recently collected specimen would have been selected as the holotype. However, Urquhart's specimen series is the only collection where males and females have been collected together and a specimen from that series was chosen for this reason.

ACKNOWLEDGEMENTS

I thank the many people who have made specimens available for this study, especially Cor Vink and Simon Pollard (Canterbury Museum, NZ), Mike Fitzgerald (Museum of New Zealand Te Papa Tongarewa, NZ), Grace Hall (Landcare Research, NZ), Cody Fraser (Otago Museum, NZ); John Marris and Jagoba Malumbres-Olarte (Lincoln University, NZ), Olivier Ball (NorthTec, NZ), Dave Seldon and Stephen Thorpe (Auckland University, NZ), Helen Smith and Graham Milledge (Australian Museum, Australia), Robert Whyte and Wendy Hebron (Queensland Museum, Australia), Bryce McQuillan (Hamilton, NZ) who also provided one of the photographs, and many more besides. I would like to thank Suresh Benjamin (Zoologisches Forschungsmuseum Alexander Koenig, Germany), David Court (Raffles University, Singapore) and Pawel Szymkowiak (A. Mickiewicz University, Poland) who provided useful insights into the complexities of the Australasian thomisid fauna. Mike Fitzgerald provided comments on an earlier draft of this chapter. Ricardo Palma (Museum of New Zealand Te Papa Tongarewa, NZ) provided taxonomic advice, while Lara Shepherd (Museum of New Zealand Te Papa Tongarewa, NZ) generated a COI sequence data for *Cymbachina albobrunnea* for me. Phil Lester (Victoria University, NZ) provided instruction on how to use R to make maps. I would also like to acknowledge the institutional support of Geoff Chambers and Phil Lester (Victoria University, NZ) and Simon Whittaker, Jenn Dalen, Carol Diebel, Claudia Orange and Anna Cowie (Museum of New Zealand Te Papa Tongarewa).



Fig 9. *Bryantymella angularis* (Urquhart, 1885). A) Female. B) Male.

A



B



Fig. 10. *Bryantymella thorini* sp. nov. A) Female. B) Male.

A



B



Fig. 11. *Bryantymella angulata* (Urquhart, 1885). A) Female. B) Male.

A



B



Fig. 12. *Bryantymella brevirostris* sp. nov. A) Female. B) Male.



Fig. 13. *Sidymella longipes* (L. Koch, 1874). A) Female. B) Male.

A



B



Fig. 14. *Sidymella trapezia* (L. Koch, 1874). A) Female. B) Male.



Fig. 15. *Cymbachina albobrunnea* (Urquhart, 1893). A) Female. B) Male.



Fig. 16. *Cymbachina albolimbata* (L. Koch, 1875). A) Female. B) Male.



Fig. 17. *Cymbachina ambara* (Urquhart, 1885). A) Female. B) Male.

A



B



Fig. 18. *Cymbachina sphaeroides* (Urquhart, 1885). A) Female. B) Male.



Fig. 19. *Cymbachina urquharti* sp. nov. A) Female. B) Male.

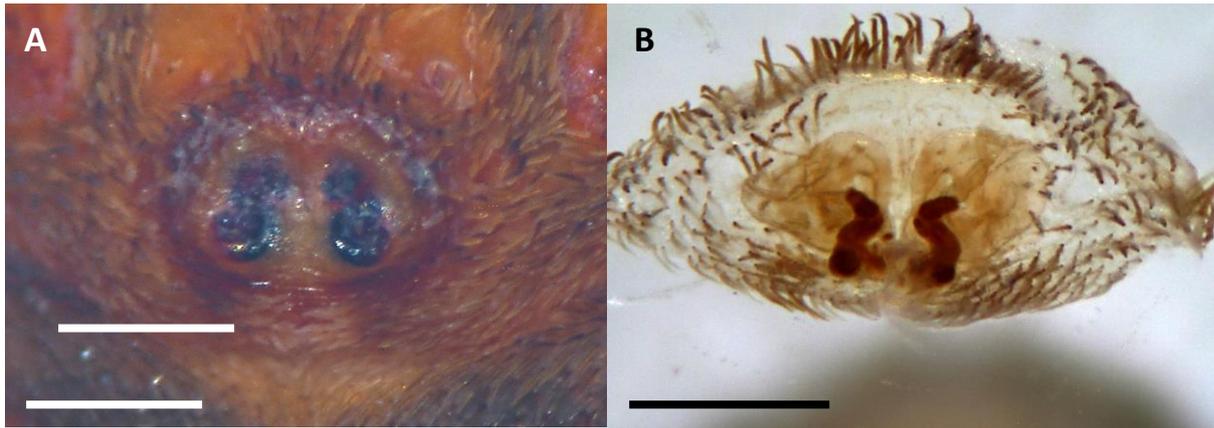


Fig. 20. Epigyne of *Bryantymella angularis* (Urquhart, 1885). A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

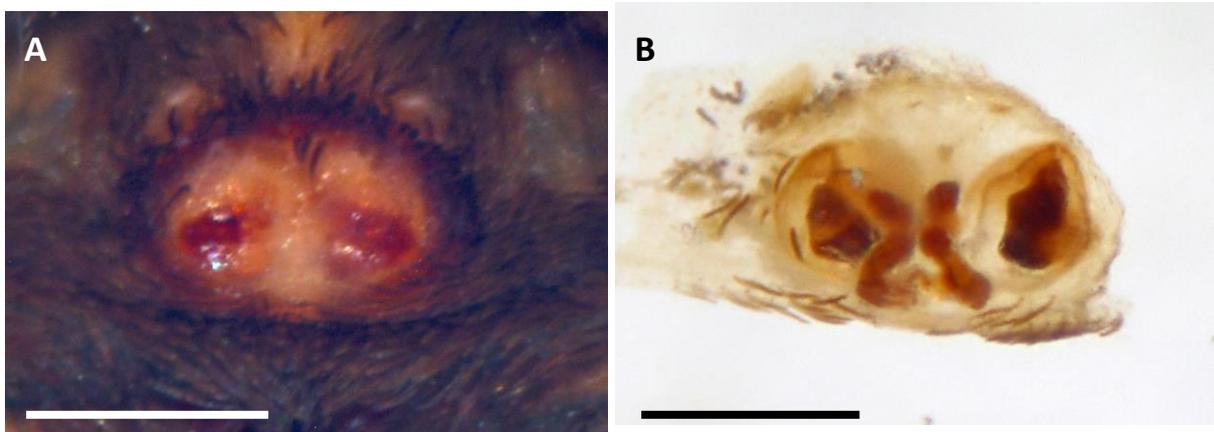


Fig. 21. Epigyne of *Bryantymella thorini* sp. nov. A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

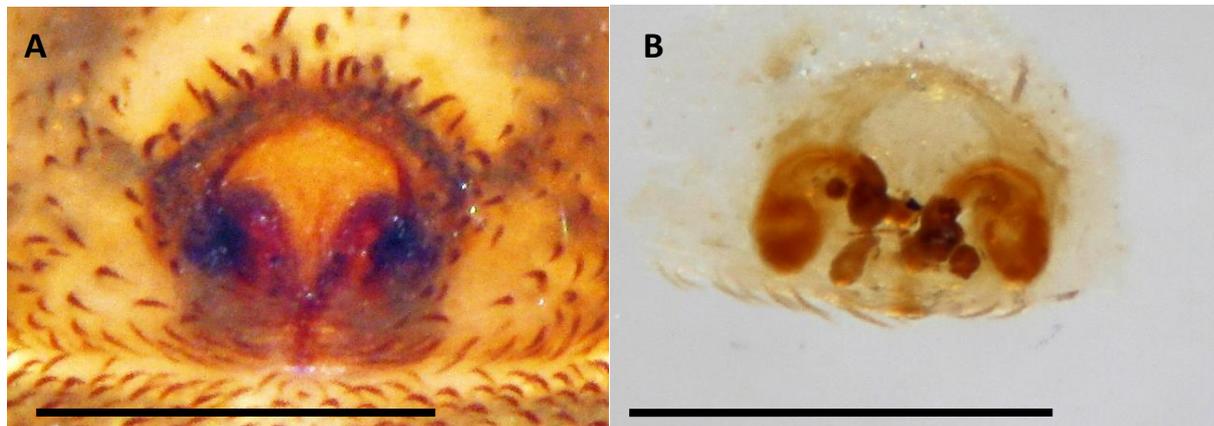


Fig. 22. Epigyne of *Bryantymella angulata* (Urquhart, 1885). A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

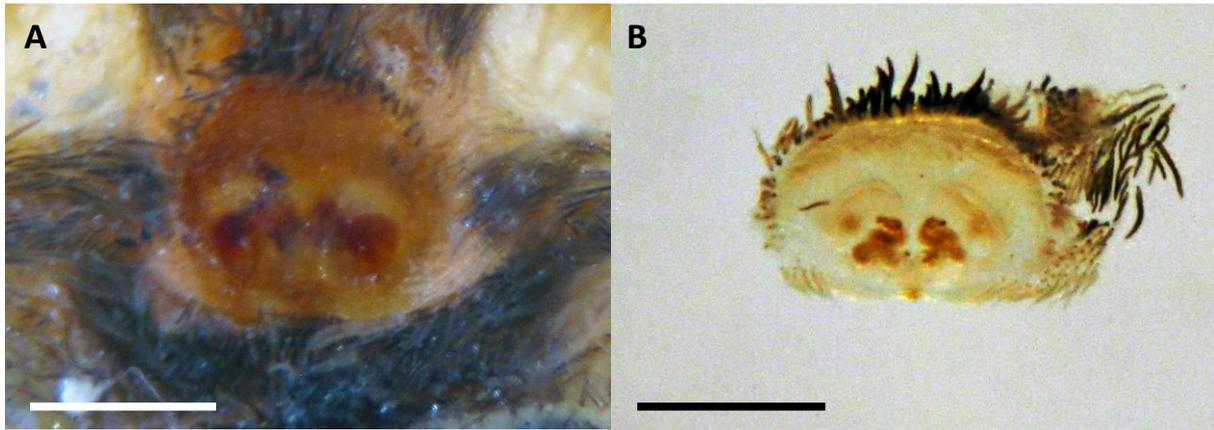


Fig. 23. Epigyne of *Bryantymella brevirostris* new sp. A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

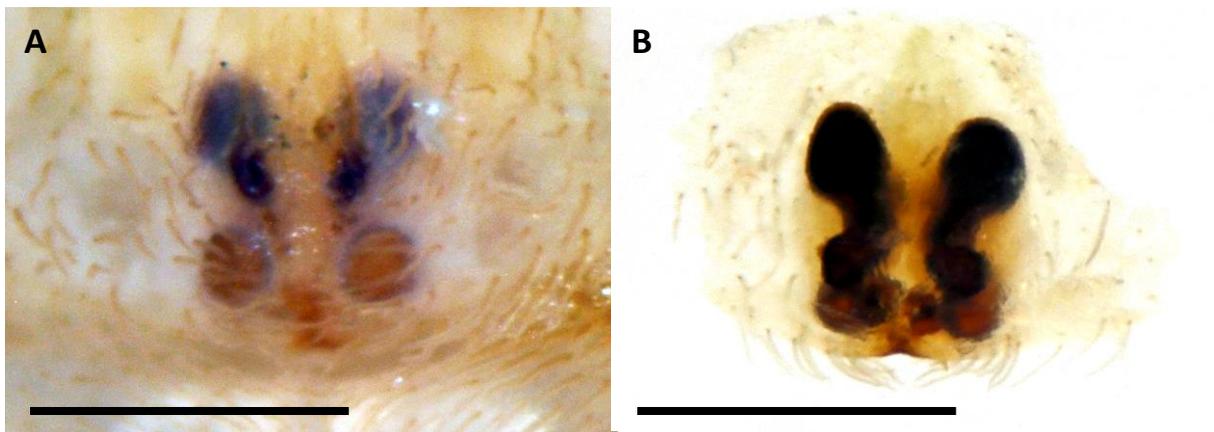


Fig. 24. Epigyne of *Sidymella longipes* (L. Koch, 1874). A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

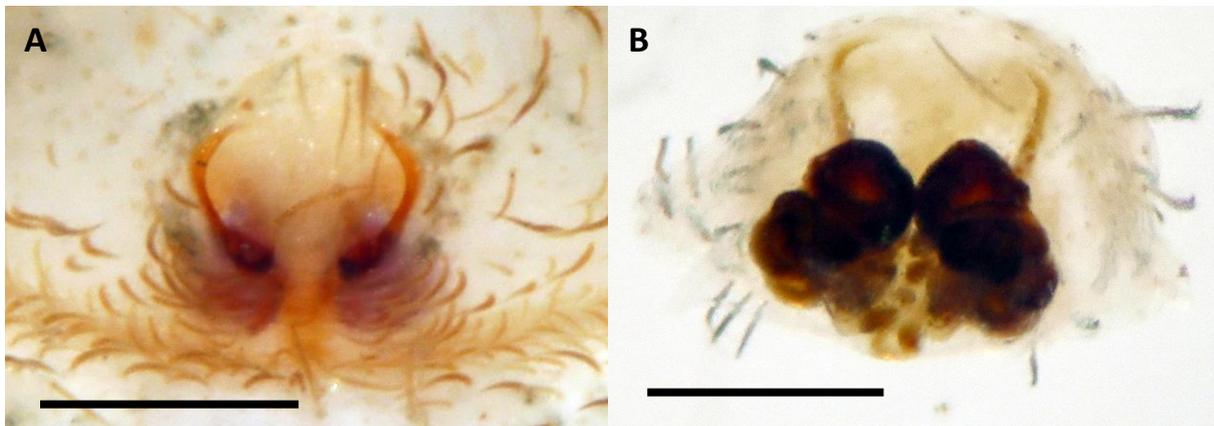


Fig. 25 Epigyne of *Sidymella trapezia* (L. Koch, 1874). A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

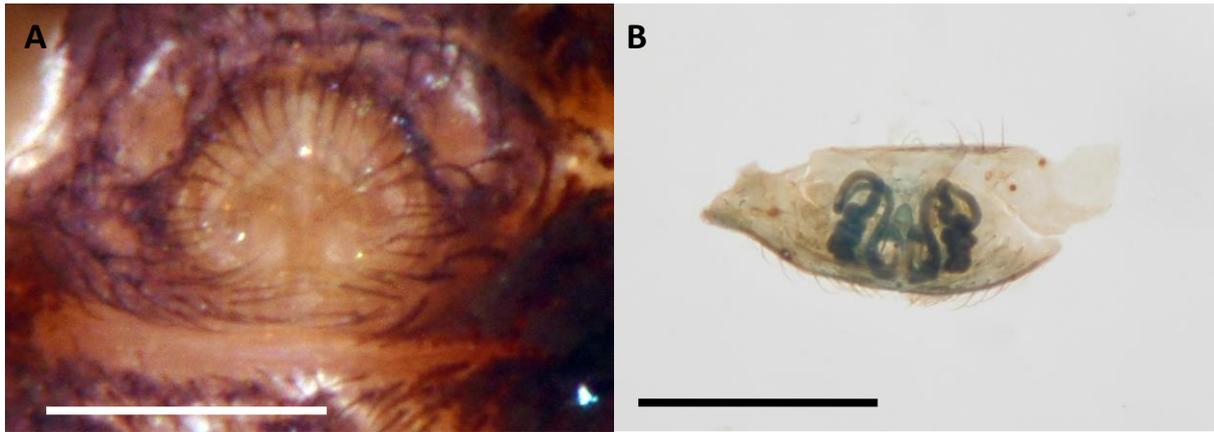


Fig. 26. Epigyne of *Cymbachina albobrunnea* (Urquhart, 1893). A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

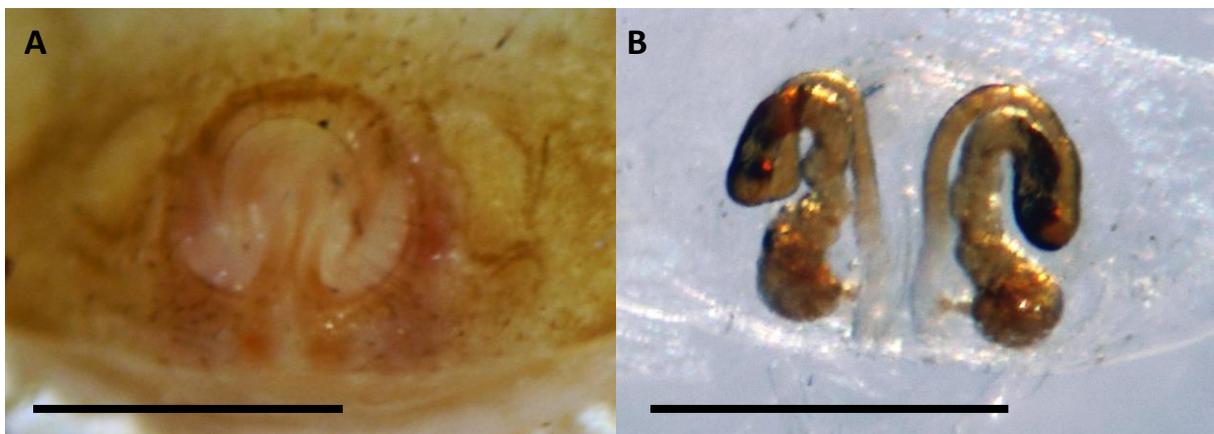


Fig. 27. Epigyne of *Cymbachina albolimbata* (L. Koch, 1875). A) Ventral external view. B) Dorsal internal view. Scale bars =0.5 mm.

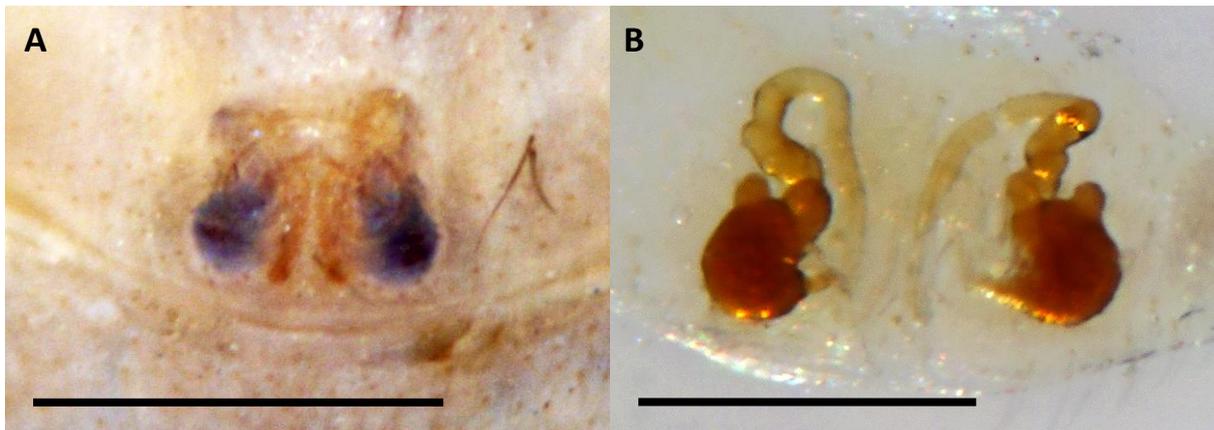


Fig. 28. Epigyne of *Cymbachina ambara* (Urquhart, 1885). A) Ventral external view. B) Dorsal internal view. Scale bar A = 0.5 mm, scale bar B = 0.25 mm.

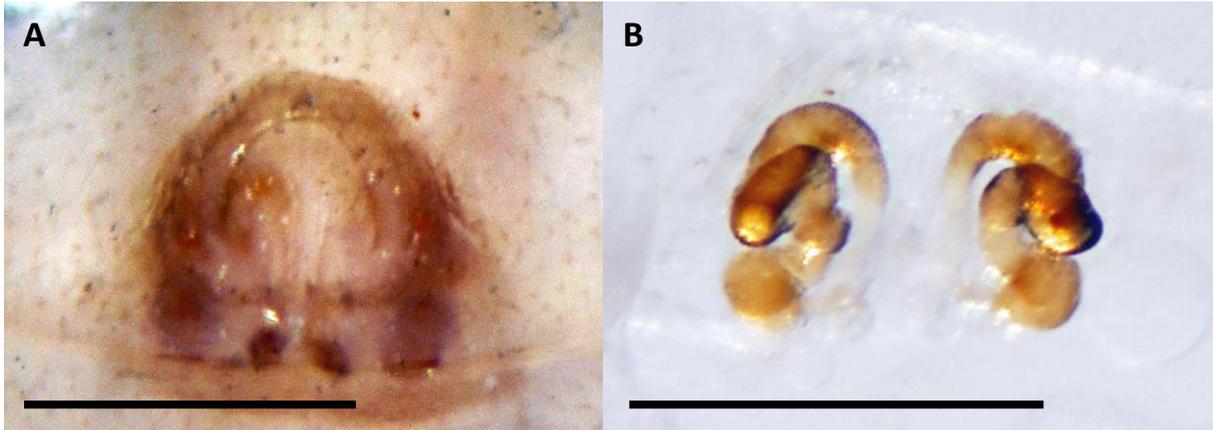


Fig. 29. Epigyne of *Cymbachina ambara* (Urquhart, 1885). A) Ventral external view. B) Dorsal internal view. Scale bars = 0.5 mm.

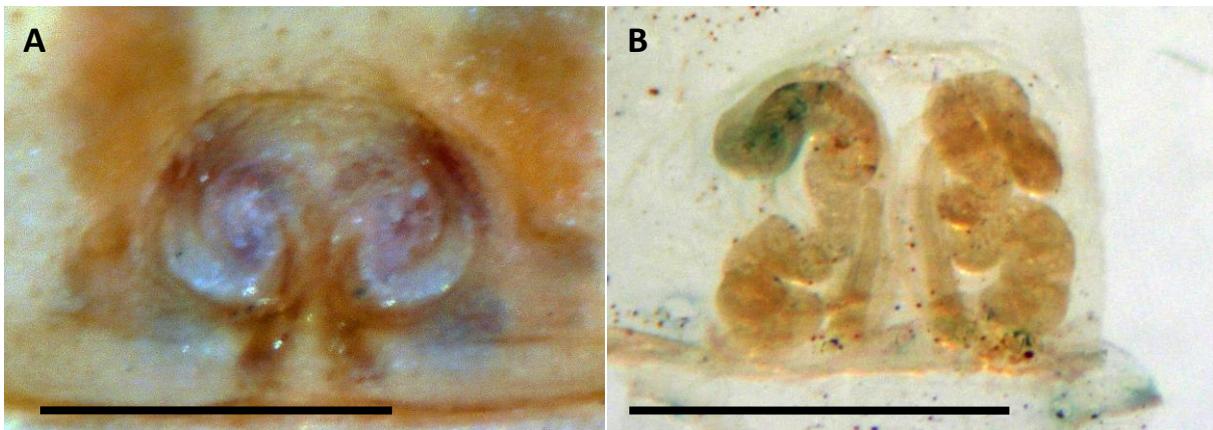


Fig. 30. Epigyne of *Cymbachina urquharti* sp. nov. A) Ventral external view. B) Dorsal internal view. Scale bars = 0.5 mm.

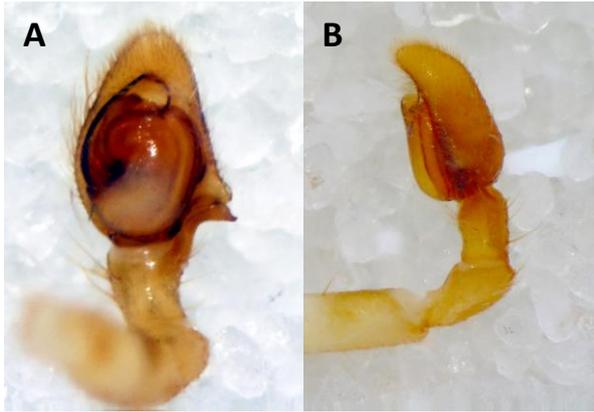


Fig. 31. Male palp of *Bryantymella angularis* (Urquhart, 1885). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.

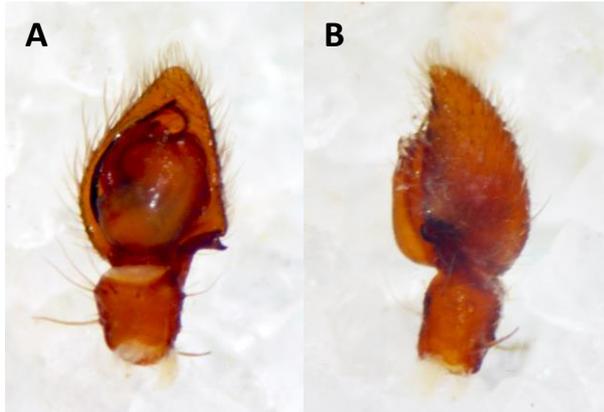


Fig. 32. Male palp of *Bryantymella thorini* sp. nov. A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.

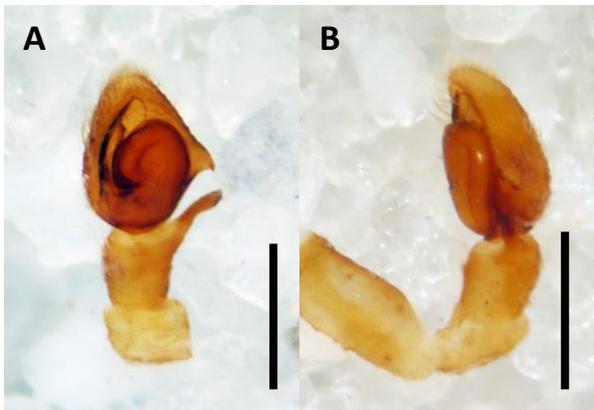


Fig. 33. Male palp of *Bryantymella angulata* (Urquhart, 1885). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.

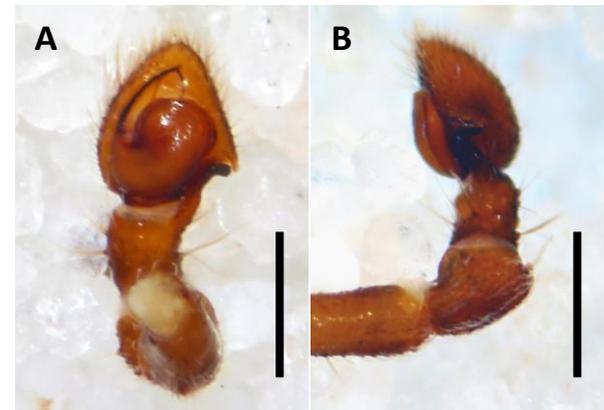


Fig. 34. Male palp of *Bryantymella brevirostris* sp. nov. A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.



Fig. 35. Male palp of *Sidymella longipes* (L. Koch, 1874). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.



Fig. 36. Male palp of *Sidymella trapezia* (L. Koch, 1874). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.

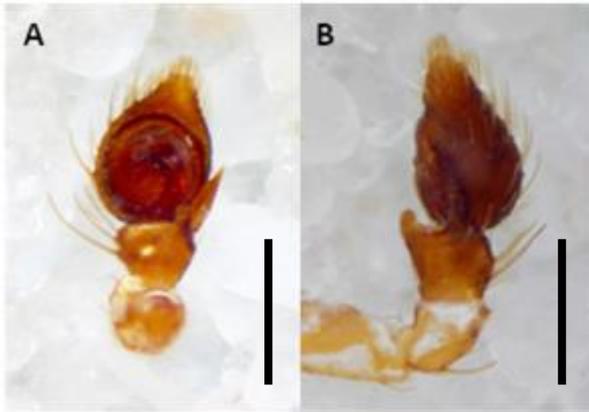


Fig. 37. Male palp of *Cymbachina albobrunnea* (Urquhart, 1893). A) Ventral view, B) Retrolateral view. Scale bars = 0.25 mm.



Fig. 38. Male palp of *Cymbachina albolimbata* (L. Koch, 1875). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.



Fig. 39. Male palp of *Cymbachina ambara* (Urquhart, 1885). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.

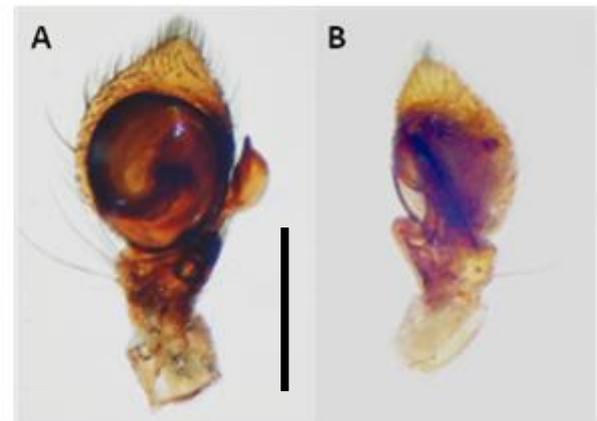


Fig. 40. Male palp of *Cymbachina sphaeroides* (Urquhart, 1885). A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.



Fig. 41. Male palp of *Cymbachina urquharti* sp. nov. A) Ventral view, B) Retrolateral view. Scale bars = 0.5 mm.



Map 1: Collection localities for *Bryantymella angularis*



Map 2: Collection localities for *Bryantymella thorini*



Map 3: Collection localities for *Bryantymella angulata*



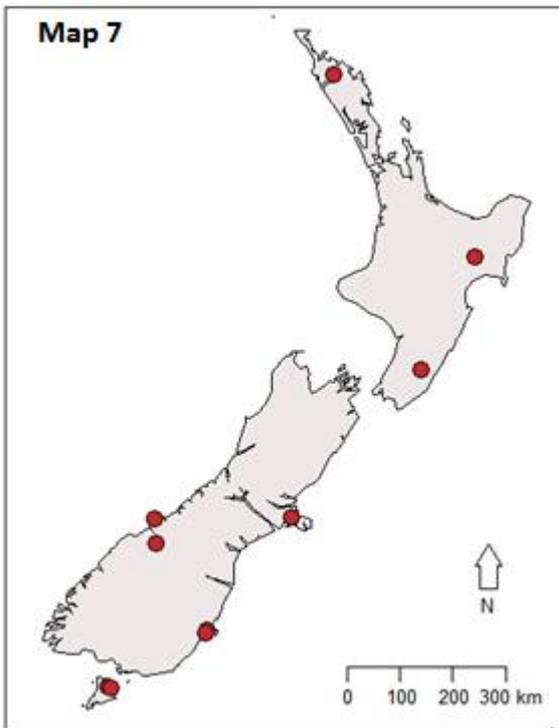
Map 4: Collection localities for *Bryantymella brevirostris*



Map 5: Collection localities for *Sidymella longipes*



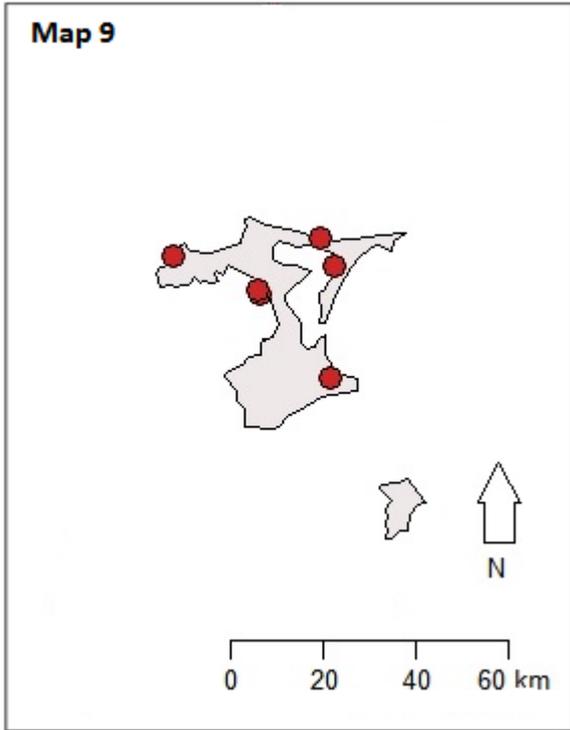
Map 6: Collection localities for *Sidymella trapezia*



Map 7: Collection localities for *Cymbachina albobrunnea*



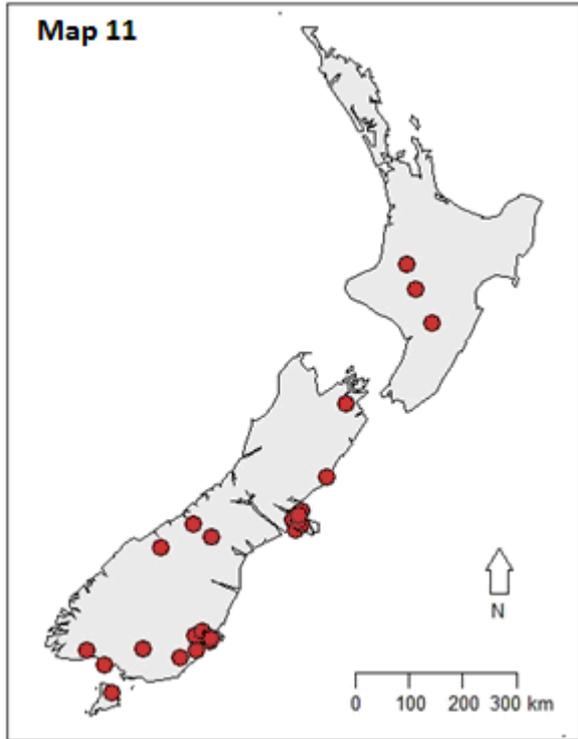
Map 8: Collection localities for *Cymbachina albolimbata* (mainland New Zealand)



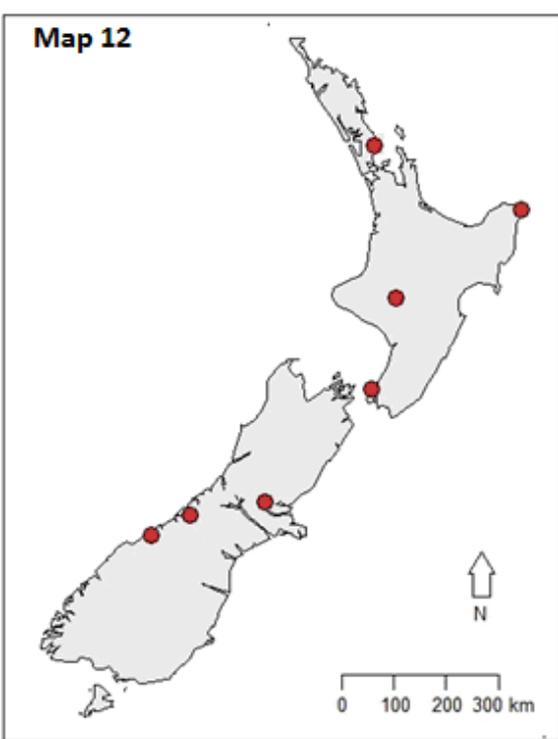
Map 9: Collection localities for *Cymbachina albolimbata* (Chatham Islands)



Map 10: Collection localities for *Cymbachina ambara*



Map 11: Collection localities for *Cymbachina sphaeroides*



Map 12: Collection localities for *Cymbachina urquharti*

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APPENDIX A: MATERIAL EXAMINED

Institutional acronyms are defined in the *Collection Repositories* subsection of *Methods and Conventions*.

Bryantmella angularis

CMNZ, Holotype, 1♀, misidentified Paralectotype 1♂ of *Sidymella angulata*, Tairua, Whangarei Harbour, 37° 01.20' S, 175° 50.40' E, T. Broun; MONZ AS.003215, 1♀, Te Pahi, North Cape, Northland, 34° 24.9468' S, 173° 01.4458' E, pit trap, O. Ball, 22 Oct. 2008; MONZ AS.003591, 1♀, Taput Hill, Te Pahi, Northland, 34° 26.527' S, 172° 42.1615' E, pit trap, O. Ball, 22 Oct. 2008; MONZ AS.003217, 1♀, Te Pahi, Darkies Ridge, Northland, 34° 27.6695' S, 172° 45.623' E, shrubland, pit trap, O. Ball, 12 Feb. 2007; MONZ AS.003216, 1♀, Te Pahi, Darkies Ridge, Northland, 34° 27.6695' S, 172° 45.623' E, shrubland, pit trap, O. Ball, 13 Apr. 2007; MONZ AS.003218, 1♀, Kerr Point Pines, Te Pahi, Northland, 34° 27.7257' S, 172° 52.962' E, pit trap, O. Ball, 14 Jul. 2006; MONZ AS.001717, 1♀, 1 juv., Matthew Reserve (Forest & Bird), near Kaitaia, Northland, 35° 09.253' S, 173° 17.507' E, regenerating puriri/kauri forest, P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010; MONZ AS.001734, 1♂, 1 juv., Mangumuka Gorge, picnic area., 35° 11.600' S, 173° 28.878' E, P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010; MONZ AS.003122, 1♂, 1♀, Tawhiti Rahi, Poor Knights Islands, 35° 27.00' S, 174° 42.60' E, I. Stringer, 15 Apr. 1996; MONZ AS.001710, 1♀, Waipoua forest, S of Tane Mahuta, Northland, 35° 36.212' S, 173° 31.937' E, kauri forest, P.J. Sirvid & B.M. Fitzgerald, 24 Mar. 2010; MONZ AS.003210, 2 juv., Waipoua forest, Northland, 35° 37.403' S, 173° 33.623' E, shrubs, beating, J. Griffiths & A.D. Blest, 13 Dec. 2003; MONZ AS.003211, 5 juv., Waipoua forest, Northland, 35° 37.403' S, 173° 33.623' E, from manuka in flower, beating, J. Griffiths, 13 Dec. 2003; MONZ AS.003209, 1 juv., Waipoua forest, Northland, 35° 37.403' S, 173° 33.623' E, beating, J. Griffiths, 14 Dec. 2003; MONZ AS.001651, 1♂, Northern end of Coronation Park (Russell Rd end), Whangarei, 35° 42.798' S, 174° 18.83' E, dry kanuka/totara/tree fern/adventive forest, P.J. Sirvid & B.M. Fitzgerald, 25 Mar. 2010; MONZ AS.001686, 1♂, 1♀, Trounson kauri Park, Northland, 35° 43.158' S, 173° 38.932' E, kauri/tree fern forest, P.J. Sirvid & B.M. Fitzgerald, 24 Mar. 2010; MONZ AS.001649, 2 juv., Kaihu Farm Hostel, Northland, 35° 45.738' S, 173° 40.410' E,

nikau/mixed forest, by creek, P.J. Sirvid & B.M. Fitzgerald, 24 Mar. 2010; MONZ AS.001650, 1♀, Kaihu Farm Hostel, Northland, 35° 45.738' S, 173° 40.410' E, nikau/mixed forest, by creek, P.J. Sirvid & B.M. Fitzgerald, 24 Mar. 2010; MONZ AS.003182, 1♂, 1♀, 7 juv., Bream Head Scenic Reserve., 35° 51.000' S, 174° 32.000' E, litter in crown of nikau and hanging dead leaves, leaf litter, B.M. Fitzgerald, 16 Oct. 2001; MONZ AS.003183, 1♀, Bream Head Scenic Reserve., 35° 51.000' S, 174° 32.000' E, litter in crown of nikau and hanging dead leaves, leaf litter, B.M. Fitzgerald, 16 Oct. 2001; MONZ AS.003220, 2♂, 5 juv., Hen Island, 35° 54.60' S, 174° 43.80' E, from shrub and fallen kanuka twigs, B.M. Fitzgerald, 19 Oct. 2001; NZAC , 1♀, 1 juv., Omeru Res., Kaipara, 36° 20' S, 174° 17' E, G. Hall, 27 Sep. 2009; MONZ AS.003592, 1♀, Lake Ototoa forest Res., valley below South Head Rd south of South Head., 36° 30.60' S, 174° 13.80' E, steep nikau/broadleaf litter Steep south-facing slope, B. Marshal & S. O'Shea, 24 Feb. 2008; OMNZ IV36643, 1♂, Kennedy Bay, Coromandel, 36° 40.20' S, 175° 33.60' E, malaise trap, H.A. Oliver, 7 Apr. 1969; OMNZ IV35954, 1♀, Riverlands Road, Kumeu, 36° 46.20' S, 174° 33.00' E, R.W. Hutton, 19 Mar. 1968; NZAC , 1♀, Kakamatua inlet, Waitakere Ranges, 37° 00' S, 174° 35.67' E, R. Hoare, 6 Jan. 2009; MONZ AS.003185, 1♂, 3 juv., Tuhua (= Mayor Island), 37° 16.80' S, 176° 15.00' E, by hand, B.M. Fitzgerald, 23 Mar. 2004; MONZ AS.003186, 1♂, 1♀, 5 juv., Tuhua (= Mayor Island), 37° 16.80' S, 176° 15.00' E, forest and scrub, on plants close to ground, by hand, B.M. Fitzgerald, 24 Mar. 2004; MONZ AS.003187, 1♀, Tuhua (= Mayor Island), 37° 16.80' S, 176° 15.00' E, forest at night, on underside of matipo leaf, by hand, B.M. Fitzgerald, 26 Mar. 2004; MONZ AS.003596, 1♀, Hamilton, 37° 46.80' S, 175° 16.20' E, B. McQuillan, Feb. 2012; MONZ AS.003597, 1♀, Hamilton, 37° 46.80' S, 175° 16.20' E, B. McQuillan, Feb. 2012; MONZ AS.003598, 1♀, Hamilton, 37° 46.80' S, 175° 16.20' E, B. McQuillan, Feb. 2012; MONZ AS.003599, 1♀, Hamilton, 37° 46.80' S, 175° 16.20' E, B. McQuillan, Feb. 2012; MONZ AS.003600, 1♀, Hamilton, 37° 46.80' S, 175° 16.20' E, B. McQuillan, Feb. 2012; MONZ AS.003601, 1♀, Hamilton, 37° 46.80' S, 175° 16.20' E, B. McQuillan, Feb. 2012; MONZ AS.003221, 1♂, Bay of Plenty, Whale Island (Moutuhora), 37° 51.000' S, 176° 58.000' E, beaten from Mariscus seed heads, beating, B.M. Fitzgerald, 29 Mar. 2005; MONZ AS.003222, 1♀, Bay of Plenty, Whale Island (Moutuhora), 37° 51.000' S, 176° 58.000' E, beaten from Mariscus seed heads, beating, B.M. Fitzgerald, 29 Mar. 2005; LUNZ , 1 juv., Mt Ngongataha, 38° 07.20' S, 176° 11.40' E, C.J. Vink, 26 May 1996; OMNZ IV36259, 1♂, 1♀, 2 juv., Purukai, 38° 36' S, 176° 13' E, under native bush canopy, malaise trap, NZ Forest inst., 31 Mar. 1977; MONZ AS.003230, 1♂, 3 juv., Control 3 site, Urewera National Park, Maranui Bay, Lake Waikaremoana, 38° 46.092' S, 177° 05.297' E, mixed

podocarp forest, beating, L.J. Boutin, 19 Nov. 1996; MONZ AS.003229, 1♂, 1♀, Lake Waikaremoana, Urewera National Park, 38° 46.20' S, 177° 04.20' E, beech forest Control 2, pit trap, G. Blackwell, 16 Feb. 1996; MONZ AS.003231, 1♂, Lake Waikaremoana, Urewera National Park, 38° 46.20' S, 177° 04.20' E, beech forest Control 2, pit trap, G. Blackwell, 16 Feb. 1996; NZAC , 1♂, Lake Waikaremoana, 38° 46.20' S, 177° 04.20' E, 7 Apr., 2005; MONZ AS.003205, 2♀, Whitecliffs, Taranaki, control line (1080 Poison study), 38° 52.80' S, 174° 32.40' E, pit trap, L. Stanley, 28 Feb. 1993; MONZ AS.003206, 1♀, Whitecliffs, Taranaki, control line (1080 Poison study), 38° 52.80' S, 174° 32.40' E, pit trap, L. Stanley, 29 Apr. 1993; MONZ AS.003204, 1♂, 1 juv., Whitecliffs, Taranaki, control line (1080 Poison study), 38° 52.80' S, 174° 32.40' E, pit trap, L. Stanley, 31 Jan. 1993; OMNZ IV36605, 1♂, 9 juv., Tuna Saddle, Taumarunui, 38° 52.80' S, 175° 15.60' E, R.R. Forster, 6 Nov. 1974; OMNZ IV36871, 1♀, Tangarakau Gorge, 38° 58.80' S, 174° 50.40' E, C.L. Wilton, 25 Feb. 1967; MONZ AS.003136, 4♂, 1 juv., Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, malaise trap, I. Stringer, 15 Apr. 2000; MONZ AS.003142, 1♂, 1 juv., Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 15 Apr. 2000; MONZ AS.003143, 1♂, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 15 Mar. 2000; MONZ AS.003139, 1♂, 1♀, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Apr. 2000; MONZ AS.003140, 1♂, 1♀, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Apr. 2000; MONZ AS.003137, 1♀, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Mar. 2000; MONZ AS.003138, 2♂, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Mar. 2000; MONZ AS.003141, 1♂, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Mar. 2000; MONZ AS.003144, 1♂, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Mar. 2000; MONZ AS.003147, 1♀, Tongariro National Park, south of Erua, 39° 15.012175' S, 175° 23.57448' E, pit trap, I. Stringer, 5 Mar. 2000; OMNZ IV36884, 2♀, Mt Egmont/Taranaki, 39° 17.40' S, 174° 03.60' E, C.L. Wilton, 24 Feb. 1967; MONZ AS.003145, 8♂, 2 juv., Tongariro National Park, 39° 17.45' S, 175° 26.05' E, I. Stringer, 5 Mar. 2000; MONZ AS.003123, 1♀, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, malaise trap, I. Stringer, 14 Jun. 2000; MONZ AS.003124, 1♀, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, malaise trap, I. Stringer, 14 Jun. 2000; MONZ AS.003125, 6♂, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E,

malaise trap, I. Stringer, 15 Apr. 2000; MONZ AS.003129, 1♂, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, pit trap, I. Stringer, 15 Apr. 2000; MONZ AS.003184, 4♂, 1♀, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, malaise trap, I. Stringer, 15 Apr. 2000; MONZ AS.003126, 2♂, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, malaise trap, I. Stringer, 5 Mar. 2000; MONZ AS.003127, 1 juv., Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, pit trap, I. Stringer, 5 Mar. 2000; MONZ AS.003128, 1 juv., Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, pit trap, I. Stringer, 5 Mar. 2000; MONZ AS.003148, 1♀, Tongariro National Park, east of Horopito, 39° 21.65110' S, 175° 22.86603' E, pit trap, I. Stringer, 9 Aug. 2000; MONZ AS.003134, 1♂, Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, pit trap, I. Stringer, 10 Aug. 2000; MONZ AS.003135, 1 juv., Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, pit trap, I. Stringer, 10 Aug. 2000; MONZ AS.003146, 1♀, Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, pit trap, I. Stringer, 10 Aug. 2000; MONZ AS.003133, 1♂, Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, pit trap, I. Stringer, 15 Apr. 2000; MONZ AS.003130, 1♀, Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, malaise trap, I. Stringer, 15 Jun. 2000; MONZ AS.003132, 1♀, Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, malaise trap, I. Stringer, 15 Jun. 2000; MONZ AS.003131, 1♂, Tongariro National Park, east of Horopito, 39° 22.028617' S, 175° 22.91400' E, malaise trap, I. Stringer, 17 Apr. 2000; OMNZ IV36048, 5♂, Vinegar Hill Reserve, 39° 55.20' S, 175° 37.20' E, R.R. Forster, 6 Jan. 1967; MONZ AS.003223, 1♀, Bruce Park Scenic Reserve, 39° 57.60' S, 175° 31.20' E, rimu forest, beating, B.M. Fitzgerald, 14 May 2007; MONZ AS.003224, 1♂, Bruce Park Scenic Reserve, 39° 57.60' S, 175° 31.20' E, rimu forest, beating, B.M. Fitzgerald, 14 May 2007; MONZ AS.003189, 1♂, 1 juv., Atiwhakatu Valley and Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 1 Jan. 1973; MONZ AS.003191, 5♂, Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 16 Jan. 1973; MONZ AS.003195, 3♂, Atiwhakatu Valley and Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 16 Jan. 1974; MONZ AS.003193, 1♂, Bush near Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 22 Dec. 1973; MONZ AS.003188, 1♀, Bush near Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, leafmould, pit trap, C.L. Wilton, 31 Jul. 1972; MONZ AS.003194, 1♂, Bush near

Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 5 Jan. 1974; MONZ AS.003190, 2♂, 1♀, Bush near Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 6 Feb. 1973; MONZ AS.003192, 1♀, Bush near Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, pit trap, C.L. Wilton, 7Dec. 1973; MONZ AS.003196, 1♂, 1♀, 1 juv., Atiwhakatu Valley and Holdsworth Lodge, Tararua forest Park, Wairarapa, 40° 54.290' S, 175° 28.340' E, C.L. Wilton, 8Feb. 1974; MONZ AS.003620, 1♂, Kaitoke Regional Park, 41° 04.13995' S, 175° 11.0067' E, pit trap, R. Barbieri, 10 Mar. 2011; MONZ AS.003621, 1♀, Kaitoke Regional Park, 41° 04.2383' S, 175° 10.95' E, pit trap, R. Barbieri, 28 Feb. 2011; MONZ AS.004062, Silverstream, Keith George Memorial Park, 41° 08.33' S, 175° 00.37' E, 1 Nov. 2011; MONZ AS.003213, 1♂, 1 Lincoln Street, Brooklyn, Wellington, 41° 10.000' S, 174° 20.000' E, A.D.B. Tennyson, 12 Apr. 2012; MONZ AS.003212, 1♂, 1 Lincoln Street, Brooklyn, Wellington, 41° 10.000' S, 174° 20.000' E, in house, A.D.B. Tennyson, 22 Feb. 2001; MONZ AS.003198, 1♀, 44 Raukawa St, Stokes Valley, WN, 41° 11.20' S, 174° 58.77' E, inside house, by hand, B.M. Fitzgerald, 14 Apr. 2103; MONZ AS.003197, 1♀, 44 Raukawa St, Stokes Valley, WN, 41° 11.20' S, 174° 58.77' E, on flower at night, by hand, B.M. Fitzgerald, 21 Mar. 1995; MONZ AS.003199, 1 juv., 44 Raukawa St, Stokes Valley, WN, 41° 11.20' S, 174° 58.77' E, in garden, by hand, B.M. Fitzgerald, 30 Mar. 1997; MONZ AS.003587, 1♀, 44 Raukawa St, Stokes Valley, 41° 11.20' S, 174° 58.77' E, in garden in litter, B.M. Fitzgerald, 5 Apr. 2009; OMNZ IV36286, 1♂, Oparara, 41° 12.60' S, 172° 07.20' E, R.R. Forster, 22 Sep. 1966; OMNZ IV36601, 1♀, Ruby Bay, 41° 13.80' S, 173° 04.80' E, C.L. Wilton, 12 Mar. 1967; MONZ AS.003214, 1♀, Allports Island, Queen Charlotte Sound, 41° 13.80' S, 174° 03.00' E, pit trap, Murphy, E, Nov. 1986; MONZ AS.003219, 1♂, 1♀, Otari-Wilton's Bush, Wellington, 41° 16.020' S, 174° 45.000' E, pit trap, 23 Mar. 2007; MONZ AS.003228, 1♀, 26 Sunshine Ave, Karori, Wellington, 41° 17.08' S, 174° 43.58' E, on outside porch, P.J. Sirvid, Mar. 2001; MONZ AS.003226, 1♂, 26 Sunshine Ave, Karori, Wellington, 41° 17.08' S, 174° 43.58' E, inside bathroom, P.J. Sirvid, 15 Feb. 2001; MONZ AS.003227, 1♂, 26 Sunshine Ave, Karori, Wellington, 41° 17.08' S, 174° 43.58' E, inside bathroom, P.J. Sirvid, 15 Feb. 2001; MONZ AS.003225, 1♀, 26 Sunshine Ave, Karori, Wellington, 41° 17.08' S, 174° 43.58' E, inside bathroom, P.J. Sirvid, 6 Mar. 2000; MONZ AS.003163, 1♀, 4♂, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, silver beech forest, B.M. Fitzgerald, 1993; MONZ AS.003175, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, 17 May 1994; MONZ AS.003169, 1♀, 2 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174°

54.000' E, hard beech forest, P. Berben & J. Alley, Dec. 1994; MONZ AS.003180, 1♂, 2♀, 2 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Feb. 1994; MONZ AS.003171, 2♀, 5 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Feb. 1995; MONZ AS.003172, 4♂, 3 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Feb. 1996; MONZ AS.003149, 1♂, 1 juv., Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, broadleaf-podocarp forest, A. Moeed & M.J. Meads, Jan. 1976; MONZ AS.003170, 1♂, 5 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Jan. 1995; MONZ AS.003177, 2♂, 1♀, 8 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Jan. 1996; MONZ AS.003181, 2♀, 8 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Mar. 1995; MONZ AS.003173, 3♂, 2 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, Mar. 1996; MONZ AS.003176, 1♂, 3 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, P. Berben & J. Alley, May 1995; MONZ AS.003156, 1 juv., Orongorongo Valley, Wellington, Station Ridge, silver beech forest, 41° 25.000' S, 174° 54.000' E, silver beech forest, B.M. Fitzgerald, 1 Feb. 1992; MONZ AS.003201, 1♂, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, silver beech, pitfall trap, B.M. Fitzgerald, 1 Mar. 1992; MONZ AS.003178, 2♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 14 Apr. 1994; MONZ AS.003159, 4♂, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, silver beech forest, B.M. Fitzgerald, 14 Feb. 1992; MONZ AS.003202, 1♂, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Apr. 1993; MONZ AS.003168, 3 juv., Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, silver beech forest, pit trap, P. Berben & J. Alley, 15 Apr. 1995; MONZ AS.003164, 1♂, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Feb. 1993; MONZ AS.003157, 1♂, Station Ridge, Orongorongo Valley, Wellington., 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Feb. 1994; MONZ AS.003158, 3♂, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Jan. 1992; MONZ AS.003200, 1♂, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Jan. 1992; MONZ AS.003161, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Jun. 1992; MONZ AS.003165, 5♂, Orongorongo Valley,

Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Mar. 1993; MONZ AS.003166, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Nov. 1993; MONZ AS.003167, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 15 Nov. 1993; MONZ AS.003160, 3♂,1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 16 Mar. 1992; MONZ AS.003179, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 16 Nov. 1992; MONZ AS.003162, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, hard beech forest, B.M. Fitzgerald, 16 Sep. 1992; MONZ AS.003203, 1♀, Orongorongo Valley, Wellington, 41° 25.000' S, 174° 54.000' E, mixed podocarp-hardwood forest under rock, by hand, B.M. Fitzgerald, 21 Jan. 1994; MONZ AS.003154, 1♀, Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, A. Moeed & M.J. Meads, 24 Aug. 1985; MONZ AS.003150, 1♂, Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, A. Moeed & M.J. Meads, 24 Feb. 1981; MONZ AS.003152, 1♂, Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, A. Moeed & M.J. Meads, 25 Feb. 1984; MONZ AS.003153, 1♂, Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, A. Moeed & M.J. Meads, 25 Feb. 1984; MONZ AS.003174, 1♀, Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, A. Moeed & M.J. Meads, 25 Jan. 1984; MONZ AS.003151, 1♂, 1♀, Orongorongo Valley Field Station, Wellington, 41° 25.000' S, 174° 54.000' E, A. Moeed & M.J. Meads, 26 Mar. 1983; MONZ AS.003155, 1♂, 1 juv., Orongorongo Valley Field Station, Wellington, Green's Stream, Doll's House, 41° 25.000' S, 174° 54.000' E, under rocks, B.M. Fitzgerald, 31 Jan. 1995; OMNZ IV36042, 1♂, Washout Creek, Upper Buller Gorge, 41° 41.40' S, 172° 34.20' E, C.L. Wilton, 12 Feb. 1969; OMNZ IV36606, 1♂, Long Creek, Hapuka River, Kaikoura, 42° 17.40' S, 173° 39.00' E, 26 Dec. 1974; MONZ AS.002548, 1♀, 1 juv., Lake Matheson, Westland, 43° 26.622' S, 169° 58.112' E, G.W. Gibbs, 14 Feb. 2010; MONZ AS.003589, 1♀, Lake Matheson, Westland, 43° 26.622' S, 169° 58.112' E, G.W. Gibbs, 14 Feb. 2010; OMNZ IV36869, 1♀, Saltwater Creek, South Westland, 43° 27.00' S, 169° 45.00' E, R.R. Forster & C.L. Wilton, 29 Sep. 1966; MONZ AS.003622, 1♂, Banks Peninsula, Tutakakahikura Scenic Res., 43° 51.20' S, 172° 59.12' E, C.J. Vink, N. Head & H. Schneider, 20 Feb. 2009; OMNZ IV36566, 1♂, 1 juv., Deep Cove, Manapouri, 45° 26.40' S, 167° 08.40' E, caught with light at night, R.R. Forster, 25 Jan. 1958; OMNZ IV36535, 4♂, 2 juv., Deep Cove, Manapouri, 45° 26.40' S, 167° 08.40' E, R.R. Forster, 25 Jan. 1958; OMNZ IV36502, 1♀, Fraser's Gully, Dunedin, 45° 45.000' S, 170° 19.000' E, C.L.

Wilton, 31 Oct. 1965; OMNZ IV38148, 9♂, 2♀, Swampy Spur, Otago, 45° 48.0000' S, 170° 30.0000' E, A.C. Harris, 19 Mar. 1980; OMNZ IV36600, 1♂, Leith Saddle, 45° 50.00' S, 170° 30.000' E, R.R. Forster, 15 Mar. 1977; MONZ AS.003232, 1♀, Waitutu Bush, Southland, 46° 11.40' S, 167° 06.00' E, beech forest Control 2, C. Rufaut, Feb. 2003; OMNZ IV38142, 1♂, 2 juv., Fern Gully, Stewart I., 46° 53.40' S, 168° 05.40' E, R.R. Forster, 9 Mar. 1986; OMNZ IV366045, 1♂, 1♀, Oban, Stewart I., 46° 53.40' S, 168° 06.00' E, C.L. Wilton, 23 Feb. 1972; OMNZ IV36139, 1♂, 3♀, 6 juv., Oban, Stewart I., 46° 53.40' S, 168° 06.00' E, A.C. Harris, 29 Mar. 1975; MONZ AS.003208, 1♂, 9 juv., Port Pegasus Camp, Southern Stewart Island, 47° 12.60' S, 167° 41.40' E, in coprosma and manuka, beating, L.C. Hudson, 21 Feb. 1972; MONZ AS.003207, 1♂, Ridge west of camp, Port Pegasus, southern Stewart Island, 47° 12.60' S, 167° 41.40' E, collected at night, F.M. Climo, 22 Feb. 1972.

Bryantymella thorini

MONZ AS.003611, Holotype, 1♂, Waimea River, 41° 18.633' S, 173° 07.728' E, in grass, C.J. Vink & S.J. Crampton, 23 Mar. 2009; MONZ AS.001720, 1 juv., Matthew Reserve (Forest & Bird), near Kaitaia, Northland, 35° 09.253' S, 173° 17.507' E, regenerating puriri/kauri forest., P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010; OMNZ IV36259, 1♂, 1♀, 2 juv., Purukai, 38° 36' S, 176° 13' E, under native bush canopy, malaise trap, NZ Forest Inst., 31 Mar. 1977; LUNZ, 1 juv., Nr Nth Egmont Chalet, 39° 08.40' S, 174° 08.40' E, C.J. Vink, 24 May 1996; MONZ AS.003595, 2♀, 44 Raukawa St, Stokes Valley, 41° 10.80' S, 174° 58.80' E, by hand, in garden, B.M. Fitzgerald, 30 Dec. 2007; MONZ AS.004041, 1♀, 44 Raukawa St, Stokes Valley, 41° 11.20' S, 174° 58.77' E, in leaf litter in garden, B.M. Fitzgerald, 11 Dec. 2012; MONZ AS.004042, 1♀, 44 Raukawa St, Stokes Valley, 41° 11.20' S, 174° 58.77' E, in leaf litter in garden, B.M. Fitzgerald, 23 Nov. 2012; MONZ AS.004046, 1♀, 44 Raukawa St, Stokes Valley, 41° 11.20' S, 174° 58.77' E, in leaf litter in garden, B.M. Fitzgerald, 7 Dec. 2012; MONZ AS.004040, 1♀, 44 Raukawa St, Stokes Valley, 41° 11.20' S, 174° 58.77' E, in leaf litter in garden, B.M. Fitzgerald, 9 Dec. 2012; MONZ AS.004058, 1♂, Iwituaroa Reserve, Queen Charlotte Sound, 41° 15.60' S, 173° 55.20' E, pit trap, C. Grose & B.M. Fitzgerald, Apr. 1997; MONZ AS.003611, 1♂, Waimea River, 41° 18.633' S, 173° 07.728' E, in grass, C.J. Vink & S.J. Crampton, 23 Mar. 2009; LUNZ, 1♀, Nr St Arnaud ice skating pond, 41° 47.40' S, 172° 50.40' E, C.J. Vink, 9 Feb. 1997; MONZ AS.004039, 1♂, Bluff Station, Clarence, Kaikoura, 42° 00.00' S, 173° 59.40' E, Department of Conservation [Wellington Conservancy Office], 12 Feb. 2005; NZAC, 2♂, 3 juv., Reefton, 42° 06.60' S, 171° 51.60' E, pit trap in pine forest, J.A. Wightman, 12 Apr. 1997; LUNZ, 1♀, Mt Fyffe Forest, nr Hinau Tk, 42° 18.60' S,

173° 36.60' E, C.J. Vink & S.J. Crampton, 3 Jul. 1995; OMNZ IV36859, 1♀, 5 miles W. of Otira, 42° 52.27' S, 171° 33.408', A.D. Blest, 30 Sep. 1966; LUNZ, 1♀, Lords Bush, Springfield, 43° 20.000' S, 171° 56.00' E, A.E. Singleton, 25 Apr. OMNZ IV36573, 1♀, Franz Josef, nr glacier, 43° 29.00' S, 170° 12.00' E, under stones, B.J. Marples, 6 Dec.1955; LUNZ, 1♂, Beckenham, Christchurch, 43° 33.60' S, 172° 38.40' E, C.J. Vink & M.A. Hudson, 7 Nov. 1999; OMNZ IV36581, 1♀, Staveley, 43° 39.00' S, 171° 26.40' E, C.L. Wilton, 20 Feb. 1972; LUNZ, 1♀, Hinewai Res., Banks Peninsula, 43° 50.72' S, 173° 03.810' E, in toitoi litter, C.J. Vink, 27 Aug. 1996; OMNZ IV36627, 1♀, Macrae's Flat, 45° 23.000' S, 170° 26.00' E, C.L. Wilton, 16 Dec. 1974; MONZ AS.002550, 1♂, Glenkraeg, Rock and Pillar Range, Otago, 45° 26' S, 170° 05' E, C. Rufaut, 2000; OMNZ IV36623, 1♀, W. of Middlemarch, 45° 30.000' S, 170° 01.00' E, matagouri scrub, 800m, J. Child, 16 Nov. 1968; OMNZ IV35965, 1 juv., Piano Flat, 45° 34.20' S, 169° 00.00' E, R.R. Forster, 13 Dec. 1981; OMNZ IV38163, 1♀, Millar's Flat, 45° 39.000' S, 169° 23.000' E, sown tussock, 500m, B.I.P. Barratt, 13 Oct. 1978; OMNZ IV38148, 1♂, Swampy Spur, Otago, 45° 48.00' S, 170° 30.00' E, A.C. Harris, 19 Mar. 1980; OMNZ IV38171, 1♂, Waipori, 45° 49.20' S, 169° 52.80' E, burnt tussock, 520m, ex pitfall, B.I.P. Barratt, 16 Feb. 1979; OMNZ IV38514, 4♀, 1 juv., Waipori, 45° 49.20' S, 169° 52.80' E, burnt tussock, 520m, ex pitfall, B.I.P. Barratt, 19 Dec. 1978; OMNZ IV36610, 1♀, Flagstaff, Dunedin, 45° 49.80' S, 170° 27.60' E, R.R. Forster, 27 Sep. 1975; OMNZ IV36343, 1 juv., Flagstaff, Dunedin, 45° 49.80' S, 170° 27.60' E, R.R. Forster, 4 Nov. 1978; OMNZ IV36350, 1♀, Flagstaff, Dunedin, 45° 49.80' S, 170° 27.60' E, R.R. Forster, 4 Nov. 1978; OMNZ IV36616, 1♀, Leith Saddle, 45° 50.00' S, 170° 30.00' E, R.R. Forster, 10 Dec. 1974; OMNZ IV36492, 1♀, Allan's Beach, 45° 52.77' S, 170° 41.370' E, sand hills, C.L. Wilton, 6 Nov. 1965; OMNZ IV36536, 1♀, Orepuki, 46° 17.000' S, 167° 44.000' E, R.R. Forster, 9. May 1949; LUNZ, 4♀, Otatara Scenic Res., 46° 26' S, 168° 18' E, in grass at bush edge, C.J. Vink, 3 Feb. 2000; OMNZ IV36485, 1♀, Catlins Highway, nr Puketiro Rd Junction, 46° 29.48' S, 169° 30.17' E, R.R. Forster, 31 Aug. 1966; OMNZ IV36642, 1♂, 1♀, 1 juv., Bluff, 46° 36.00' S, 168° 19.80' E, C.L. Wilton, 10 Mar. 1970; OMNZ IV36139, 1♀, Oban, Stewart I., 46° 53.40' S, 168° 06.00' E, A.C. Harris, 29 Mar. 1975; LUNZ, 2♀, Deep Stream, 11 Jan. 2005.

Bryantymella angulata

CMNZ, Lectotype, 1♀, Whangarei Harbour, 37° 01.20' S, 175° 50.40' E, T. Broun; NZAC, 1♀, Tasman Valley, Three Kings I., 34° 09.60' S, 172° 04.20' E, G. Kuschel, 18 Nov. 1970; NZAC, 3♀, 3 juv., East end of Great King I., Three Kings Is, 34° 09.60' S, 172° 06.60' E, E.S. Gourlay, Jan. 1963; MONZ AS.001718, 1 juv., Matthew

Reserve (Forest & Bird), near Kaitaia, Northland, 35° 09.253' S, 173° 17.507' E, regenerating puriri/kauri forest, P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010; NZAC, 1♂, Tawhiti Rahi I., Poor Knights Is., 35° 27.00' S, 174° 42.60' E, sifted litter, by track near lighthouse, G. Kuschel, 8 Dec. 1980; NZAC, 1♂, Parakao, 35° 42.60' S, 173° 57.00' E, leaf litter, R.A. Cumber, 19 Oct. 1962; MONZ AS.001653, 2♀, Northern end of Coronation Park (Russell Rd end), Whangarei, 35° 42.798' S, 174° 18.83' E, dry kanuka/totara/tree fern/adventive forest, P.J. Sirvid & B.M. Fitzgerald, 25 Mar. 2010; OMNZ IV36233, 1♂, 1♀, Nr Kaitoke, Northland, 36° 13.80' S, 175° 28.20' E, toi toi litter, A.D. Blest, 6 Feb. 1994; MONZ AS.002549, 2♀, 2 juv., Red Mercury Island, Mercury Islands, 36° 37.80' S, 175° 55.80' E, beaten from *Muehlenbeckia* and reared out, B.M. Fitzgerald, 27 Nov. 1998; NZAC, 1♀, Motuhoropapa I., Noises Is, 36° 41.40' S, 174° 57.60' E, J.S. Dugdale, 19 Feb. 1978; NZAC, 1♂, Onetangi Res., Waiheke I., 36° 47.10' S, 175° 03.97' E, P.A. Maddison, 27 Oct. 1984; NZAC, 1♀, Mt Albert, Auckland, 36° 52.80' S, 174° 43.20' E, beating shrubs, G. Hall, 14 Jun. 1991; MONZ AS.002547, 1♀, Waharau Regional Park, Hunua Ranges, Auckland, 37° 02.40' S, 175° 15.00' E, ex fern fronds at night, D. Seldon, 13 Mar. 2010; MONZ AS.003610, 1♀, 1 juv., Waharau Regional Park, Hunua Ranges, Auckland, 37° 02.40' S, 175° 15.00' E, ex fern fronds at night, D. Seldon, 13 Mar. 2010; NZAC, 1♀, Thames Estuary, Tahuna Torea, 37° 10.000' S, 175° 32.000' E, litter, D. Russell, 13 Oct. 1983; NZAC, 1♀, Onewhero, 37° 19.80' S, 174° 54.60' E, lichen, K. Walter, 19 Mar. 1985; NZAC, 1♂, Onewhero, 37° 19.80' S, 174° 54.60' E, *Beilschmiedia tarairi* forest, malaise trap, R.A. Galbreath & S. Grant, 23 Feb. 1985; NZAC, 1♂, Onewhero, 37° 19.80' S, 174° 54.60' E, moss in *Beilschmiedia tarairi* forest, malaise trap, R.A. Galbreath & S. Grant, 8 Apr. 1985; NZAC, 1♂, Te Araroa, Lighthouse Tk, 37° 25' S, 178° 19' E, G.Hall, R. Hoare, T. Buckley & D. Seldon, 1 Dec. 2009; NZAC, 1♀, 1 juv., Lottin Pt Rd, Waenga Bush, Otanga, 37° 33.00' S, 178° 09.00' E, beating at night, G. Hall, 16 Sep. 1992; NZAC, 1♀, Waenga Bush, Otanga, 37° 33.00' S, 178° 09.00' E, J.S. Dugdale, 16 Sep. 1992; NZAC, 1♀, 1 juv., Rereauira swamp, 37° 33.60' S, 178° 01.80' E, malaise trap, J.S. Dugdale, 9 Mar. 1993; MONZ AS.003608, 1♂, East Cape, 37° 41.433' S, 178° 32.768' E, litter, C.J. Vink, 28 Feb. 2012; OMNZ IV36594, 1♀, Matamata, 37° 48.00' S, 175° 46.20' E, D.J. Court, 26 Dec. 1983; MONZ AS.004048, 1♂, 1♀, Bay of Plenty, Whale Island (Moutuhora), 37° 51.000' S, 176° 58.000' E, B.M. Fitzgerald, 2 Feb. 1999; OMNZ IV36191, 2♂, 1♀, 3 juv., Lake Rotehu, nr Hongi's Track, 38° 01.20' S, 176° 31.20' E, C.L. Wilton, 4 Dec. 1969; OMNZ IV35947, 1♂, Aniwanuiwa, Waikaremoana, 38° 44.40' S, 177° 09.60' E, R.W. Hutton, 21 Oct. 1966; NZAC, 1♀, Orate Forest, Te Puia Hut, 39° 10.20' S, 176° 24.00' E, beating *Dacrydium* branch trap, J.S. Dugdale, 8 Apr. 1993; OMNZ

IV36879, 1♂, Okato, 39° 11.40' S, 173° 52.20' E, C.L. Wilton, 23 Feb. 1967; NZAC, 1♂, 1♀, Munroe's Bush, Palmerston North, 40° 21.00' S, 175° 36.60' E, malaise trap, P. Watt, Mar. 1981; OMNZ IV36761, 1♀, Greville Harbour, Nelson, 40° 49.80' S, 173° 47.40' E, cliff face, M. Williams, 28 Aug. 1960; OMNZ IV36035, 1♂, Mikimiki, 40° 50.40' S, 175° 36.00' E, C.L. Wilton, 14 Sep. 1967; OMNZ IV36722, 1♀, Kapiti I., 40° 51.00' S, 174° 52.20' E, R.R. Forster, Apr. 1947; OMNZ IV36763, 2♂, 5 juv., Waikanae, 40° 51.60' S, 175° 00.00' E, R.R. Forster, 6 Jun. 1943; OMNZ IV36472, 1♀, Solway, 40° 57.60' S, 175° 36.60' E, C.L. Wilton, 28 Aug. 1967; OMNZ IV36539, 1♀, Solway, 40° 57.60' S, 175° 36.60' E, R.W.Hutton, 29 Jun. 1966; MONZ AS.002380, 1♀, Mana Island (2011 Bioblitz), 41° 04.80' S, 174° 45.60' E, P.J. Sirvid, 25 Feb. 2011; MONZ AS.003604, 1♀, 44 Raukawa St, Stokes Valley, WN, 41° 10.80' S, 174° 58.80' E, in garden, B.M. Fitzgerald, 11 Dec. 2005; MONZ AS.003014, 1♂, 1 juv., Maitu/Somes Island, Wellington Harbour, 41° 15.00' S, 174° 50.40' E, beaten from trackside vegetation, P.J. Sirvid & R.L. Palma, 13 Nov. 2012; MONZ AS.003588, 1♀, 57 Rona St, Rona Bay, Eastbourne, Wellington, 41° 17.000' S, 174° 46.000' E, beaten from ferns, P.J. Sirvid, 3 Mar. 2005; MONZ AS.003613, 1♀, 57 Rona St, Rona Bay, Eastbourne, Wellington, 41° 17.000' S, 174° 46.000' E, beaten from ferns, P.J. Sirvid, 3 Mar. 2005; MONZ AS.004060, 1♀, Butterfly Creek, 41° 20.000' S, 174° 53.000' E, L.J. Boutin, 9Dec. 1996; OMNZ IV36498, 1♀, Okaratahi Bridge, N. of Conway R., 42° 24.60' S, 173° 15.60' E, C.L. Wilton, 22 Sep. 1967; OMNZ IV36617, 1♀, Fox Glacier, 43° 27.60' S, 170° 00.60' E, unknown, unknown; OMNZ IV38203, 2♂, Dean's Bush, Christchurch, 43° 32.000' S, 172° 36.000' E, ? Halldane & J.S. Dugdale, 19 Dec. 1949; OMNZ IV36190, 1♂, Riccarton Bush, Christchurch, 43° 32.000' S, 172° 36.000' E, R.R. Forster, 29 Jan. 1968; OMNZ IV36729, 1♂, 1♀, Riccarton Bush, Christchurch, 43° 32.000' S, 172° 36.000' E, R.R. Forster, 29 Jan. 1968; OMNZ IV36640, 1♀, Taumaka I., Open Bay Is, 43° 51.00' S, 168° 52.20' E, D.S. Horning, 20 Aug. 1970; OMNZ IV36248, 1 juv., Silver I., 44° 27.00' S, 169° 19.80' E, kanuka, litter, 9 Mar. 1997; NZAC, 1♂, 1 juv., Secretary I., 45° 13.80' S, 166° 55.20' E, beating astelia, C.F. Butcher, 18 Mar. 1984; MONZ AS.003612, 1♀, Opoho Bush, Dunedin, 45° 51.50' S, 170° 32.50' E, M. Wakelin, 1 Feb. 2011; OMNZ IV36308, 1♂, Brighton Beach, Dunedin, 45° 56.40' S, 170° 19.20' E, R.R. Forster, Feb. 1991; OMNZ IV36473, 1♂, Bull Creek, 45° 58.80' S, 170° 07.20' E, bush, R.W.Hutton & C.L. Wilton, 14 May 1967; NZAC, 1♀, 6 juv., Cannibal Bay, E. of Owaka, 46° 28.20' S, 169° 45.00' E, sifted kelp, debris and plants, G. Kuschel, 14 Jan. 1978; NZAC, 1♂, Cannibal Bay, E. of Owaka, 46° 28.20' S, 169° 45.00' E, sifted litter, G. Kuschel, 18 Jan. 1978; OMNZ IV36642, 1♂, 1♀, 5 juv., Bluff, 46° 36.00' S, 168° 19.80' E, C.L. Wilton, 10 Mar. 1970; OMNZ IV36591, 2♀, 1 juv.,

Oban, Stewart I., 46° 53.40' S, 168° 06.00' E, C.L. Wilton, 23 Feb. 1972; OMNZ IV36207, 1♂, 4♀, 2 juv., Aker's Pt, Stewart I., 46° 53.40' S, 168° 09.60' E, R.R. Forster, 24 Nov. 1946.

Bryantymella brevisrostris

LUNZ, Holotype 1♂, Three Kings Is, South West I., 34° 10.20' S, 172° 04.20' E, ex litter under puka forest, south west slope. A. Booth, 5 Apr. 2000; NZAC, 20 juv., Tasman Valley, Great I., Three Kings Is. , 34° 05' S, 172° 05' E, sifting leaf litter and in rotten wood, T. Buckley & R. Leschen, 10 Nov. 2008; MONZ AS.001473, 1 juv., Te Paki, Kohuronaki, Northland, 34° 29.4658' S, 172° 50.2647' E, pit traps, O. Ball, 14 May 2007; MONZ AS.001310, 1 juv., Te Paki, Kohuronaki, Northland, 34° 29.4658' S, 172° 50.2647' E, pit traps, O. Ball, Jun. 2007; MONZ AS.001470, 1 juv., Te Paki, Kohuronaki, Northland, 34° 29.4658' S, 172° 50.2647' E, pit traps, O. Ball, Jun. 2007; MONZ AS.001468, 1 juv., Te Paki, Kohuronaki, Northland, 34° 29.4658' S, 172° 50.2647' E, native bush, pit traps, O. Ball, Mar. 2007; MONZ AS.003605, 1♀, Te Paki, Kohuronaki, Northland, 34° 29.4658' S, 172° 50.2647' E, pit traps, O. Ball, 12 Feb. 2007; MONZ AS.001277, 1 juv., Te Paki, Kohuronaki, Northland, 34° 29.4658' S, 172° 50.2647' E, pit traps, O. Ball, 14 Aug. 2006; MONZ AS.001720, 1 juv., Matthew Reserve (Forest & Bird), near Kaitaia, Northland, 35° 09.253' S, 173° 17.507' E, regenerating puriri/kauri forest, P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010.

Sidymella longipes

AM KS115193, 1♂, Mt Colah, Berowra Valley R., N.S.W., Australia, 33° 40.98' S, 151° 07.00' E, G. Milledge, 1 May 2011; MONZ AS.004034, 1♀, Houhora, Northland, 34° 47.40' S, 173° 06.00' E, sand hills., C.L. Wilton, 23 Jul. 1975; MONZ AS.001668, 1♂, Mangumuka Summit, Northland, 35° 11.402' S, 173° 27.367' E, mixed forest below road., P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010; MONZ AS.001654, 1♀, 1 juv., Northern end of Coronation Park (Russell Rd end), Whangarei, 35° 42.798' S, 174° 18.83' E, dry kanuka/totara/tree fern/adventive forest, P.J. Sirvid & B.M. Fitzgerald, 25 Mar. 2010; MONZ AS.004029, 1♀, Whangarei, 35° 43.20' S, 174° 17.40' E, Aug. 1970; NZAC, 1 juv., Nr Waipawa Track, Little Barrier I., 36° 11.40' S, 175° 06.60' E, G. Hall & D.M. Gleeson, 27 Mar. 1987; NZAC, 1♂, Te Maraeroa, Little Barrier I., 36° 11.40' S, 175° 06.60' E, C.T. Duval, MONZ AS.004028, 3♀, 2 juv., Cuvier Island, 36° 26.05' S, 175° 46.300' E, beaten from mariscus seed heads., B.M. Fitzgerald, 26 Mar. 1994; MONZ AS.004037, 1 juv., Double Island (Western side),

Mercury Islands, Coromandel, 36° 37.20' S, 175° 53.40' E, summit, in grassy litter., B.M. Fitzgerald, 1 Mar. 2000; MONZ AS.004053, 1♂, 1♀, Mercury Islands, Korapuki Island, 36° 39.62' S, 175° 50.920' E, beaten from manuka., B.M. Fitzgerald, 2 Mar. 1998; MONZ AS.004038, 7 juv., Mercury Islands, Korapuki Island, 36° 39.62' S, 175° 50.920' E, beaten from manuka and matipo., B.M. Fitzgerald, 26 Feb. 1998; NZAC, 1♀, Ike I., Noises Is, 36° 41.40' S, 174° 57.00' E, litter, J.C. Watt, 15 Jun. 1978; MONZ AS.004031, 1♀, Waiheke Island, Hauraki Gulf, 36° 48.60' S, 175° 04.20' E, Chamberlain, G, Dec. 1939; NZAC, 1♀, Auckland University Campus, 36° 51.00' S, 174° 45.60' E, S.E. Thorpe, 13 Jun. 2004; MONZ AS.004035, 1♂, Preston Rd, Henderson, Auckland, 36° 51.10' S, 174° 37.70' E, B.M. Fitzgerald, 24 Feb. 1999; NZAC, 1♂, Kohimarama vet clinic, 36° 51.60' S, 174° 50.40' E, ex cat, Mar. 1992; NZAC, 1♀, Avondale, 36° 53.40' S, 174° 41.40' E, G. Hall, Jun. 2001, MONZ AS.004032, 1♀, Mount Albert, Auckland, 36° 53.40' S, 174° 43.20' E, Chamberlain, G, 1942; MONZ AS.004059, 2 juv., Waharau Regional Park, Hunua Ranges, Auckland, 37° 02.40' S, 175° 15.00' E, ex dead branches, D. Seldon, 13 Mar. 2010; MONZ AS.003609, 1♀, Tuhua (= Mayor Island), 37° 16.80' S, 176° 15.00' E, beating, B.M. Fitzgerald, Mar. 2004; MONZ AS.003594, 2♂, Lighthouse, Tuhua (= Mayor Island), 37° 16.80' S, 176° 15.00' E, hanging dying coprosma leaves., by hand, B.M. Fitzgerald, 26 Mar. 2004; MONZ AS.004036, 3 juv., Tuhua (= Mayor Island), 37° 16.80' S, 176° 15.00' E, beaten from shrub and dead branch., B.M. Fitzgerald, 29 Mar. 2004; MONZ AS.004033, 1♀, Mount Maunganui, 37° 37.20' S, 176° 09.60' E, sand hills., C.L. Wilton, 22 Jul. 1976; MONZ AS.004061, 1♀, 1 juv., Bay of Plenty, Whale Island (Moutuhora), 37° 51.000' S, 176° 58.000' E, beaten from kanuka and mariscus seed heads, B.M. Fitzgerald, 2 Feb. 1999.

Sidymella trapezia

NZAC, 1♂, Ocean Beach, Havelock North, 39° 44.40' S, 177° 00.60' E, Sand dunes, 18 Apr. 2010; NZAC, 1♂, Foxton Beach, 40° 28' S, 175° 13' E, Dunes, ex *Pimelia*, R. Hoare, 16 Jan. 2009; NZAC, 2 juv., Masterton, 40° 57.60' S, 175° 39.60' E, 9 Mar. 2009; MONZ, AS.003593, 1♀, Southern Wairarapa, Lake Onoke, Onoke Spit carpark, 41° 17.82332' S, 175° 14.17695' E, Amongst *Juncus maritimus* and *Lolium* sp., K. Chamberlain, 4 Apr. 2009; MONZ, AS.004051, 1♂, 44 Raukawa St, Stokes Valley, 41° 11.20' S, 174° 58.77' E, by hand, B.M. Fitzgerald, Mar. 2011; MONZ, AS.004052, 1♀, 185 Riverside Drive, Lower Hutt, 41° 13.20' S, 174° 54.60' E, In garden, by hand, C. McGuinness, 19 Apr. 2003; MONZ, AS.004054, 1♀, Waiwhetu, Lower Hutt, 41° 13.20' S, 174° 54.60' E, On windowsill, by hand, C. McGuinness, 19 Jun. 2009.

Cymbachina albobrunnea

CMNZ, Holotype, 1♀, bush near Ohaupo, 37° 55.20' S, 175° 18.00' E A.T. Urquhart; MONZ AS.004027, 1♀, Waipapa River track, Puketi Forest, Northland, 35° 16.53' S, 173° 41.17' E, ex tree fern fronds, D.S. Seldon, 20 Jan. 2010; OMNZ IV36122, 1♂, Aniwanui, Waikaremoana, 38° 44.40' S, 177° 09.60' E, H.A. Oliver, 9-16 Mar. 1969; OMNZ IV36787, 1 juv., Mangareia, 40° 51.68' S, 175° 51.53' E, unknown, 13 Mar. 1960; LUNZ, 1♂, Ahuriri Res., 43° 40' S, 172° 37' E, C.J. Vink, 22 Jan. 2000; OMNZ IV360968, 1♂, Nr Whakapohi R., 43° 42.00' S, 169° 13.20' E, D.A. McHugh, 13 Feb. 1966; OMNZ IV36886, 1♂, Makarora Valley, 44° 09.60' S, 169° 16.20' E, ex moss, R.R. Forster, 12 Feb. 1977; OMNZ IV36300, 1 juv., Pidgeon Flat Rd, nr Mt Cargill, 45° 48.60' S, 170° 33.00' E, R.W.Hutton & C.L. Wilton, 3 Mar. 1969; OMNZ IV36111, 1♂, Dunedin, 45° 52.20' S, 170° 30.00' E, J. Kikkawa, 25 Oct. 1959; OMNZ IV38146, 1♀, Fern Gully, Stewart I., 46° 53.40' S, 168° 05.40' E, R.R. Forster, 9 Mar. 1986; OMNZ IV36255, 1♀, Bluecliffs, Sandhill Pt., Southland, 46° 54.60' S, 168° 09.00' E, A. Mercer, 25 Oct. 1998.

Cymbachina albolimbata

CMNZ, Holotype of *Philodromus ovatus*, 1♀, Waiwera, 36° 32.40' S, 174° 42.60' E, A.T. Urquhart; AMNZ AMNZ6852, 1♀, East end of Great King I., Three Kings, 34° 09.60' S, 172° 06.60' E, E.G. Turbott, 15 Jan. 1951; MONZ AS.001667, 1 juv., Mangumuka Summit, Northland, 35° 11.402' S, 173° 27.367' E, mixed forest below road., P.J. Sirvid & B.M. Fitzgerald, 23 Mar. 2010; OMNZ IV46489, 1♀, Waipoua Forest, 35° 36.60' S, 173° 32.40' E, R.R. Forster, 6 Jan. 1967; MONZ AS.001655, 1♀, Northern end of Coronation Park (Russell Rd end), Whangarei, 35° 42.798' S, 174° 18.83' E, dry kanuka/totara/tree fern/adventive forest., P.J. Sirvid & B.M. Fitzgerald, 25 Mar. 2010; MONZ AS.001694, 1♂, Southern end of Coronation Park (Wilson Rd end), Whangarei, 35° 43.480' S, 174° 18.462' E, regenerating kauri/nikau/tree fern/adventive forest., P.J. Sirvid & B.M. Fitzgerald, 26 Mar. 2010; MONZ AS.001683, 1♂, Mas Olivier, near Whangarei, Northland, 35° 51.842' S, 174° 10.150' E, puriri/nikau/totara forest., P.J. Sirvid, B.M. Fitzgerald & O. Ball, 25 Mar. 2010; AMNZ AMNZ20216, 1♂, Summit, Cuvier I., 36° 25.80' S, 175° 43.80' E, bracken, K.A.J.Wise, 12 Jan. 1972; NZAC, 1♂, Hicks Bay Motel, Glow Worm Grotto, 37° 21' S, 178° 11' E, G. Hall, 4 Dec. 2009; NZAC, 1♀, East Cape, Lighthouse Tk, 37° 25' S, 178° 19' E, ex manuka flowers, D. Seldon, 1 Dec. 2009; OMNZ IV36437, 2♀, Matamata, 37° 48.00' S, 175° 46.20' E, D.J. Court, 1 Dec. 1983; MONZ AS.003615, 1♂, Mangareia Road, Wairarapa, 40° 51.68' S, 175° 51.53' E, by road,

beaten from mainly kanuka, J. Malumbres-Olarte, 29 May 2011; MONZ AS.003011, 1♂, Matiu/Somes Island, Wellington Harbour, 41° 15.00' S, 174° 50.40' E, beaten from trackside vegetation, P.J. Sirvid & R.L. Palma, 13 Nov. 2012; MONZ AS.001077, 1♂, 1 juv., Ocean Mail Scenic Reserve, Chatham Island, 43° 44.8290' S, 176° 24.030' W, grassy sand dunes with low shrubs and trees., beating, P.J. Sirvid, 1 Feb. 2007; MONZ AS.000927, 1♂, Ocean Mail Scenic Reserve, Chatham Island, 43° 44.8290' S, 176° 24.030' W, sand dunes, grasses/med shrubs, beating, N. Curtis & M. McIntosh, 11 Nov. 2005; MONZ AS.000932, 2 juv., Waitangi West, Chatham Island, 43° 47' S, 176° 48' W, sandy soil, grass/med shrubs., beating, N. Curtis & A.M. Paterson, 1 Nov. 2005; MONZ AS.000933, 1 juv., Waitangi West, Chatham Island, 43° 47' S, 176° 48' W, sand dunes/grasses/low shrubs, beating, N. Curtis & A.M. Paterson, 1 Nov. 2005; MONZ AS.000934, 2 juv., Waitangi West, Chatham Island, 43° 47' S, 176° 48' W, beach litter/driftwood, N. Curtis & A.M. Paterson, 10 Nov. 2005; MONZ AS.000928, 1 juv., Hapupu Scenic Reserve, Chatham Island, 43° 48' S, 176° 21.50' W, sand dune/grasses/low shrubs, N. Curtis & A.M. Paterson, 1 Nov. 2005; MONZ AS.000930, 2 juv., Hapupu Scenic Reserve, Chatham Island, 43° 48' S, 176° 21.50' W, sand dune/grasses/low shrubs, pit traps, N. Curtis & A.M. Paterson, 1 Nov. 2005; MONZ AS.000931, 2 juv., Hapupu Scenic Reserve, Chatham Island, 43° 48' S, 176° 21.50' W, sandy soil, grass/med-large shrubs/trees., N. Curtis & A.M. Paterson, 1 Nov. 2005; MONZ AS.000929, 2 juv., Hapupu Scenic Reserve, Chatham Island, 43° 48' S, 176° 21.50' W, sand dunes, grasses/med shrubs, beating, N. Curtis & M. McIntosh, 11 Nov. 2005; MONZ AS.001014, 2♂, 2♀, Henga Scenic Reserve, Chatham Island (beating)., 43° 51' S, 176° 34' W, beating, P.J. Sirvid, 2 Feb. 2007; MONZ AS.003616, 1♀, Henga Scenic Reserve, Chatham Island, 43° 51' S, 176° 34' W, beating, P.J. Sirvid, 2 Feb. 2007; MONZ AS.004047, 1♀, Henga Scenic Reserve, Chatham Island, 43° 51.3020' S, 176° 33.9230' W, sand dunes, beating, N. Curtis & A.M. Paterson, 1 Nov. 2005; MONZ AS.000926, 1♂, 2♀, 3 juv., Henga Scenic Reserve, Chatham Island, 43° 51.3020' S, 176° 33.9230' W, sand dunes/grasses/low shrubs., beating, N. Curtis & M. McIntosh, 11 Nov. 2005; MONZ AS.001137, 1♂, roadside ferns by Maipito Lodge, Maipito Rd, SE of Waitangi, Chatham Island, 43° 58.230' S, 176° 32.810' W, beating, P.J. Sirvid, 27 Jan. 2005; MONZ AS.001080, 1♀, Roadside ferns near Owenga, Chatham Island, 44° 01.500' S, 176° 22.250' W, grassy sand dunes with low shrubs and trees., beating, P.J. Sirvid, 3 Feb. 2007; OMNZ IV36497, 1♂, Makarora, 44° 13.80' S, 169° 13.80' E, R.R. Forster, 16 Mar. 1966; OMNZ IV36733, 1♂, Hollyford-Pyke R., 44° 19.80' S, 168° 03.00' E, M.A. Chapman, Nov. 1960; NZAC, 1♂, Borland Rd Tk, Limestone Cave, 45° 45.000' S, 167° 30.000' E, sweeping, G. Hall & D.M. Gleeson, 24 Jun. 1998;

OMNZ IV36482, 1♀, Leith Saddle, 45° 50.00' S, 170° 30.000' E, R.R. Forster, 15 Dec. 1966; OMNZ , 1♀, Taieri, 45° 54.00' S, 170° 19.80' E, 1 Apr. 1971; OMNZ IV38182, 1♀, L. Hauroko, 45° 56.40' S, 167° 18' E, R.R. Forster & C.L. Wilton, 25 Nov. 1970; OMNZ IV38143, 1♀, 1 juv., Fern Gully, Stewart I., 46° 53.40' S, 168° 05.40' E, R.R. Forster, 9 Mar. 1986; MONZ AS.001138, 1♀, Lanauze Bush (on Lanauze farm), SE of Waitangi, Chatham Island, bush (mostly ferns) on swampy ground by a limestone outcrop., by hand, P.J. Sirvid, 29 Jan. 2005; AMNZ AMNZ6854, 1♀, Unknown.

Cymbachina ambara

CMNZ, 5 immature ♀, 2♂ syntypes, Tairua, Whangarei Harbour, 37° 01.20' S, 175° 50.40' E, T. Broun; ZMH 20867, Syntypes of *Synema suteri* Dahl, 1907, 3 ♀, 2 ♂, New Zealand; OMNZ IV36486, 1♂, Cape Reinga, 34° 25.20' S, 172° 40.20' E, R.R. Forster, 7 Jan. 1967; OMNZ IV36754, 1♀, 1 juv., Kohukohu, "The Skyline", Tapuae, 35° 21.31' S, 173° 27.58' E, B.J.Marples, 28 Aug. 1953; OMNZ IV36337, 1♂, Matamata, 35° 25.20' S, 173° 21.00' E, D.J. Court, 1 Oct. 1982; OMNZ IV36478, 1♀, Waipoua Forest, 35° 36.60' S, 173° 32.40' E, R.R. Forster, 6 Jan. 1967; MONZ AS.001647, 1♀, 1 juv., Kaihu Farm Hostel, Northland, 35° 45.738' S, 173° 40.410' E, nikau/mixed forest, by creek., P.J. Sirvid & B.M. Fitzgerald, 24 Mar. 2010; MONZ AS.004050, 1♂, 1♀, 2 juv., Bream Head Scenic Reserve., 35° 51.000' S, 174° 32.000' E, B.M. Fitzgerald, 16 Oct. 2001; AMNZ AMNZ6802, 1♂, Pumphouse Stream, Cuvier I., 36° 25.80' S, 175° 43.80' E, yellow pan trap in forest, 120m, J.W. Early & S.E. Thorpe, 10 Nov. 1999; OMNZ IV36057, 7♂, 3♀, 5 juv., Cuvier I., 36° 25.80' S, 175° 43.80' E, R.R. Forster, Jul. 1943; AMNZ AMNZ202777, 1♀, Cuvier I., 36° 25.80' S, 175° 43.80' E, P.F. Jenkins, Nov.-Dec. 1971; AMNZ AMNZ20279, 1♀, Cuvier I., 36° 25.80' S, 175° 43.80' E, P.F. Jenkins, Nov.-Dec. 1971; AMNZ AMNZ20276, 1♂, 2♀, 3 juv., Cuvier I., 36° 25.80' S, 175° 43.80' E, swept trees, low vegetation, P.F. Jenkins, Nov-Dec 1971; OMNZ IV38149, 2♂, 1 juv., Waiheke I., 36° 48.60' S, 175° 04.20' E, D.J. Court, 5 Sep. 1970; AMNZ AMNZ6873, 1♀, Auckland Museum, 36° 52.00' S, 174° 46.00' E, K.A.J. Wise, 22 Mar. 1948; AMNZ AMNZ6865, 1♂, Kauaeranga Valley, Thames, 37° 08.40' S, 175° 36.00' E, R. Rowe, 25 Feb. 1976; NZAC, 1♂, 2 juv., Lottin Pt Rd, Waenga Bush, Otanga, 37° 33.00' S, 178° 09.00' E, G. Hall, 16 Sep. 1992; NZAC, 1♀, 3 juv., Waiaroho, 37° 36.00' S, 178° 09.00' E, J.S. Dugdale, 29 Apr. 1993; AMNZ AMNZ6869, 2 juv., S. end of Green Lake, Rotorua, 38° 12.60' S, 176° 19.20' E, sweeping shrubs, K.P. Rennell, 23 May 1971; MONZ AS.004055, 1♂, Whanganui, 39° 55.80' S, 175° 01.20' E, regenerating native forest., J. Malumbres-Olarte, 11 May 2011; OMNZ IV36882, 1♂, Kitchener Pk,

Feilding, 40° 14.40' S, 175° 31.80' E, R.R. Forster, 29 Dec. 1966; OMNZ IV36876, 2 juv., Nr Pakawau, 40° 35.40' S, 172° 40.80' E, C.L. Wilton, 8 Mar. 1967; MONZ AS.004057, 1♂, Mangareia Road, Wairarapa, 40° 51.68' S, 175° 51.53' E, by road, beaten from mainly kanuka., J. Malumbres-Olarte, 29 May 2011; MONZ AS.003614, 2♂, Belmont Regional Park, track next to Korokoro dam, 41° 09.350' S, 174° 56.30' E, regenerating native bush, beating, J. Malumbres-Olarte, 21 Apr. 2011; OMNZ IV36284, 1♂, Karamea Coast, 41° 15.00' S, 172° 06.00' E, R.R. Forster & C.L. Wilton, 28 Sep. 1966; OMNZ IV36268, 1♂, Karamea Coast, 41° 15.00' S, 172° 06.00' E, R.R. Forster, 28 Sep. 1966; MONZ AS.003022, 1♀, 1 juv., Matiu/Somes Island, Wellington Harbour, 41° 15.00' S, 174° 50.40' E, beaten from trackside vegetation, P.J. Sirvid & R.L. Palma, 13 Nov. 2012; MONZ AS.003590, 1♂, 27 Waitohu Road, York Bay, Wellington, 41° 15.73' S, 174° 54.58' E, reared to adulthood (july 2009), by hand, P.J. Sirvid, May 2009; MONZ AS.003607, 1♂, 1♀, Wairarapa, Road side shrub, 41° 18.84533' S, 175° 10.19133' E, ex buckthorn?. single shrub amongst grass., K. Chamberlain, 2 Apr. 2009; MONZ AS.003606, 1♂, Wairarapa, Ocean beach area, roadside bank exposed to coast., 41° 22.47227' S, 175° 04.78042' E, K. Chamberlain, 2 Apr. 2009; OMNZ IV36457, 1♂, North of Conway R., 42° 24.60' S, 173° 15.60' E, beech forest, C.L. Wilton, 25 Mar. 1969; OMNZ IV36073, 5♂, 5 juv., Greymouth, 42° 27.00' S, 171° 10.20' E, P.J. Hughson, 2 Apr. 1950; OMNZ IV36658, 5 juv., Milton Rd, Greymouth, 42° 27.00' S, 171° 10.20' E, L.R. Jackson, Jul. 1956-Jan. 1957; OMNZ IV36205, 1♀, Rough Ck, Arthurs Pass, 42° 57.00' S, 171° 33.00' E, 3 Aug. 1974; LUNZ, 1♂, Harihari, Saltwater Forest, 43° 08.40' S, 170° 33.00' E, beaten from shrubs, A.R.G. McLachlan, 29 Aug. 1997; LUNZ, 1♂, 2♀, 4♀, Travis Marsh, Christchurch, 43° 29.25' S, 172° 41.37' E, R.P. MacFarlane, 20 Dec. 1995; LUNZ, 1♂, 1♀, Christchurch, 43° 33.60' S, 172° 38.40' E, beaten from heather in garden, C.J. Vink, 2 Jan. 1997; LUNZ, 2♂, 1 juv., Ahuriri Res., 43° 40' S, 172° 37' E, C.J. Vink, 22 Jan. 2000; OMNZ IV36662, 1♂, 1♀, Peel Forest, 43° 54.60' S, 171° 15.60' E, C.W. O'Brien, 9 Mar. 1960; OMNZ IV36355, 1♂, Dunedin, 45° 52.20' S, 170° 30.00' E, 20 Dec. 1978; OMNZ IV36331, 1♀, Leith Stream, 45° 52.20' S, 170° 31.20' E, P. Taane, 22 Sep. 1982; OMNZ IV35972, 1♂, Mosgiel, 45° 52.80' S, 170° 19.80' E, 15 Jun. 1981; OMNZ IV36810, 1♂, 2♀, 1 juv., Tapanui, 45° 56.40' S, 169° 15.60' E, R.R. Forster, Nov. 1958; OMNZ IV36358, 6♂, Bull Creek Bush, 45° 58.80' S, 170° 07.20' E, R.W. Hutton & C.L. Wilton, 19 May 1967; OMNZ IV38184, 3♂, 3 juv., Bull Creek, 45° 58.80' S, 170° 07.20' E, C.L. Wilton, 27 Mar. 1970; OMNZ IV36340, 1♂, 1♀, Tautuku, Catlins, 46° 34.80' S, 169° 25.20' E, R.R. Forster, 14 Feb. 1979; OMNZ IV36204, 1♀, 3 juv., Lee Bay, Stewart I., 46° 51.60' S, 168° 07.20' E, A.C. Harris, 25 Dec. 1975; OMNZ IV36650, 1♀, Fern Gully, Stewart I., 46° 53.40' S,

168° 05.40' E, R.R. Forster, 9 Mar. 1986; OMNZ IV36656, 1♂, Fern Gully, Stewart I., 46° 53.40' S, 168° 05.40' E, R.R. Forster, 9 Mar. 1986.

Cymbachina sphaeroides

CMNZ, Holotype 1♀, Lake Tekapo, Canterbury, 43° 47.40' S, 170° 31.80' E, A.T. Urquhart (CMNZ); OMNZ IV36520, 1♀, 1 juv., Tuna Saddle, Taumarunui, 38° 52.80' S, 175° 15.60' E, R.R. Forster, 6 Nov. 1974; OMNZ IV36377, 1♂, Waitetoko, 38° 54.00' S, 175° 55.20' E, R.W. Hutton, 8 Nov. 1968; NZAC, 2♂, 2 juv., Blyth Tk, Ohakune, 39° 20.40' S, 175° 29.40' E, Sweeping, G. Hall & R.Hoare, 15 Feb. 2007; OMNZ IV36271, 1♀, Apiti, 39° 58.20' S, 175° 52.20' E, R.R. Forster, 29 Dec. 1966; MONZ AS.003618, 1♂, Onamalutu Reserve, 41° 29.000' S, 173° 47.000' E, Beaten from ferns, P.J. Sirvid, Feb. 2010; OMNZ IV36202, 3♂, 3♀, 1 juv., Gore, 42° 51.60' S, 173° 18.60' E, 20 Oct. 1975; LUNZ, 1♂, 1 juv., Travis Marsh, Christchurch, 43° 29.25' S, 172° 41.37' E, R.P. MacFarlane, 18 Dec. 1995; OMNZ IV36017, 1♂, Christchurch, 43° 31.80' S, 172° 37.80' E, F. McGregor, 22 Dec. 1950; LUNZ, 1♂, 1♀, Christchurch, 43° 33.60' S, 172° 38.40' E, beaten from heather in garden, C.J. Vink, 2 Jan. 1997; MONZ AS.003619, 1♂, 1♀, Port Hills, Kennedy's Bush, 43° 37.88' S, 172° 37.15' E, very exposed habitat, C.J. Vink, 30 Mar. 2009; MONZ AS.003602, 1♂, Liffey Domain, Lincoln, Canterbury (Bioblitz), 43° 38.30' S, 172° 29.13' E, C.J. Vink, 4 Apr. 2009; MONZ AS.003603, 1♂, Liffey Domain, Lincoln, Canterbury (Bioblitz), 43° 38.30' S, 172° 29.13' E, C.J. Vink, 4 Apr. 2009; LUNZ, 2♂, 1♀, Ahuriri Res., 43° 40' S, 172° 37' E, C.J. Vink, 22 Jan. 2000; OMNZ IV36698, 1♀, The Hermitage, Mt Cook, 43° 43.80' S, 170° 04.80' E, R.R. Forster, 20 Jan. 1951; OMNZ IV36065, 1♂, 1 juv., The Hermitage, Mt Cook, 43° 43.80' S, 170° 04.80' E, 2500' [762m], J.S. Sellacek, 4 Feb. 1961; OMNZ, 4♂, 2♀, Kaituna Valley, Banks Pen., 43° 43.80' S, 172° 41.40' E, R.R. Forster, 2 Nov. 1966; OMNZ IV36499, 1♂, Kaituna Valley, Banks Pen., 43° 43.80' S, 172° 41.40' E, R.R. Forster, 29 May. 1966; MONZ AS.004049, 1♂, 1♀, 2 juv., Kaitorete Spit, Canterbury, 43° 49.80' S, 172° 32.40' E, ex *Muehlenbeckia complexa*, J. Griffiths, 18 Oct. 2013; OMNZ IV36887, 1♂, Makarora Valley, 44° 09.60' S, 169° 16.20' E, ex moss, R.R. Forster, 12 Feb. 1977; OMNZ IV36464, 1♂, Nr Hindon, 45° 43.80' S, 170° 18.00' E, C.L. Wilton, 30 Nov. 1969; OMNZ IV36456, 1♂, Nr Hindon, 45° 43.80' S, 170° 18.00' E, C.L. Wilton, 30 Nov. 1969; OMNZ IV36461, 1♀, Lee Str. Bridge, 45° 48.00' S, 170° 07.20' E, C.L. Wilton, 30 Nov. 1969; OMNZ IV38172, 1♂, Flagstaff, Dunedin, 45° 49.80' S, 170° 27.60' E, R.R. Forster, 20 Dec. 1983; OMNZ IV36285, 1♀, Halfway Bush, 45° 51.00' S, 170° 27.60' E, Mrs Jolly, Dec. 1965; ; OMNZ IV36265, 1♂, Harbour Tce Bush, Dunedin, 45° 52.20' S, 170° 30.00' E, T. Bruce, 25 Apr. 1966; OMNZ IV36458, 1♂, St

Clair, Dunedin, 45° 54.60' S, 170° 28.80' E, R.R. Forster, 11 Dec. 1965; OMNZ IV36294, 1♂, 2♀, St Clair, Dunedin, 45° 54.60' S, 170° 28.80' E, R.R. Forster, 7 Jun. 1969; OMNZ IV38143, 1♀, 1 juv., Nr Dolamore Park, Gore, 46° 03.60' S, 168° 49.80' E, ex tussock, R.R. Forster, 19-Sep-79, ; OMNZ IV36269, 1♂, Akatore, 46° 04.80' S, 170° 07.80' E, C.L. Wilton, 4 Dec. 1965; OMNZ IV36451, 1♂, Rowallen Str., Southland, 46° 05.40' S, 167° 28.20' E, C.L. Wilton, 11 Mar. 1970; OMNZ IV36487, 1♂, Plant Res., Balclutha, 46° 13.80' S, 169° 43.80' E, R.R. Forster, 21 Apr. 1966; OMNZ IV36199, 1♂, 2 juv., Colac Bay, 46° 22.20' S, 167° 54.00' E, A.C. Harris, 19 Mar. 1975; OMNZ IV36653, 1♂, Fern Gully, Stewart I., 46° 53.40' S, 168° 05.40' E, R.R. Forster, 9 Mar. 1986

Cymbachina urquharti

CMNZ, Holotype 1♂, Waiwera, 36° 32.40' S, 174° 42.60' E, A.T. Urquhart, [early 1886]; CMNZ, 2♂, 1♀, Waiwera, 36° 32.40' S, 174° 42.60' E, A.T. Urquhart, [early 1886]; NZAC, 1♂, Te Araroa, Lighthouse Tk, 37° 41' S, 178° 32' E, G.Hall, R. Hoare, T. Buckley & D. Seldon, 1 Dec. 2009; OMNZ IV36338, 1♂, Tongariro National Park, 39° 21.96' S, 175° 22.53' E, D.J. Court, 4 Apr. 1972; MONZ AS.003617, 1♀, Mana Island (2011 Bioblitz), 41° 04.80' S, 174° 45.60' E, P.J. Sirvid, 25 Feb. 2011; OMNZ IV36215, 1♂, Oxford, White's Creek, 43° 13.20' S, 172° 05.40' E, J. Veale, 6 Sep. 1950; OMNZ IV36299, 1♂, Franz Josef Glacier, 43° 29.00' S, 170° 12.00' E, Ex moss., J. Child, Sep. 1970; LUNZ, 1♂, Mataketake Range, 43° 50.993' S, 169° 13.882' E, 1200m, tussock tops, W.G.H. Chinn, 1 Jan. 2003.

APPENDIX B: GLOSSARY (Modified from Paquin *et al.* 2010)

Abdomen: Fig. 2A, 2C. Posterior division of the spider body. Bears the spinnerets.

Apical embolic bend (AEB): Fig. 4. A sharp bend at the distal-most point in the sperm duct seen in some stephanopine Thomisidae.

Atrium: A concavity in the epigynal plate in entelgyne females containing the copulatory openings.

Carapace: Fig. 2A. Dorsal part of the cephalothorax.

Cephalic area: Fig 2A. Anterior part of carapace. Bears the eyes.

Cephalothorax: Fig 2A. The anterior portion of the spider body. Bears the legs and palps.

Chelicerae: Fig. 2C. The biting appendages of a spider. Consists of a basal segment or paturon and a fang. The paturon may bear cheliceral teeth.

Cheliceral teeth: Fig. 2C. Tooth-like projections that border the fang furrow on the paturon.

Copulatory ducts: Fig. 5B. Tube-like structures in female internal genitalia connecting the copulatory openings to the spermathecae:

Copulatory openings: Fig. 5. External openings in the epigyne allowing insertion of the male embolus for sperm transfer.

Coxa: Fig 2C. Leg segment attached to the spider's body.

Cymbium: Figs 3-4. Terminal (distal) segment of male palp. Bears the genital bulb.

Embolus: Figs 3-4. Distal termination of sperm duct used in copulation.

Entelgyne: A form of epigyne with external copulatory openings.

Epigastric furrow: A transverse groove across the antero-ventral part of the abdomen.

Epigyne: Fig 2C. Sclerotised external portion of the female genitalia. Located towards the anterior end of the ventral surface of the abdomen between the book lungs and the epigastric furrow.

Fang: Fig 2C. Distal segment of chelicera used to pierce prey and inject venom.

Fang furrow: Groove in the distal portion of paturon into which the fang closes.

Femur: Fig 2C. Third segment of spider leg and usually the longest. Located between trochanter and patella.

Genital bulb: Fig. 3. The genitalic structure of the male palp borne on the cymbium.

Guide pockets: Fig. 5A. Accessory sclerotised structures on epigyne to help in positioning of embolus during copulation.

Labium: Fig 2C. Median sclerite immediately anterior of sternum and between maxillae.

Maxillae: Fig. 2C. Expanded lobes of palpal coxae that flank the labium.

Metatarsus: Fig. 2C. Penultimate leg segment, located between tibia and tarsus.

Palps: Fig 2C. A pair of leg-like appendages between the front leg. Palps lack the metatarsus of the legs and the coxae are modified to form maxillae, but the segments are otherwise similarly labelled. In female and juveniles are tipped with a single claw.. In males, the palps are modified to the genital bulb.

Patella: Fig 2C. Fourth leg segment. Knee-like and located between the femur and tibia.

Paturon: Large basal portion of chelicera. Bears the fang.

Prolateral: On the anterior or inner surface of an appendage.

Retrolateral: On the posterior or outer surface of an appendage.

Retrolateral cymbial projection (RCP): Fig 4. A thickening of the retrolateral margin of the cymbium seen in some stephanopine Thomisidae.

Retrolateral tibial apophysis (RTA): Figs 3-4. Tibial apophysis originating on the retrolateral side of the tibia of the male palp.

Sperm duct: Fig. 3. Connects sperm reservoir to embolus in male palp.

Spinnerets: Fig. 2C. Silk spinning organs, typically located towards the rear of the abdomen.

Sternum: Fig. 2C. Ventral sclerite of cephalothorax.

Tarsus: Fig. 2C. Terminal segment of spider leg located distally of the metatarsus. Usually the smallest segment and tipped with claws.

Tegulum/tegular area: Figs 3-4. Middle sclerite of male palp bearing sperm duct and embolus.

Thorax/thoracic area: Fig. 2A. Posterior portion of carapace.

Tibia: Fig. 2C. Fifth segment of spider leg. Usually second longest and located between patella and metatarsus.

Tibial apophysis: Figs 3-4. Sclerotised structures arising from the tibia of male palp.

Trochanter: Fig. 2C. Second segment of leg and located between coxa and femur.

Ventral tibial apophysis (VTA): Fig. 3. Tibial apophysis originating on the ventral side of the tibia of the male palp.

CHAPTER 3:
**A PRELIMINARY MOLECULAR ANALYSIS OF PHYLOGENETIC AND
BIOGEOGRAPHIC RELATIONSHIPS OF NEW ZEALAND THOMISIDAE
(ARANEAE) USING A MULTI-LOCUS APPROACH**

Notes

This chapter is based on a manuscript that has been accepted for publication in the journal *Invertebrate Systematics*. While the font has been changed for ease of reading, there is some variation in format from the rest of the thesis. This section is co-authored and details of each co-author's contribution are given in Chapter 1. Taxon names used reflect the state of knowledge prior to the taxonomic revision of Chapter 2. Table 2 in Chapter 2 updates names used here.

**A preliminary molecular analysis of phylogenetic and
biogeographic relationships of New Zealand
Thomisidae (Araneae) using a multi-locus approach**

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Abstract

We tested competing theories on the origins of the New Zealand fauna using thomisid spiders as a model group. These theories can be broadly described as old and vicariant versus young and recent (dispersal). To test these theories, a phylogenetic analysis was undertaken based on cytochrome *c* oxidase subunit I (COI) and 28S rRNA sequence data, with smaller datasets (histone H3, nicotinamide adenine dinucleotide (NADH) dehydrogenase subunit 1 and a combined dataset) used to improve resolution of internal branches. The monophyly of New Zealand thomisid subfamilies and of individual taxa were also assessed using these data. Our data supports the separation of New Zealand clades from their Australian counterparts. Evidence of recent dispersal to New Zealand by Australian stephanopines combined with our proposed maximum divergence date of 5.3 mya indicates that the New Zealand thomisids are a younger lineage than previously suspected. Several other gene targets (internal transcribed spacer units 1 and 2, wingless and 18S rRNA) were examined but did not generate sufficient

reliable data to contribute to the analysis. Corrected p -distance values for COI indicate that *Sidymella angularis*, a widely distributed and morphologically variable stephanopine species, is a single taxon. Three undescribed endemic species exhibited molecular and morphological distinctiveness from previously described New Zealand thomisids.

Additional keywords: 28S, Australia, COI, *Diaea*, DNA, H3, ND1, phylogenetics, *Sidymella*, Stephanopinae, Thomisinae.

Introduction

Origins of the New Zealand spider fauna

There are two markedly differing views with respect to origins of the New Zealand spider fauna. Forster (1975) suggested the fauna arose in the late Mesozoic and later inferred a Gondwanan distribution for several spider families e.g. Forster and Platnick's (1985) revision of Orsolobidae based on their present-day geographical ranges. Landis *et al.* (2008) presented a radically different hypothesis. They found no evidence to suggest that any part of the New Zealand landmass was above sea level during the Oligocene period (34–23 mya). If New Zealand was completely inundated, then the entire biota (spiders included) must be formed from more recent episodes of colonisation and subsequent radiation. These two competing hypotheses to explain New Zealand's current spider biota can be broadly described as a vicariance- versus dispersal-based origins.

In exploring questions of origin, molecular studies have one advantage over the classical morphology-based approach of Forster and others (e.g. Forster and Platnick 1985) in that they allow estimates of evolutionary divergence times to be calculated based on genetic distances. Molecular studies on the origins of New Zealand spiders are still few in number. Vink and Paterson's (2003) study of the wolf spider genus *Anoteropsis* L. Koch, 1878 suggests it probably colonised New Zealand sometime after the breakup of Gondwana. Using Brower's (1994) arthropod molecular clock rate (2.3 million years per percentage point difference), they tied the radiation of the genus to the uplift of the Southern Alps (~5 mya). Vink and Dupérré's (2010) revision of New Zealand Pisauridae does not give a specific divergence time estimate for the

family, but with a maximum uncorrected p -distance of 3% (for cytochrome c oxidase subunit I (COI)) between species, it appears that their radiation would have been even more recent than that of the lycosid *Anoteropsis* if the same molecular clock is applied. Both families are strongly represented in Australia, have excellent dispersal abilities (Vink and Paterson 2003; Vink and Dupérré 2010) and appear to have undergone recent radiations, so may not be a good fit for Forster's vicariance-based Gondwanan hypothesis.

The New Zealand Thomisidae was chosen as a model group for this study because known distributional data suggested the possibility that both vicariance-based and dispersal-based speciation may have occurred. Of the two most speciose genera (see Table 1), *Diaea* Thorell, 1869 (subfamily Thomisinae) is known to be a capable disperser and is distributed across a wide expanse of the Pacific, including Australia, New Zealand, New Caledonia and many Pacific Islands (Lehtinen 1993, Garb and Gillespie 2006). The stephanopine genus *Sidymella* Strand, 1942 is currently known from Australia, New Zealand and South America, but not New Caledonia or other Pacific Islands (Platnick 1993, 2013). While inference of ancient faunal origins based solely on modern distributions is highly speculative, the current geographic range of *Sidymella* appears to match Forster's (1975) view of a Gondwanan taxon. Bryant (1933) suggested that New Zealand *Sidyma* (now *Sidymella*) possess features such as cephalothoracic ridges that separate them from their South American congeners and that a new genus should probably be erected for them. David Court (pers. comm.) states Australian and New Zealand *Sidymella* form their own clade based on synapomorphies such as a narrow cephalic region.

Systematics

With over 1100 described species, New Zealand has a rich spider fauna characterised by a high degree of endemism (Sirvid *et al.* 2010). However, many taxa still await description and families such as Thomisidae have never been taxonomically revised (Paquin *et al.* 2010).

Thomisidae merit their common name of crab spiders because of their ability to move sideways and backwards (Forster and Forster 1999). They are

ambush predators (Jocqué and Dippenaar-Schoeman 2007), but one New Zealand species, simply identified as *Diaea* sp., has been recorded as augmenting this strategy by using silk as an aid in prey capture (Jackson *et al.* 1995). Thomisids are common in New Zealand and can be encountered in habitats ranging from suburban gardens to native forests (Forster and Forster 1999). They are known from the three main islands of New Zealand as well as more distant islands such as Three Kings and the Chathams (PJS, pers. obs.), but are not recorded from any of the subantarctic islands (e.g. Berland 1931; Forster 1964).

In terms of world spider diversity, Thomisidae rank sixth of 112 families with 2151 currently recognised species (Platnick 2013). At the outset of this study, the known New Zealand thomisid fauna (Table 1) consisted of eight described endemic species in four genera: *Sidymella*; *Diaea*; *Synema* Simon, 1864; and *Cymbachina* Bryant, 1933. The subfamily Stephanopinae is represented by *Sidymella* (Fig. 1a), while the other genera are members of the Thomisinae (Fig. 1b). As will be seen later (see *Study objectives*), the list of taxa in Table 1 is incomplete. Most New Zealand thomisids were described in the late 1800s by Urquhart (1885, 1887, 1893), with the most recent description (*Sidymella benhami*) published in 1910 (Hogg 1910). Bryant's (1933, 1935) redescription and transfer of Urquhart's thomisid species to other genera represents the most recent taxonomic work on New Zealand thomisids but does not constitute a full revision.

Subfamily Thomisinae

Cymbachina albobrunnea (Urquhart, 1893)
Diaea albolimbata L. Koch 1875
Diaea ambara (Urquhart, 1885)
Diaea sphaeroides (Urquhart, 1885)
Synaema suteri Dahl, 1907

Subfamily Stephanopinae

Sidymella angularis (Urquhart, 1885)
Sidymella angulata (Urquhart, 1885)
Sidymella benhami (Hogg, 1911)

Table 1: The described endemic New Zealand thomisid fauna



Fig. 1a. The most common of New Zealand stephanopines, *Sidymella angularis*, from Hamilton (Photo credit. B. McQuillan).



Fig. 1b. A typical New Zealand thomisine, *Diaea albolimbata*, from Chatham Island. (Photo credit. M. Hall, Te Papa).

Full taxonomic revisions exist for many other New Zealand spider families (e.g. Forster and Wilton 1973), but the great majority were produced before the turn of 21st century and are based on classical morphological methods with no genetic data to support them. While it is possible that the great majority of New Zealand spider species delineated on morphological criteria will prove to be valid species, recent studies including a molecular component in the analysis have shown that this is not always the case. For instance Vink *et al.* (2008) used a combination of molecular, morphological and cross-breeding evidence to conclude that the two previously recognised species of New Zealand katipo spider (*Latrodectus katipo* Powell, 1871 and *L. atritus* Urquhart, 1890) were conspecific. More recently, Vink *et al.* (2011b) examined four species in four genera that were all described on the basis of specimens from one sex only (female *Cambridgea reinga* Forster & Wilton, 1973, male *Nanocambridgea grandis* Blest & Vink, 2000, female *Nuisiana arboris* (Marples, 1959) and male *Matachia magna* Forster, 1970). Using molecular, morphological and distributional data, they showed these four species were actually the male and female pairs of *C. reinga* and *N. arboris*.

Other New Zealand family-level revisions for spiders, while heavily reliant on morphological characters, are also backed by molecular data. Vink's (2002) taxonomic revision of the Lycosidae (wolf spiders) is reinforced by a companion study exploring the phylogeny of Australasian lycosid genera (Vink *et al.* 2002). Vink and Dupérré's (2010) revision of Pisauridae (nursery web and water spiders) includes a phylogenetic analysis based on COI and Actin 5C data.

Phylogenetic studies on thomisids exist with resolution at both the family (Benjamin *et al.* 2008) and species level (Garb 1999; Garb and Gillespie 2006). However, given the long-standing taxonomic neglect of New Zealand thomisids, it is not surprising they have not featured prominently in molecular studies. Indeed, a single New Zealand thomisid (identified as *Diaea* sp.) used as an outgroup taxon in a study of Austral Island colonisation by thomisids (Garb and Gillespie 2006) appears to be the only example. Benjamin *et al.* (2008) used several loci (COI, 16S rRNA, histone H3) to explore the

phylogeny of Thomisidae. While the study did not include any New Zealand taxa, it concluded that Thomisidae is monophyletic.

Study objectives

A preliminary examination of thomisid specimens held by New Zealand entomological collections indicates there are more species of crab spiders in New Zealand than are historically documented (PJS, pers. obs.). Furthermore, some previously recorded species appear to be widespread and exhibit morphological variation (PJS, pers. obs.) with respect to somatic characters such as colour, size and leg spine counts. Our study analyses sequence data generated from nuclear and mitochondrial gene regions to: (1) test the monophyly of the two New Zealand thomisid subfamilies; (2) determine if putative new species exhibit molecular distinctiveness; (3) assess if *Sidymella angularis* (Urquhart, 1885), a common and widely distributed species exhibiting somatic variation is a single species or several; and (4) examine the level of evolutionary divergence between species with a view to exploring the origin and diversification of the New Zealand thomisid fauna relative to included Australian endemic specimens and two Australian species suspected to be recent introductions.

Materials and methods

Taxon sampling

Specimens sampled for this study are listed in Table 2, along with repository information, registration numbers and GenBank accession numbers. This table also shows which gene targets were successfully amplified for each specimen. Specimens we sampled were either identified by, or had their original determinations verified by one of us (PJS). Three taxa (*Sidymella* 'dwarf' *angularis* and *Sidymella* 'snouty' and *Diaea* sp.) are distinct morphospecies suspected of being undescribed endemic New Zealand species. Non-NZ endemic material is a combination of Australian species collected from both Australia and New Zealand as well as sequence data available on GenBank.

GenBank Accession Number										
Specimen Code	Species	Locality	COI	28S	H3	ND1	18S	ITS	Collection	Req. Number
7.3	<i>Diaea ambara</i>	Wairarapa	KF669339	KF669294	-	-	-	-	MONZ	AS.003606
7.4	<i>Diaea ambara</i>	Wairarapa	KF669340	KF669295	KF669314	-	-	-	MONZ	AS.003607
8.4	<i>Diaea ambara</i>	Whanganui	-	KF669296	-	-	-	-	NZAC	-
8.8s	<i>Diaea ambara</i>	Belmont Regional Park, Wellington	-	KF669297	-	-	-	-	MONZ	AS.003614
19	<i>Diaea ambara</i>	Eastbourne, Wellington	KF669338	-	-	-	-	-	MONZ	AS.003590
4.3	<i>Diaea albolimbata</i>	East Cape	KF669331	KF669292	-	-	-	-	NZAC	-
4.4	<i>Diaea albolimbata</i>	Hicks Bay	KF669331	-	-	-	-	-	NZAC	-
4.4	<i>Diaea albolimbata</i>	Mangareia Rd, Wellington	KF669332	-	-	-	-	-	NZAC	-
8.7	<i>Diaea albolimbata</i>	Chatham I.	KF669333	KF669293	-	KF669316	-	-	MONZ	AS.003615
18	<i>Diaea albolimbata</i>	Peery Nat. Park, NSW, Australia	KF669341	KF669298	-	-	-	-	AM	AS.003616
11595	<i>Diaea sp.</i>	NSW, Australia	KF669343	KF669299	-	-	-	-	AM	KS.115195
6.07	<i>Diaea sp.</i>	Freshwater Lake, Australia	KF669344	-	-	-	-	-	AM	-
90150	<i>Diaea sp.</i>	Mana Island	KF669336	-	-	-	-	-	MONZ	KS.90150
6.02	<i>Diaea sp.</i>	Te Anaroa	KF669337	KF669291	-	-	-	-	NZAC	AS.003617
6.1aa	<i>Diaea sp.</i>	Onamalutu Res., Christchurch	-	KF669290	-	-	-	KF669329	MONZ	-
115b	<i>Diaea sp.</i>	Tonga	-	-	-	DQ174365.1	-	-	-	AS.003618
D.Q.174365.1	<i>Diaea praetexta</i>	Liffey Domain, Lincoln	KF669334	KF669288	KF669315	KF669317	KF669303	-	MONZ	AS.003603
20	<i>Diaea sphaeroides</i>	Liffey Domain, Lincoln	KF669335	KF669289	-	-	-	-	MONZ	AS.003602
27	<i>Diaea sphaeroides</i>	NZ	-	-	-	DQ174355.1	-	-	-	-
D.Q.174355.1	<i>Diaea sphaeroides</i>	Kennedy's Bush, Christchurch	-	KF669286	-	-	-	-	MONZ	AS.003619
115a	<i>Diaea sphaeroides</i>	Kennedy's Bush, Christchurch	-	KF669287	-	-	-	-	MONZ	AS.003619
115e	<i>Diaea sphaeroides</i>	Brisbane, QLD, Australia	KF669342	-	KF669313	KF669318	-	-	QM	22901
22901	<i>Thomisus spectabilis</i>	Peninsula	-	-	-	-	-	-	MONZ	AS.003591
2	<i>Sidyrella angularis</i>	Tapu Hill, North Cape	KF669363	-	-	-	-	-	MONZ	AS.003592
3	<i>Sidyrella angularis</i>	Lake Otdtoa	KF669359	KF669268	-	-	-	-	MONZ	AS.003587
4	<i>Sidyrella angularis</i>	Stokes Valley, Wellington	KF669362	-	KF669305	-	-	-	MONZ	AS.003621
6.11a	<i>Sidyrella angularis</i>	Kaitoke, Wellington	KF669348	-	-	-	-	-	MONZ	AS.001686
7.1	<i>Sidyrella angularis</i>	Trounson Kauri Park, Northland	KF669354	KF669270	-	-	-	-	MONZ	AS.001650
7.2	<i>Sidyrella angularis</i>	Kaihu Farm Hostel, Northland	KF669355	-	-	-	-	-	MONZ	AS.003622
8.2	<i>Sidyrella angularis</i>	Tutakakahikura Res., Banks Peninsula	KF669349	KF669272	-	-	-	-	MONZ	AS.003620
8.11	<i>Sidyrella angularis</i>	Kaitoke, Wellington	KF669360	KF669271	-	-	-	-	NZAC	-
9.2	<i>Sidyrella angularis</i>	Watakeres	KF669357	-	-	-	-	-	NZAC	-
9.13	<i>Sidyrella angularis</i>	Kaipara	KF669358	KF669273	-	KF669321	-	-	NZAC	-
9.14	<i>Sidyrella angularis</i>	Lake Matheson	KF669350	KF669274	KF669306	-	KF669300	-	MONZ	AS.003589
9.22	<i>Sidyrella angularis</i>	Coronation Park, Whangarei	KF669356	-	-	-	-	-	MONZ	AS.001651
10	<i>Sidyrella angularis</i>	Lake Waikaremoana	KF669361	-	-	-	-	-	MONZ	AS.001447
BM Q1	<i>Sidyrella angularis</i>	Hamilton	KF669351	KF669275	-	-	-	-	MONZ	AS.003596
BM Q2	<i>Sidyrella angularis</i>	Hamilton	KF669346	KF669276	-	-	-	-	MONZ	AS.003597
BM Q3	<i>Sidyrella angularis</i>	Hamilton	-	KF669277	-	-	-	-	MONZ	AS.003598
BM Q4	<i>Sidyrella angularis</i>	Hamilton	KF669347	KF669278	-	-	-	-	MONZ	AS.003599
BM Q5	<i>Sidyrella angularis</i>	Hamilton	KF669353	KF669279	-	-	-	-	MONZ	AS.003600
BM Q6	<i>Sidyrella angularis</i>	Hamilton	KF669345	KF669280	-	-	-	-	MONZ	AS.003601
K13	<i>Sidyrella angularis</i>	Tuhua (Mayor) Island	KF669352	KF669269	-	-	-	-	MONZ	AS.003187

Specimen Code	Species	Locality	GenBank Accession Number							Collection	Req. Number
			COI	28S	H3	ND1	18S	ITS			
SKOF	<i>Sidymella 'dwarf' angularis'</i>	Waimea River	KF669364	KF669281	KF669307	KF669323	KF669302	-	MONZ	AS.003611	
7	<i>Sidymella 'dwarf' angularis'</i>	Stokes Valley, Wellington	-	KF669282	-	KF669324	-	-	MONZ	AS.003595	
9.24	<i>Sidymella 'dwarf' angularis'</i>	Stokes Valley, Wellington	KF669365	KF669283	-	KF669325	-	-	MONZ	AS.003595	
6.03	<i>Sidymella angulata</i>	Dunedin	KF669366	KF669256	-	-	-	-	MONZ	AS.003612	
14	<i>Sidymella angulata</i>	Eastbourne, Wellington	KF669369	KF669257	-	KF669320	-	-	MONZ	AS.003613	
15	<i>Sidymella angulata</i>	Eastbourne, Wellington	KF669370	KF669258	-	-	-	-	MONZ	AS.003588	
115c	<i>Sidymella angulata</i>	Hunua Ranges	KF669367	KF669259	-	-	-	-	MONZ	AS.003610	
115d	<i>Sidymella angulata</i>	Hunua Ranges	KF669368	KF669260	-	-	-	-	MONZ	AS.003610	
12403	<i>Sidymella angulata</i>	East Cape	-	-	KF669308	KF669319	KF669301	-	MONZ	AS.003608	
9.3	<i>Sidymella longipes</i>	Tuhua (Mayor) Island	KF669373	KF669284	KF669311	KF669326	KF669304	-	MONZ	AS.003594	
Pos9676P3	<i>Sidymella longipes</i>	Tuhua (Mayor) Island	KF669374	-	-	-	-	-	MONZ	AS.003609	
Pos9677P3	<i>Sidymella longipes</i>	Tuhua (Mayor) Island	KF669374	-	-	-	-	-	MONZ	AS.003609	
11593	<i>Sidymella longipes</i>	Mt Colah NSW	KF669377	-	-	-	-	-	AM	KS115193	
22899	<i>Sidymella longipes</i>	Brisbane, Queensland, Australia	KF669285	KF669285	-	-	-	-	QM	22899	
69163	<i>Stephanopsis nr corticalis</i>	Glenbuck, Australia	KF669378	-	-	-	-	-	QM	69163	
69167	<i>Stephanopsis nr corticalis</i>	Brisbane, Queensland, Australia	KF669379	KF669262	-	-	-	-	QM	69167	
SC1	<i>Stephanopsis nr corticalis</i>	Brisbane, Queensland, Australia	KF669380	-	KF669312	KF669328	-	-	QM	-	
6.6	<i>Sidymella 'snouty'</i>	Three Kings Is	KF669372	KF669261	KF669309	KF669322	-	-	NZAC	-	
6.9	<i>Sidymella 'snouty'</i>	Te Pahi, Northland	KF669371	-	-	-	-	-	MONZ	AS.003605	
1	<i>Sidymella trapezia</i>	Lake Onoke, Wairarapa	KF669381	KF669266	-	-	-	-	MONZ	AS.003593	
6.01	<i>Sidymella trapezia</i>	Ocean Beach, Havelock North	-	KF669265	-	-	-	-	NZAC	-	
6.2	<i>Sidymella trapezia</i>	Foxton	KF669382	KF669263	KF669310	KF669327	-	-	NZAC	-	
9.1	<i>Sidymella trapezia</i>	Masterton	KF669384	KF669264	-	-	-	-	NZAC	-	
9.6	<i>Sidymella trapezia</i>	Masterton	KF669383	KF669267	-	-	-	-	NZAC	-	
EU157117.1	<i>Stephanopsis sp</i>	Australia	-	-	EU157117.1	-	-	-	-	-	
AF374172.1	<i>Eresus cinnabermus</i>	-	-	-	-	AF374172.1	-	-	-	-	
AD328016	<i>Marpissa sp.</i>	-	AD328016	-	-	-	-	-	-	-	
EF419135.1	<i>Spartaeus platnicki</i>	-	-	-	EF419135.1	-	-	-	-	-	

Table 2. Specimen sampling table (this page and previous page). GenBank numbers in bold denote previously published sequences used in this study. Collection repository abbreviations are: MONZ = Museum of New Zealand Te Papa Tongarewa, Wellington, NZ; NZAC = NZ Arthropod Collection, Auckland, NZ; AM = Australian Museum, Sydney, Australia; QM = Queensland Museum, Brisbane Australia. Collection specimen registration numbers are provided where available

Not all species listed in Table 1 were available for molecular study. Attempted DNA extraction from specimens thought to be *Sidymella benhami* was unsuccessful. We were not able to collect fresh material of *Cymbachina albobrunnea* (Urquhart, 1893). Lastly, the identity of the thomisine *Synema suteri* Dahl, 1907 is unclear, so this species was not considered in this study.

DNA extraction

DNA was extracted using a Zymo ZR Genomic Tissue Miniprep kit (Zymo Research, Irvine, CA, USA). Genomic DNA was typically extracted using 1–2 legs from each specimen and proteinase-K to digest the muscle tissue, although some small specimens required the cephalothorax and legs to provide sufficient DNA template. This extraction method allowed exoskeletal material to remain intact and body parts were able to be returned to source specimens after extraction for later study of external morphological characteristics (Paquin and Vink 2009).

Gene targets and primers

A multi-locus molecular approach was used to target a variety of nuclear (histone 3 (H3), 18S rDNA (18S), 28S rDNA (28S), internal transcribed spacer units 1 and 2 (ITS-1 and ITS-2) and wingless (wg)) and mitochondrial gene regions (COI, nicotinamide adenine dinucleotide (NADH) dehydrogenase subunit 1 (ND1)). Although our study primarily focussed on COI and 28S, representatives of major clades identified from preliminary phylogenetic analysis of this sequence data were subjected to further testing using the other gene targets.

Histone 3 has been studied specifically in thomisids (Benjamin *et al.* 2008), making it a logical choice for inclusion. Both 18S and 28S have relatively slow rates of evolution and have been used to test deep divergences in spider phylogenetic studies (e.g. Spagna and Gillespie 2008; Satler *et al.* 2011). In contrast, ITS1 and ITS2 have been used at the species and population level in spiders (Hedin 1997; Arnedo and Gillespie 2006; Chang *et al.* 2007) and are potentially useful in separating cryptic species that may be present in somatically variable taxa such as *Sidymella angularis*. The final nuclear gene region chosen was *wingless* (wg), a relatively novel gene target in spider

studies. Blackledge *et al.* (2009) and Satler *et al.* (2011) have used *wg* in studies of orb-web evolution and on trapdoor spiders respectively.

The chosen mitochondrial gene regions (COI and ND1) are fast evolving and have been used to generate taxonomic information at the population, genus and species levels in spiders (e.g. Vink *et al.* 2008; Rix and Harvey 2012). ND1 is also useful as it is more divergent than COI in most spiders (Vink and Paterson 2003; Vink *et al.* 2008) and has been studied in thomisids by Garb and Gillespie (2006). Nonetheless, relationship patterns revealed from these data should be comparable with those obtained from COI. These gene targets, along with ITS1 and ITS2, were used to test whether *Sidyrella angularis*, a morphologically variable species found throughout New Zealand, constitutes a complex of species rather than just a single species.

Details of each primer pair used for amplification, expected fragment sizes and source references are given in Table 3.

PCR amplification

Standard 25 μ L polymerase chain reactions were used and thermocycling conditions for amplification of each gene target are given in Table 4. PCR amplification was carried out in a Mastercycler-S thermocycler (Eppendorf, Hamburg, Germany). Amplicons were run on a 1% agarose gel, digitally photographed and PCR product fragment sizes were checked against a 100 bp DNA Ladder (Invitrogen, Carlsbad, CA, USA) on the resulting image.

PCR product purification, quantation and sequencing

PCR products were purified with Zymo DNA Clean and Concentrator-5 kits (Zymo Research, Irvine, CA, USA). The final elution volume was 20 μ L of DNA template in double-distilled H₂O. DNA yields were measured on a NanoDrop 1000 spectrophotometer (Thermo Fisher Scientific, Franklin, MA, USA), followed by sequencing in both directions using Big Dye sequencing chemistry at the Massey Genome Service (Massey University, Palmerston North, New Zealand). Novel sequence data were deposited in GenBank. See Table 2 for accession numbers.

Table 3: Gene targets and primer data used in this study.

Gene Target	Forward Primer	5'-Sequence-3'	Reverse Primer	5'-Sequence -3'	Expected fragment size (bp)	Reference
CO1	LCO-1490	GGTCAACAAATCATAAAGATATTGG	C1-N-2568	GCTACAAACATAATAAGTATCATG	1054	Vink <i>et al.</i> (2008) Hedin & Maddison (2001)
	C1-J-1718	GGNGATTGGAAATTGRTTRGTTC	C1-N-2568	GCTACAAACATAATAAGTATCATG	850	Folmer <i>et al.</i> (1994) C. Vink (Pers. comm. 2009)
28S	28S O	GAAACTGCTCAAAGGTAAACGG	28S C	GGTTCGATTAGTCTTTCGCC	800	Spagna & Gillespie (2008) Hedin & Maddison (2001)
ITS	CAS18SF1	TACACACGCGCCGTCGCTACTA	CAS28SBid	TTCTTTTCTCCSCTTAYTRATATGCTTAA	1040	Vink <i>et al.</i> (2008)
H3	H3aF	ATGGCTCGTACCAAGCAGACVGC	H3aR	ATATCCTTRGGCATRATRGTGAC	350	Clogan <i>et al.</i> (1997) Benjamin <i>et al.</i> (2008)
ND1	N1-J-12261	TORTAAGAAATTA TTTGAGC	LR-N-12945	CGACCTCGATGTTGAA TTAA	548	Johansen & Veith (2001) Hedin & Maddison (2001)
18S	1F	TACCTGGTTGATCCTGCCAGTAG	9R	GATCCTTCCGCAGGTTCAACCTAC	1800	Bond & Hedin (2006)
Wg	Spwgf1	GYAAATGCCAYGGWATGTCMGG	Spwgr1	ACTTGRCAACACCARTGAAA AWG	352	Blackledge <i>et al.</i> (2009)

Table 4. PCR conditions used in this study. (R) indicates reverse primers.

Gene target	Primers	Cycling profile					
		Initial denaturation	Cycle numbers	Denaturation	Annealing	Extension	Final extension
COI	LCO-1490 C1-N-2568 C1-J-1718 (R)	94°C 3.5 min	37 cycles	94°C 30s	46°C 50s	72°C 80s	72°C 5 min
28S	28S O 28S C (R)	95°C 2 min	35 cycles	95°C 30s	52°C 30s	72°C 45s +3s per cycle	72°C 7 min
ITS	CAS18SF1 CAS28SBld (R)	94°C 3 min	40 cycles	94°C 30s	55°C 40s	72°C 1 min	72°C 5 min
H3	H3aF H3aR (R)	94°C 3 min	40 cycles	94°C 30s	48°C 40s	72°C 1 min	72°C 5 min
ND1	N1-J-12261 LR-N- 12945 (R)	95°C 2 min	35–37 cycles	95°C 30s	47°C 1 min	72°C 1.5 min	72°C 10 min
18S	1F 9R (R)	94°C 2 min	30 cycles	94°C 45s	48°C 45s +0.2°C per cycle	72°C 90s	72°C 10 min
Wg	Spwgf1 Spwgr1 (R)	94°C 2 min	45–50 cycles	94°C 30s	46°C 30s	72°C 30s	72°C 2 min

Sequence editing, alignment and quality assurance

Raw sequence data files were inspected visually and edited manually using a combination of the SeqMan and EditSeq modules of LaserGene (DNASTar, Madison, WI, USA) and AB Sequence Scanner (Life Technologies, Carlsbad, CA, USA) to assemble consensus sequences. The sequence quality was checked by translation of open reading frames using the invertebrate mitochondrial genome in EditSeq. Protein-coding DNA sequences were considered to be in the correct reading frame if stop codons were absent. Alignments using default parameters were created using either the Muscle function in MEGA version 5.10 (Tamura *et al.* 2011) or PRANKSTER (<http://www.ebi.ac.uk/goldman-srv/prank/prankster/>). Alignment files were trimmed to eliminate primers and overhanging sequences (including a portion

of 16S amplified with ND1) before export in both .meg and .nexus formats for later analysis.

Because low annealing temperature can generate non-target PCR products (e.g. see Rychlik *et al.* 1990), a further test of sequence quality was conducted by aligning COI protein sequences from a representative of each of the two main New Zealand subfamilies (Thomisinae: *Diaea* 4.3, Stephanopinae: *Sidymella angularis* 7.1 – See Table 2 for details) with a protein sequence of the salticid species *Marpissa* (GenBank # AD328016; Hedin and Maddison 2001) in MEGA and mapping them against the structural model of Hedin and Maddison 2001). The overall similarity of these sequences was used as a gauge of sequence authenticity.

As a further test of quality assurance, published sequence data (see Table 2) were also aligned and visually compared with sequences generated for this study in order to verify that authentic thomisid sequence data had been produced.

Data analysis: p-distances

In line with other spider barcoding studies such as Robinson *et al.* (2009), a Kimura 2-parameter (K2P) *p*-distance matrix (Kimura 1980) using the gamma (+G) and pairwise deletion options was computed for each alignment using MEGA. Additional matrices were generated using the same parameters for subfamilial or species groupings for COI and 28S data. Tables for H3 and ND1 are given in the supplementary material (Tables S1–S2, available on the Journal website).

Data analysis: maximum likelihood (ML)

The appropriate evolutionary model was chosen by running the ‘find best DNA/protein model (ML)’ option in MEGA and selecting the model with the lowest Bayesian and Akaike Information Criteria (BIC and AIC respectively) scores. The model chosen for H3 was K2P+G, while all other analyses used general time reversible (GTR)+G. Bootstrapped trees (1000 replicates) were generated in MEGA using these models. Trees generated by these analyses were edited in MEGA.

Data analysis: Bayesian analysis using BEAST

BEAST v1.7.3 (Drummond *et al.* 2012) requires data to be converted to .xml format. Alignments were exported from MEGA in .nexus format and were imported into BEAUti (BEAST software) to create a BEAST file (.xml). Bayesian analyses were then run using BEAST for 1×10^7 generations, sampling every 1000th tree, with two simultaneous and completely independent analyses run for each target region. The simultaneous analyses were combined using LogCombiner (BEAST software). Trees were built using TreeAnnotator (BEAST software) and edited using FigTree 1.4 (Rambaut 2012). Based on prior analysis of log files in Tracer (Rambaut and Drummond 2007), the first 10% of trees were discarded as burn-in, while the remaining trees were reconstructed using a 50% posterior probability (pp) limit. Evolutionary model choice was identical to that chosen for ML where possible. The sole exception was H3, where a K2+G option was not supported by BEAST. Hasegawa, Kishino and Yano (HKY) model + G (Hasegawa *et al.* 1985) had the lowest BIC score of the available options and was used instead. Note that the Bayesian trees are available as supplementary material (Figs S1–S5, on the journal website).

Results

DNA extraction and sequence data generation

Table 2 records gene targets that were successfully sequenced for each specimen. Production of useful quantities of sequence data was successful for several gene targets (COI, 28S, ND1 and H3). As noted previously, generation of COI sequence data required a low annealing temperature to successfully amplify PCR products. Despite the risk of amplification of non-target DNA under such conditions (Rychlik *et al.* 1990), the sequence data passed all quality assurance testing. Paralogues of 28S have been observed in other spider species (e.g. Vink *et al.* 2011a) and may potentially have been amplified here. Attempted amplification of ND1 using Hedin and Maddison's (2001) PCR conditions was unsuccessful. Johannesen and Veith's (2001) protocol proved satisfactory, although in a few cases an increase from 35 cycles to 37 was necessary in order to generate sufficiently large quantities of

PCR products for analysis. Amplification of H3 proceeded without difficulty under conditions given in Table 4.

Not every gene target yielded sufficient high quality sequence data for analysis. For 18S, only five sequences were produced, so this target was dropped but the data have been deposited in GenBank (Table 2). Similarly, despite experimentation with lowered annealing temperatures and an increase in the number of cycles, only three wg sequences of the correct fragment size were generated, but these did not demonstrate any similarity to GenBank wg sequences so are not considered reliable. Additional smaller fragments were sometimes observed in gel electrophoresis imaging. These may represent paralogues (T. Blackledge, pers. comm.) but as wg was not included in the analysis, this possibility was not tested. Only a single high quality usable sequence was generated for ITS1 and ITS2 (GenBank KF669329). Multiple variants of ITS appeared to be amplified and overlaid each other in sequence data. Good quality sequence data has been generated for this target in other spiders (e.g. Vink *et al.* 2008) but at this time it does not appear to be a practical option for Thomisidae.

Phylogenetic analysis

Several clear trends are apparent under both ML (see Figs 2–6) and Bayesian analysis (not shown). Stephanopines and thomisines form distinct clades and within each subfamily clade, New Zealand endemic species group separately from Australian relatives. Putative new species (*S.* ‘*snouty*’, *S.* ‘*dwarf*’ *angularis* and a new *Diaea*) appear to be distinguishable on the basis of genetic as well as morphological data.

For New Zealand stephanopines, the general trend in the majority of analyses featured a pairing of *S. angularis* and *S.* ‘*dwarf*’ *angularis* with *S. angulata* and *S.* ‘*snouty*’ as sister taxa. Bootstrap support is not always high for the stephanopine arrangement, but there is nonetheless generally consistent repetition of a pattern of distinct Australian and New Zealand groupings across gene targets. The major exception is with 28S and this may be due to difficulty in aligning several key taxa as noted previously. This led to the exclusion of *S. longipes*, leaving only one Australian stephanopine in the

analysis and it grouped with two New Zealand taxa (*S. angulata* and *S. 'snouty'*).

The arrangement of Thomisines is consistent across analyses, with New Zealand and Australian species forming separate groupings and the New Zealand clade consisting of *Diaea ambara* as sister to a group containing *D. albolimbata*, *D. sphaeroides* and a new species of *Diaea*.

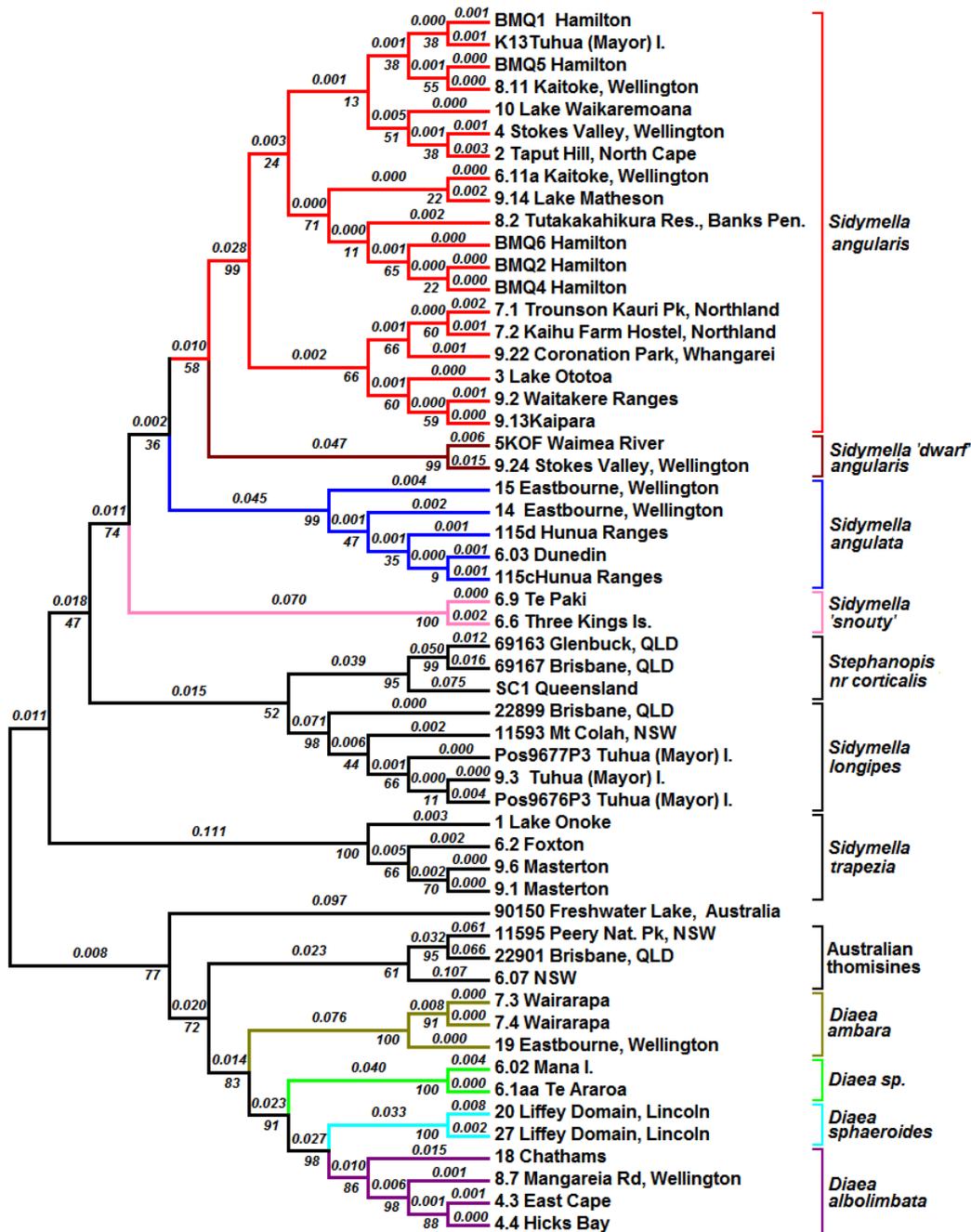


Fig. 2. Maximum likelihood (ML) topological tree based on COI sequence data. Branch lengths are given above branches and bootstrap values are given below them. Branches representing non-New Zealand endemic taxa are in black.

COI (see Fig. 2)

The general trends reported above were also observed here (Fig. 2). There were some minor differences in stephanopine tree topologies generated by ML and Bayesian analysis. Under Bayesian analysis (Fig. S1), support for a 'dwarf' + 'angularis' clade is much stronger (pp 0.9927) than under ML. Bayesian analysis (not shown) also generated a weakly supported (pp 0.444) *angulata* + 'snouty' subclade. Under ML (Fig. 2), these species form weakly supported separate sister clades. Australian stephanopines formed separate sister clades under Bayesian analysis, while under ML, *Sidymella trapezia* was sister to a *corticalis* + *longipes* clade. Both forms of analysis returned the same thomisine clades.

The single table of corrected (K2P+G) distances for all sampled taxa is very large, so tables for each subfamily are given instead. Table 5 covers thomisines, while Table 6 covers a representative set containing two examples of each stephanopine taxon present in Fig. 2.

28S (see Fig. 3)

Both Bayesian analysis (Fig. S2) and ML (Fig. 3) returned much the same arrangement of thomisine species as observed for COI (Fig. 2). However, there was some disagreement in the arrangement of stephanopine clades. Under ML, the stephanopines formed two clades: *angularis* + 'dwarf' was sister to a clade containing *S. trapezia* + (*angulata* + 'snouty'). Under Bayesian analysis, the position of *S. 'dwarf' angularis* could not be sensibly resolved and it was placed outside all other thomisid taxa. As noted previously, sequence data for this species proved difficult to align and this may be the reason for this placement. The arrangement of major clades varied, with *S. angularis* sister to two clades containing the thomisines and the remaining stephanopines respectively. Note that the arrangement of species within these clades matched that shown under ML (Fig. 2), even though the

placement of the clades varied. Repeating the Bayesian analysis without *S. 'dwarf' angularis* did not change the placement of clades.

Corrected (K2P+G) distances for thomisines and a representative set containing two examples of each stephanopine taxon featured in Fig. 3 except *S. 'snouty'* (one example only) are given in Tables 8 and 9 respectively. Note that the stephanopine table also includes *S. longipes*, a species excluded from the analysis because of alignment difficulties.

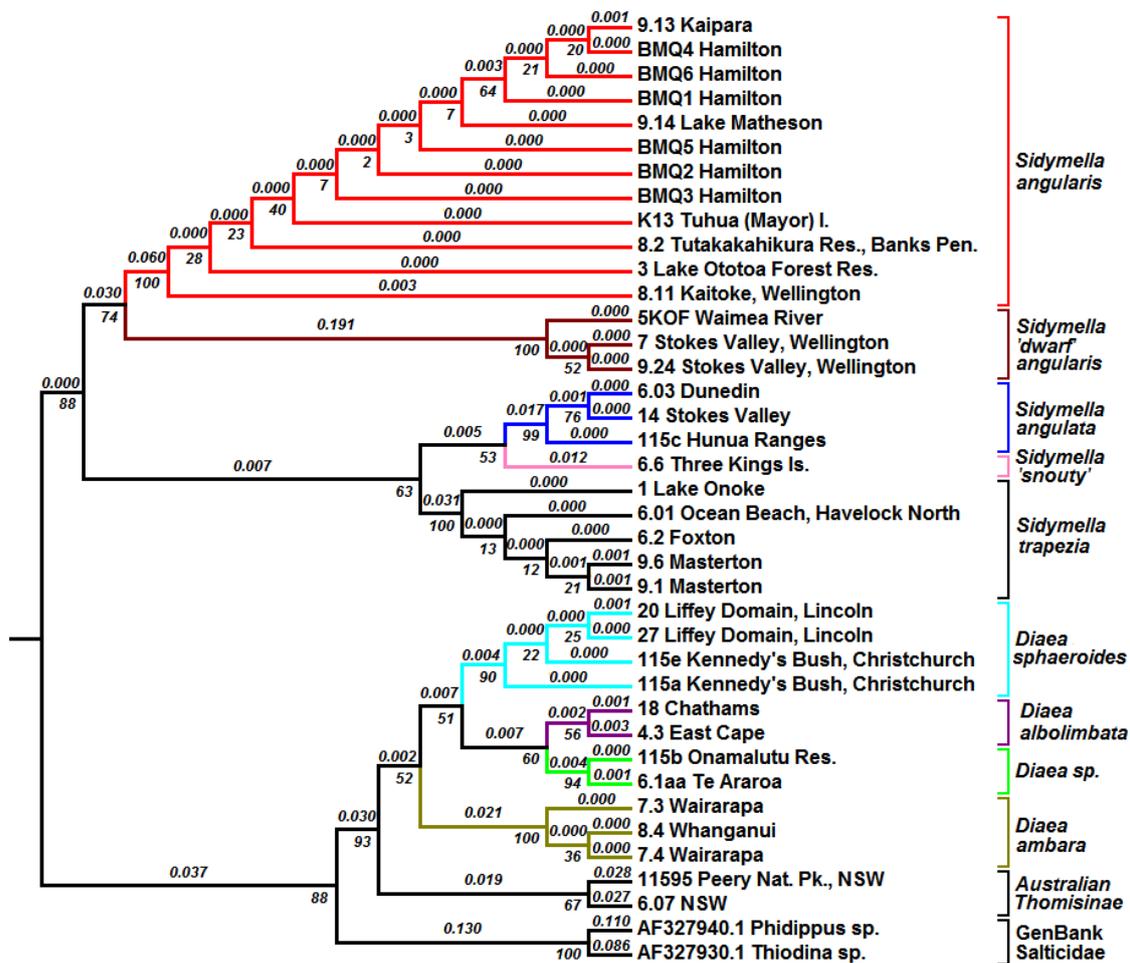


Fig. 3. Maximum likelihood (ML) topological tree based on 28S sequence data. Branch lengths are given above branches and bootstrap values are given below them. Branches representing non-New Zealand endemic taxa are in black.

Other gene targets

H3 (see Fig. 4)

Both forms of analysis returned clear New Zealand species clades within the two subfamilies. The arrangement of New Zealand stephanopines was weakly supported under both forms of analysis and this may explain their topological differences. Bayesian analysis (Fig. S3) produced a clade containing ((*'dwarf'* + *angularis*) + *angulata*) + *'snouty'* while ML (Fig. 4) produced ((*angulata* + *'dwarf'*) + *angularis*) + *'snouty'*. The arrangement of thomisines was identical in both analyses. Note that GenBank sample DQ174355.1 previously recorded as *Diaea* sp. appears to be a specimen of *D. sphaeroides*.

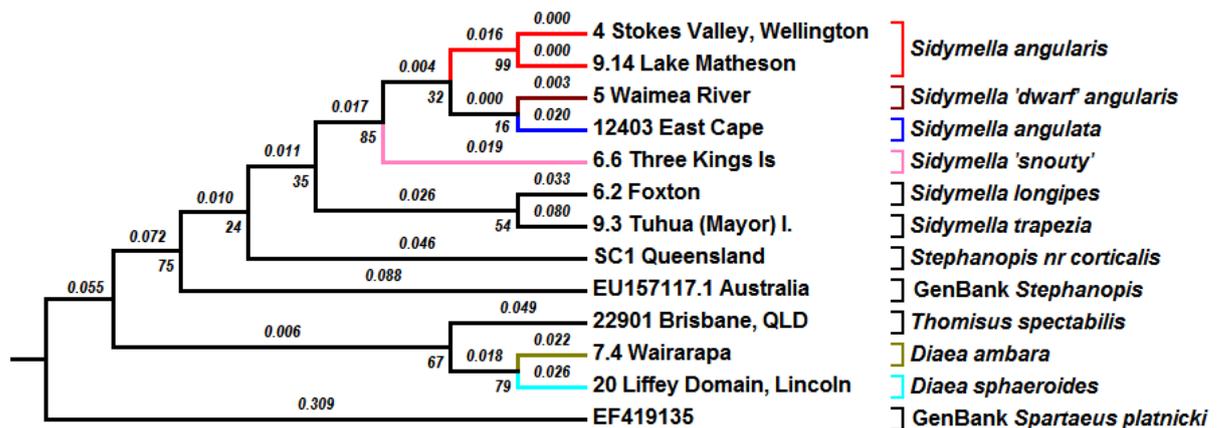


Fig. 4. Maximum likelihood (ML) topological tree based on H3 sequence data. Branch lengths are given above branches and bootstrap values are given below them. Branches representing non-New Zealand endemic taxa are in black.

Corrected (K2P+G) distances are given for species sampled for H3 in the supplementary material (Table S1).

ND1 (see Fig. 5)

Once again, a pattern of distinct New Zealand groupings within each subfamily was observed under both ML (Fig. 5) and Bayesian analysis (Fig. S4). The only difference between the two forms of analysis was the positioning of *S. angularis*. Under ML, both it and *S. 'dwarf' angularis* formed sister clades to (*snouty* + *angulata*) while under Bayesian analysis it grouped

Both forms of analysis returned a distinct Australia–New Zealand split, with ('dwarf' + *angularis*) recovered for New Zealand stephanopines and (*albolimbata* + *sphaeroides*) + *ambara* for New Zealand thomisines. *Sidymella angulata* and *S.* 'snouty' paired under ML but not under Bayesian analysis. Additionally *Sidymella longipes* and *Stephanopis corticalis* form a weakly supported pairing under ML (bootstrap value 51). Under Bayesian analysis, the three included Australian stephanopines are separate. The number of positions for each component in this dataset under partial deletion is COI: 546, 28S: 646, H3: 296 and ND1: 555.

Discussion

DNA sequence data generation and alignment

The extraction of DNA and successful amplification of PCR products proved challenging in several respects. Specimen quality varied greatly in terms of suitability for DNA extraction, with many more specimens than listed here failing to yield sufficient high quality DNA for successful amplification and subsequent sequencing. Amplification of one gene target from a given specimen was not a guarantee that amplification of other targets from the same individual would also succeed. This explains the inconsistency in terms of specimens used in different analyses and the absence of some New Zealand taxa (e.g. *Sidymella benhami*) from this study. This phenomenon was not confined to older or suboptimally preserved specimens. For example, the BMQ series of six *S. angularis* specimens from Hamilton (see Table 2) were sampled shortly after capture. All six specimens produced 28S amplicons but amplification of COI was not successful for BMQ3.

There was some initial difficulty in generating PCR products for COI. The unmodified protocol of Vink *et al.* (2008) rarely produced any amplicons. A combination of lowered annealing temperature and increased annealing and extension times (Table 4) usually resolved the issue. Occasionally, amplification of a shorter fragment (850 bp versus 1154) using C-1-J-1718 and C-1-N-2568 (Hedin and Maddison 2001) was tried when LCO-1490 and C-1-N-2568 failed.

While at least modest numbers of sequences were obtained for ND1, 28S and H3, other gene targets did not fare as well. Only one usable sequence was obtained for ITS1 and ITS2. Rix and Harvey (2012) noted multiple length-variable rDNA amplicons for this gene target in Australian archaeid spiders and that observation appears equally applicable to Australasian Thomisidae. The primers used in this study are designed to flank a large fragment encompassing both ITS regions and 5.8S rRNA. Attempts to amplify ITS1 and ITS2 as separate, smaller fragments rather than a single large one using the protocols and primers of Ji *et al.* (2003) did not result in any improvement. Amplification of wg proved consistently difficult. Very high quality genomic DNA is usually required (T. Blackledge, pers. comm.) and we may have amplified paralogues in several of our experiments. Only three clean wg sequences were generated. Generation of sequence data for 18S failed to yield any for New Zealand thomisines although several stephanopine sequences were produced.

Alignment of 28S sequence data was reasonably straightforward for most species. However, the stephanopines *S. angularis*, *S. 'dwarf' angularis* and *S. longipes* produced sequences containing indels not observed in other species. The same pattern was observed consistently in multiple samples for each species, but we cannot rule out amplification 28S paralogues. For at least some groups of spiders, it appears there may be three copies of 28S present, two of which are functional and of similar size (C. J. Vink, pers. comm.). Thus, there is a possibility that the equivalent copy of 28S has not been amplified in all species and this may explain the consistently anomalous sequence data for species such as *S. longipes*. Even after excision of obviously problematic sequence portions, alignment of *S. 'dwarf' angularis* and *S. longipes* proved particularly difficult. Ultimately, the latter species had to be excluded from the analysis as it could not be sensibly aligned at all and always placed as a separate long branch outside the other thomisids in every form of analysis attempted. This was also true for *S. 'dwarf' angularis* under Bayesian analysis, although the ML algorithm seemed better able to place this taxon. These three species did not present any particular alignment difficulties for other surveyed gene targets.

Phylogenetic analysis

Two general trends are apparent in the trees (Figs 2–6). First, there is a clear separation of subfamilies and second, exclusively New Zealand clades are typically recovered within those subfamilies. For New Zealand thomisines, *Diaea ambara* appears to be sister to a clade containing a trio of closely related *Diaea* species. This is in keeping with the expected pattern based on morphological characters such as male palp architecture (PJS, pers. obs.). In the New Zealand stephanopines, there is less consistency between analyses with respect to the arrangement of taxa, but, as expected on the basis of morphological synapomorphies (e.g. cephalothoracic ridges), *Sidymella angularis* was paired with *S. 'dwarf angularis'* in the majority of cases. For ML, the sole exception was H3 (Fig. 4), where composition of the New Zealand clade was resolved with very weak bootstrap support. Under Bayesian analysis, the ND1 tree (Fig. 5) differed and *S. 'dwarf angularis'* was placed as sister to a clade containing the other three included New Zealand stephanopines. The placement of *S. angularis* and *S. 'dwarf angularis'* proved problematic under Bayesian analysis of 28S (not shown), although they paired under ML analysis of the same dataset (Fig. 3). As noted earlier, these species, along with *S. longipes*, proved difficult to align and that may explain the lack of congruence with other trees.

There was some variation in the placement of *S. angulata* and *S. 'snouty'* in the New Zealand stephanopine clade. They were usually placed as sister taxa to the (*dwarf* + *angularis*) clade, either singly or as a pair. The exceptions were in the Bayesian ND1 tree, where they formed a clade with *S. angularis*, and H3 under ML analysis, where, as noted earlier, the composition of the New Zealand stephanopine clade was weakly resolved.

Distinct New Zealand clades were recovered for the thomisines and, with the exception of 28S, recovered for the stephanopines. Alignment difficulties meant that *S. longipes* was excluded from 28S analysis and this, along with the difficulties in aligning and accurately placing *S. angularis* and *S. 'dwarf angularis'*, is probably a factor in the Australian *S. trapezia* being placed with *S. angularis* and *S. 'snouty'*.

Overall, the general picture that emerges is one of distinct New Zealand clades within both subfamilies. This seemed particularly consistent for New Zealand thomisines regardless of gene target or analytical method. Only the 28S Bayesian analysis failed to return a clearly separate New Zealand stephanopine clade.

Are cryptic species present?

A K2P+G distance matrix of COI data (Table 7) for *Sidymella angularis*, the most common and widespread of the New Zealand stephanopines, suggests this is a single species. The highest difference of 1.6% was recorded between a specimen from the upper North Island (Trounson Kauri Park) and one from Tuhua (Mayor) Island. This is well below 2.15%, the figure given by Robinson *et al.* 2009 as the mean of intraspecific corrected distances in their study of COI-based DNA 'barcoding' for 361 spider species. Fig. 2 suggests there is some haplotype diversity, as might be expected from a widespread and somewhat variable species. However, while many specimens from the same general geographic region group together, a consistent biogeographic pattern is not evident. Specimens from quite disparate localities (e.g. Lake Matheson, midway down the South Island and Hamilton in the upper North Island) are paired in the same subclades, suggesting that long-distance dispersal may be occurring. Only two ND1 sequences were produced for this species, but their K2P+G distances were also low. As noted earlier, amplification of ITS1 and ITS2 was unsuccessful.

New species

Three taxa, *Sidymella* 'snouty', *S.* 'dwarf' *angularis* and a *Diaea* specimen with similarities to *D. albolimbata* and *D. sphaeroides*, are all considered to be morphologically distinct taxonomic units (PJS, pers. obs.). Genetic data presented here are further evidence of their distinctiveness. These taxa will be formally described as species in a forthcoming taxonomic revision on the New Zealand Thomisidae (PJS, unpubl. data).

Bryant (1933) noted that the generic position of New Zealand stephanopines was unclear as they possessed characters not found in the type species of *Sidyra* (now *Sidymella*). New generic assignments are thus

probable for the New Zealand stephanopines, but regardless of final generic placement, *S. 'dwarf' angularis* is congeneric with *S. angularis*. Not only did these two species typically pair in the analyses presented here, but they also share several unique morphological characters, such as paired cephalothoracic ridges (PJS, pers. obs.).

The taxon known as *Sidymella 'snouty'* has several unique characters, the most obvious of which is the presence of a small forward-pointing protuberance near the eye region. Numerous specimens from New Zealand entomological collections have been examined and on the basis of collection records, the known geographical range for these spiders is restricted to Te Paki in the northern part of Northland, the Three Kings Islands and Great Barrier Island (PJS, pers. obs.). Unfortunately, nearly all the available material comprises juvenile specimens. Adult specimens are usually required in order to make a reliable species identification as they possess the morphological characters (often genitalic) that are unique to each species (Paquin *et al.* 2010). The reliance on genitalic character states to identify species has arisen because they often evolve faster than other morphological markers, possibly due to sexual selection, and are valuable to distinguish even closely related species (Barrett and Hebert 2005; Garb and Gillespie 2006). Currently only two adult '*snouty*' specimens are known from existing collections, specifically a male from Three Kings and a female from Te Paki. As the only adult specimens are from different places and are different sexes, morphological study cannot currently determine how many '*snouty*' species are present in institutional collections. However, as the COI sequence data from the Te Paki female (6.6) and a juvenile from Three Kings (6.9) differ by ~0.2%, it appears very likely they represent a single species as this value is below the 2.15% average intraspecific divergence figure of Robinson *et al.* (2009). This finding needs to be treated cautiously given that only a single specimen from each of the two localities has been sampled. No firm conclusions can be drawn on the status of the Great Barrier Island population until more material is available for study. Note that the Great Barrier Island specimen along with the Three Kings male specimen were not included in this analysis because they have been in long-term storage in conditions that are adequate to preserve them for

morphological study (70% ethanol, 16°C or more), but are suboptimal for yielding molecular data according to Vink *et al.* (2005).

Evolution and phylogeny of the New Zealand Thomisidae

As noted in the introduction, stephanopine thomisids such as *Sidymella* are apparently absent from the South Pacific region outside of Australia and New Zealand (Platnick 2013). Taken together with the fact that, at the outset of this study, no Australian stephanopines had been officially recorded from New Zealand, it seemed likely that these spiders lacked the capacity for long-range dispersal. In contrast, although no Australian members of *Diaea* are known from New Zealand, dispersal by ballooning (Blandenier and Fürst 1998) and a distribution across the Pacific (Lehtinen 1993) is documented for this genus. On the basis of historically recorded distributions, it would appear that New Zealand *Sidymella* fits Forster's (1975) 'Gondwanan' model.

However, two pieces of evidence suggest this model is unlikely to be correct. First, two Australian species appear to have recently become established here. The presence of *Sidymella longipes* (L. Koch, 1874) in New Zealand was reported for the first time in Sirvid *et al.* (2010). Museum collection records indicate that it has been present in the upper North Island for several decades. The method of arrival in New Zealand is not known, but its presence on offshore islands that are not normally occupied by humans, such as Tuhua (PJS, pers. obs.), suggest it is capable of dispersal over water. A second stephanopine species currently thought to be *Sidymella trapezia* appears to have very recently become established in New Zealand (PJS, pers. obs.). The earliest known museum collection record is from Lake Onoke in the Wairarapa in 2008 (PJS, pers. obs.). It appears to be absent from New Zealand museum collections before this time even though specimens continue to be collected from other lower North Island localities (PJS, pers. obs.). Note that full records will be included in a planned taxonomic revision of this family for New Zealand. How this species came to be in New Zealand is not known but as all early records are from coastal regions rather than urban areas (PJS, pers. obs.), natural dispersal to New Zealand (perhaps by ballooning) seems more probable than anthropogenic dispersal. If Australian stephanopines can naturally disperse to New Zealand now, they may also

have done so in the past. Similarity of COI distance data for *Sidymella angularis* specimens from widely different New Zealand localities also suggests the possibility of a higher degree of dispersal capability in this species than previously realised.

Fossil exemplars of thomisid spiders are rare and the most recent examples are from the Paleogene era (Selden and Penney 2010) with none recorded from the Australasian subregion (Dunlop *et al.* 2011). Furthermore, there are no known stephanopine fossils, so it is not currently possible to corroborate subfamilial divergence dates derived from sequence data with paleontological evidence. This makes it difficult to calibrate our molecular data against a fossil record. One option is to apply a molecular clock model that seems most applicable on the basis of prior use with similar organisms. Studies of New Zealand lycosids (Vink and Paterson 2003) and pisaurids (Vink and Dupérré 2010) used the Brower (1994) rate of 2.3% per million years pairwise divergence for arthropods. The lowest COI K2P+G value between Australian and New Zealand stephanopines is 12.1% for *Sidymella longipes* and *S. angularis*. Applying the same rate model here, it would appear New Zealand stephanopines diverged from their Australian relatives no more than 5.2 mya. For thomisines, the lowest COI K2P+G value between Australian and New Zealand taxa is 12.3% for *Diaea* sp. (Peery Pk, NSW) and *D. ambara*. This gives a divergence date of 5.3 mya. Both figures are similar to the five million year divergence date suggested for the New Zealand lycosid genus *Anoteropsis* (Vink and Paterson 2003) and clearly much later than might be expected if Australian and New Zealand stephanopines were evolving in complete isolation from each other since the Mesozoic. The prospective divergence date is also well after the Oligocene. The consistent recovery of single New Zealand clades in each subfamily also suggests they are each descended from single colonisation events but this result should be treated with caution given the limited range of Australian taxa successfully sampled. The K2P distance value for *S. 'snouty'* and *S. 'dwarf' angularis* (13.4%) may also hint at an earlier colonisation event. Sharma and Wheeler (2013) suggested that the evolutionary lineages that survive mass extinctions are difficult to distinguish from scenarios of rapid radiation. Thus, it could be

argued that the New Zealand thomisid clades may have radiated from remnant endemic elements, but if so, we would expect to see higher levels of divergence from Australian relatives. Such a scenario would also be more plausible (although not proven) if Australian thomisids were not found in New Zealand.

The phylogenetic structure for New Zealand stephanopines appears to be *S. angularis* + *S. 'dwarf angularis'* although the relative positions of *S. 'snouty'* and *S. angulata* within this clade varied between analyses. Additional sequence data, particularly from *S. benhami* and *S. 'snouty'* may resolve this. The phylogenetic structure of the New Zealand thomisines has *D. ambara* as sister to a trio of *Diaea* species (*D. sphaeroides*, *D. albolimbata* and an undescribed taxon).

Summary and conclusions

Overall, the molecular data supported separate New Zealand lineages within the Australasian stephanopines and thomisines. No Australian species of thomisid were recorded for New Zealand in the late nineteenth and early twentieth century, when all currently known New Zealand thomisids were described. More recent collection records prove that Australian stephanopines can reach New Zealand. Although the mechanism for this has not been established, some circumstantial evidence suggests it may be dispersal via ballooning. Stephanopines were considered a potential model 'Gondwanan' group (*sensu* Forster 1975) and not thought to disperse well. However, evidence of dispersal ability, combined with prospective maximum divergence date of 5.3 mya, suggests this view is no longer accurate. This date is also well after the Oligocene 'drowning', meaning that hypothesis cannot be falsified for this spider family.

Low corrected K2P-distance values based on COI sequences indicate that the widely distributed yet morphologically variable taxon *S. angularis* is a single species. Three undescribed endemic species (two stephanopines and one thomisine) distinguished by morphological characters also appeared distinct on the basis of molecular data. Our study has shown that New Zealand is home to a unique but recently derived assemblage of thomisid

spiders. We have successfully demonstrated the monophyly of both New Zealand subfamilial groupings and individual species. We suggest our approach may serve as a model for future exploration of the origins of the New Zealand spider fauna.

Acknowledgements

We thank the many people who have made specimens available for this study, especially Cor Vink and Simon Pollard (Canterbury Museum, NZ), Mike Fitzgerald (Museum of New Zealand, Te Papa Tongarewa, NZ), Grace Hall (Landcare Research, NZ), Cody Fraser (Otago Museum, NZ); John Marris and Jagoba Malumbres-Olarte (Lincoln University, NZ), Olivier Ball (NorthTec, NZ), Dave Seldon and Stephen Thorpe (Auckland University, NZ), Helen Smith and Graham Milledge (Australian Museum, Australia), Robert Whyte and Wendy Hebron (Queensland Museum, Australia) and Bryce McQuillan (Hamilton, NZ) who also provided one of the photographs. PJS would like to thank Suresh Benjamin (Zoologisches Forschungsmuseum Alexander Koenig, Germany), David Court (Raffles University, Singapore) and Pawel Szymkowiak (A. Mickiewicz University, Poland) who provided useful insights into the complexities of the Australasian thomisid fauna. Ann Wood, Kelly Prendergast (all Victoria University of Wellington), Todd Blackledge (University of Akron, USA) and Cor Vink all provided much needed technical advice or aid and assistance in the laboratory. PJS would also like to acknowledge the institutional support of Phil Lester (Victoria University) and Simon Whittaker, Carol Diebel, Claudia Orange and Anna Cowie (Museum of New Zealand Te Papa Tongarewa).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 18 <i>D. albolimbata</i> Chatham I.														
2 4.3 <i>D. albolimbata</i> East Cape	0.025													
3 8.7 <i>D. albolimbata</i> Mangareia Rd	0.023	0.009												
4 4.4 <i>D. albolimbata</i> Hicks Bay	0.023	0.001	0.008											
5 6.02 <i>D. sp</i> Mana Island	0.095	0.089	0.093	0.085										
6 6.1aa <i>D. sp</i> Te Araroa	0.075	0.073	0.074	0.07	0.004									
7 19 <i>D. ambara</i> Eastbourne, Wellington	0.105	0.113	0.109	0.112	0.109	0.104								
8 7.3 <i>D. ambara</i> Wairarapa	0.115	0.109	0.113	0.108	0.113	0.106	0.008							
9 7.4 <i>D. ambara</i> Wairarapa	0.115	0.113	0.113	0.109	0.115	0.108	0.008	0						
10 20 <i>D. sphaeroides</i> Liffey Domain, Lincoln	0.06	0.05	0.055	0.05	0.094	0.085	0.112	0.114	0.114					
11 27 <i>D. sphaeroides</i> Liffey Domain Lincoln	0.052	0.045	0.049	0.045	0.094	0.081	0.107	0.113	0.113	0.008				
12 90150 <i>D. sp.</i> Freshwater Lake, Australia	0.151	0.138	0.144	0.135	0.14	0.137	0.143	0.141	0.143	0.142	0.144			
13 11595 <i>D. sp.</i> Peery Nat. Park, NSW	0.149	0.138	0.151	0.138	0.135	0.129	0.128	0.123	0.123	0.149	0.148	0.164		
14 6.07 <i>D. sp.</i> NSW	0.152	0.148	0.151	0.145	0.139	0.135	0.154	0.15	0.151	0.146	0.147	0.181	0.145	
15 22901 <i>T. spectabilis</i> Brisbane, QLD	0.155	0.144	0.154	0.144	0.145	0.144	0.154	0.144	0.144	0.162	0.158	0.153	0.102	0.146

Table 5. K2P+G corrected pairwise deletion distance distances for thomisine COI sequences

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
7.1 <i>S. angularis</i> Trounson													
1 Kauri Pk., Northland													
8.2 <i>S. angularis</i>													
Tutakakahikura Res., Banks													
2 Pen.	0.025												
5KOF <i>S. 'dwarf angularis'</i>													
3 Waimea River	0.072	0.09											
9.24 <i>S. 'dwarf angularis'</i>													
4 Stokes Valley, Wellington	0.097	0.113	0.024										
14 <i>S. angularata</i> Eastbourne,													
5 Wellington	0.077	0.096	0.089	0.12									
115c <i>S. angularata</i> Hunua													
6 Ranges	0.081	0.09	0.091	0.122	0.006								
9.3 <i>S. longipes</i> Tuhua													
7 (Mayor) Island	0.124	0.131	0.134	0.169	0.128	0.132							
22899 <i>S. longipes</i> Brisbane,													
8 QLD	0.123	0.128	0.137	0.166	0.133	0.135	0.007						
69163 <i>St. nr corticalis</i>													
9 Glenbuck, Australia	0.121	0.123	0.133	0.155	0.125	0.123	0.132	0.133					
10 SC1 <i>St. nr corticalis</i> QLD	0.129	0.133	0.126	0.148	0.121	0.119	0.127	0.127	0.109				
6.9 <i>S. 'snouty'</i> Te Pahi,													
11 Northland	0.104	0.111	0.104	0.135	0.112	0.111	0.134	0.13	0.143	0.145			
12 6.6 <i>S. 'snouty'</i> Three Kings Is	0.102	0.104	0.104	0.134	0.111	0.11	0.13	0.126	0.143	0.147	0.002		
13 6.2 <i>S. trapezia</i> Foxton	0.132	0.151	0.152	0.175	0.147	0.149	0.164	0.165	0.161	0.156	0.139	0.136	
14 9.6 <i>S. trapezia</i> Masterton	0.131	0.131	0.14	0.162	0.146	0.144	0.154	0.153	0.16	0.129	0.129	0.003	

Table 6. K2P+G corrected pairwise deletion distance distances for a selection of stephanopine COI sequences.

<i>Sidymella angularis</i>	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	2 Taput Hill North Cape																	
2	3 Lake Ototoa	0.007																
3	4 Stokes Valley	0.005	0.009															
4	6.11a Kaitoke	0.007	0.007	0.005														
5	7.1 Trounson Kauri Park	0.01	0.007	0.012	0.01													
6	7.2 Kaihu Farm Hostel	0.009	0.005	0.01	0.009	0.005												
7	9.2 Waitakeres	0.009	0.002	0.01	0.009	0.009	0.007											
	8.2 Tutakakahikura Res.																	
8	Banks Pen.	0.007	0.007	0.005	0	0.01	0.009	0.009										
9	8.11 Kaitoke Wellington	0.005	0.009	0	0.005	0.012	0.01	0.01	0.005									
10	9.13 Kaipara	0.007	0	0.009	0.007	0.007	0.005	0.002	0.007	0.009								
11	9.14 Lake Matheson	0.007	0.007	0.005	0	0.01	0.009	0.009	0	0.005	0.007							
	9.22 Coronation Park																	
12	Whangarei	0.005	0.005	0.007	0.009	0.005	0.003	0.007	0.009	0.007	0.005	0.009						
	Spider10 Lake																	
13	Waikaremoana	0.003	0.007	0.002	0.003	0.01	0.009	0.009	0.003	0.002	0.007	0.003	0.005					
14	BMQ1 Hamilton	0.007	0.01	0.002	0.003	0.014	0.012	0.012	0.003	0.002	0.01	0.003	0.009	0.003				
15	BMQ2 Hamilton	0.009	0.009	0.007	0.002	0.012	0.01	0.01	0.002	0.007	0.009	0.002	0.01	0.005	0.005			
16	BMQ4 Hamilton	0.009	0.009	0.007	0.002	0.012	0.01	0.01	0.002	0.007	0.009	0.002	0.01	0.005	0.005	0		
17	BMQ5 Hamilton	0.005	0.009	0	0.005	0.012	0.01	0.01	0.005	0	0.009	0.005	0.007	0.002	0.002	0.007	0.007	
18	BMQ6 Hamilton	0.009	0.009	0.007	0.002	0.012	0.01	0.01	0.002	0.007	0.009	0.002	0.01	0.005	0.005	0	0	0.007
19	K13 Tuhua (Mayor) Islan ^v	0.009	0.012	0.003	0.005	0.016	0.014	0.014	0.005	0.003	0.012	0.005	0.01	0.005	0.002	0.007	0.003	0.007

Table 7. K2P+G corrected pairwise deletion distance distances for *Sidymella angularis* COI sequences.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
115a <i>D. sphaeroides</i>													
Kennedy's Bush, Christchurch													
115e <i>D. sphaeroides</i>													
Kennedy's Bush, Christchurch	0												
20 <i>D. sphaeroides</i> Liffey													
Domain, Lincoln	0.001	0.001											
27 <i>D. sphaeroides</i> Liffey													
Domain, Lincoln	0	0	0										
115b <i>D. sp.</i> Onamalutu													
Res., Christchurch	0.015	0.015	0.016	0.015									
6.1aa <i>D. sp.</i> Te Atarua	0.015	0.015	0.016	0.015	0.001								
4.3 <i>D. albolimbata</i> East													
Cape	0.014	0.014	0.015	0.014	0.008	0.008							
18 <i>D. albolimbata</i>													
Chatham I.	0.012	0.012	0.013	0.012	0.005	0.005	0.004						
7.3 <i>D. ambara</i>													
Wairarapa	0.026	0.026	0.024	0.024	0.031	0.032	0.029	0.032					
7.4 <i>D. ambara</i>													
Wairarapa	0.026	0.026	0.024	0.024	0.031	0.032	0.029	0.032	0				
8.4 <i>D. ambara</i>													
Whanganui	0.024	0.024	0.023	0.023	0.03	0.031	0.027	0.031	0	0			
8.8s <i>D. ambara</i>													
Belmont Reg. Pk., Wellington	0.024	0.024	0.023	0.023	0.03	0.031	0.027	0.031	0	0	0		
11595 <i>D. sp.</i> Peery													
Nat. Park, NSW	0.052	0.052	0.054	0.052	0.051	0.051	0.051	0.054	0.049	0.049	0.048	0.048	0.048
6.07 <i>D. sp.</i> NSW,													
Australia	0.048	0.048	0.048	0.046	0.045	0.047	0.046	0.045	0.055	0.055	0.054	0.054	0.048

Table 8. K2P+G corrected pairwise deletion distance distances for thomisine 28S sequences.

Taxon	1	2	3	4	5	6	7	8	9	10
1 9.1 <i>S. trapezia</i> Masterton										
2 6.01 <i>S. trapezia</i> Ocean Beach, Havelock North	0									
3 115c <i>S. angularata</i> Hunua Ranges	0.044	0.043								
4 14 <i>S. angularata</i> Eastbourne, Wellington	0.045	0.043	0.001							
5 5KOF <i>S. 'dwarf'</i> <i>angularis'</i> Waimea River	0.169	0.172	0.18	0.173						
6 7 <i>S. 'dwarf'</i> <i>angularis'</i> Stokes Valley	0.17	0.174	0.182	0.174	0					
7 9.3 <i>S. longipes</i> Tuhua (Mayor) Island	0.121	0.121	0.134	0.128	0.167	0.168				
8 22899 <i>S. longipes</i> Brisbane, QLD	0.123	0.123	0.131	0.125	0.167	0.169	0.001			
9 6.6 <i>S. 'snouty'</i> Three Kings Is	0.041	0.041	0.03	0.029	0.16	0.161	0.13	0.127		
10 9.14 <i>S. angularis</i> Lake Matheson	0.113	0.11	0.119	0.115	0.172	0.174	0.143	0.142	0.092	
11 BMQ5 <i>S. angularis</i> Hamilton	0.111	0.11	0.119	0.116	0.172	0.172	0.143	0.142	0.093	0.003

Table 9. K2P+G corrected pairwise deletion distance distances for a selection of stephanopine 28S sequences.

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SUPPLEMENTARY MATERIAL

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
1 4 <i>S. angularis</i> Stokes Valley												
2 9.14 <i>S. angularis</i> Lake Matheson	0											
3 5KOF <i>S. 'dwarf angularis'</i> Waimea River	0.018	0.018										
4 12403 <i>S. angularata</i> East Cape	0.03	0.03	0.023									
5 6.6 <i>S. 'snoufy'</i> Three Kings Is	0.031	0.031	0.022	0.033								
6 6.2 <i>S. trapezia</i> Foxton	0.077	0.081	0.064	0.082	0.081							
7 9.3 <i>S. longipes</i> Tuhua (Mayor) Island	0.106	0.109	0.092	0.125	0.11	0.091						
8 EU157117.1 <i>Stephanopsis</i> sp. Australia	0.116	0.119	0.109	0.124	0.125	0.111	0.128					
9 SC1 <i>Stephanopsis</i> nr <i>corticalis</i> QLD	0.079	0.078	0.069	0.08	0.069	0.093	0.114	0.11				
10 22901 <i>Thomismus spectabilis</i> Brisbane, QLD	0.12	0.123	0.125	0.137	0.126	0.131	0.151	0.147	0.107			
11 7.4 <i>D. ambara</i> Wairarapa	0.111	0.114	0.108	0.119	0.108	0.133	0.14	0.141	0.112	0.071		
12 EF419135.1 <i>Spartaeus platnicki</i>	0.221	0.224	0.222	0.211	0.222	0.243	0.239	0.23	0.206	0.226	0.189	
13 20 <i>D. sphaeroides</i> Liffey Domain, Lincoln	0.121	0.124	0.118	0.129	0.126	0.135	0.138	0.151	0.118	0.081	0.041	0.217

Table S1. K2P+G corrected pairwise deletion distances for H3 sequences.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
1 AF374172.1 <i>Eresus cinnaberinus</i>													
2 9.13 <i>S. angularis</i> Kaipara	0.307												
3 5KOF <i>S. 'dwarf angularis'</i> Waimea River	0.327	0.097											
4 7 <i>S. 'dwarf angularis'</i> Stokes Valley	0.338	0.097	0.002										
5 6.6 <i>S. 'snouty'</i> Three Kings Is	0.354	0.128	0.116	0.116									
6 14 <i>S. angularata</i> Eastbourne, Wellington	0.334	0.084	0.077	0.077	0.093								
7 12403 <i>S. angularata</i> East Cape	0.337	0.086	0.079	0.079	0.095	0.002							
8 9.3 <i>S. longipes</i> Tuhua (Mayor) Island	0.324	0.141	0.132	0.135	0.164	0.124	0.126						
9 6.2 <i>S. trapezia</i> Foxton	0.357	0.184	0.166	0.167	0.186	0.155	0.153	0.204					
10 22901 <i>T. spectabilis</i> Brisbane, QLD	0.356	0.203	0.189	0.189	0.221	0.182	0.185	0.216	0.252				
11 18 <i>D. albolimbata</i> Chatham I.	0.331	0.183	0.185	0.185	0.231	0.196	0.196	0.225	0.243	0.162			
12 20 <i>D. sphaeroides</i> Liffey Domain, Lincoln	0.315	0.186	0.18	0.186	0.239	0.184	0.184	0.213	0.254	0.156	0.051		
13 DQ174355.1 <i>D. sphaeroides</i> NZ	0.332	0.189	0.194	0.197	0.241	0.194	0.194	0.218	0.262	0.159	0.048	0.005	
14 DQ174365.1 <i>D. praetexta</i> Tonga	0.357	0.197	0.207	0.207	0.247	0.206	0.209	0.241	0.266	0.161	0.15	0.146	0.144

Table S2. K2P+G corrected pairwise deletion distances for ND1 sequences.

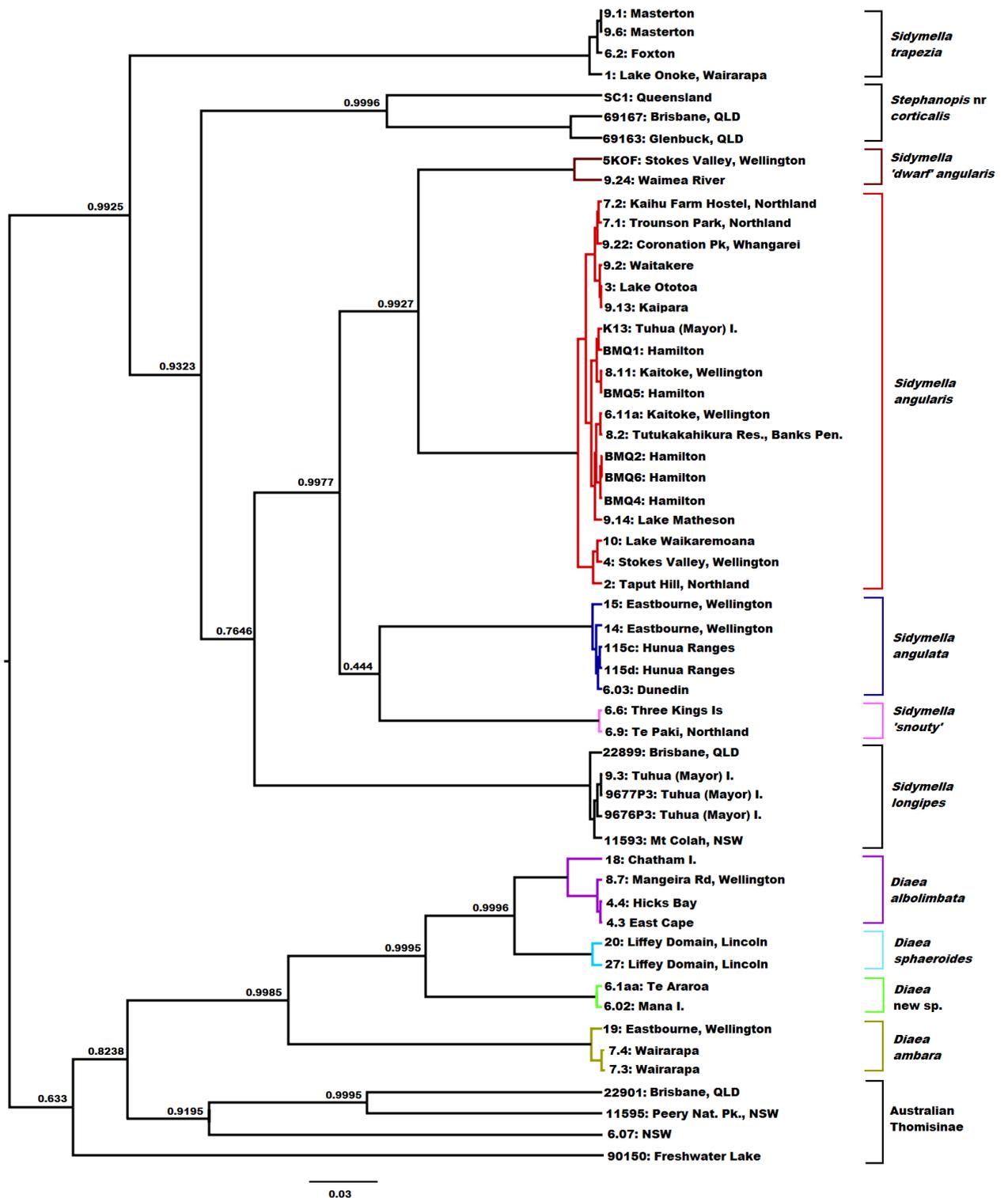


Fig. S1. Bayesian tree based on CO1 sequence data. Posterior probability values are given above branches. Branches representing non-New Zealand endemic taxa are in black.

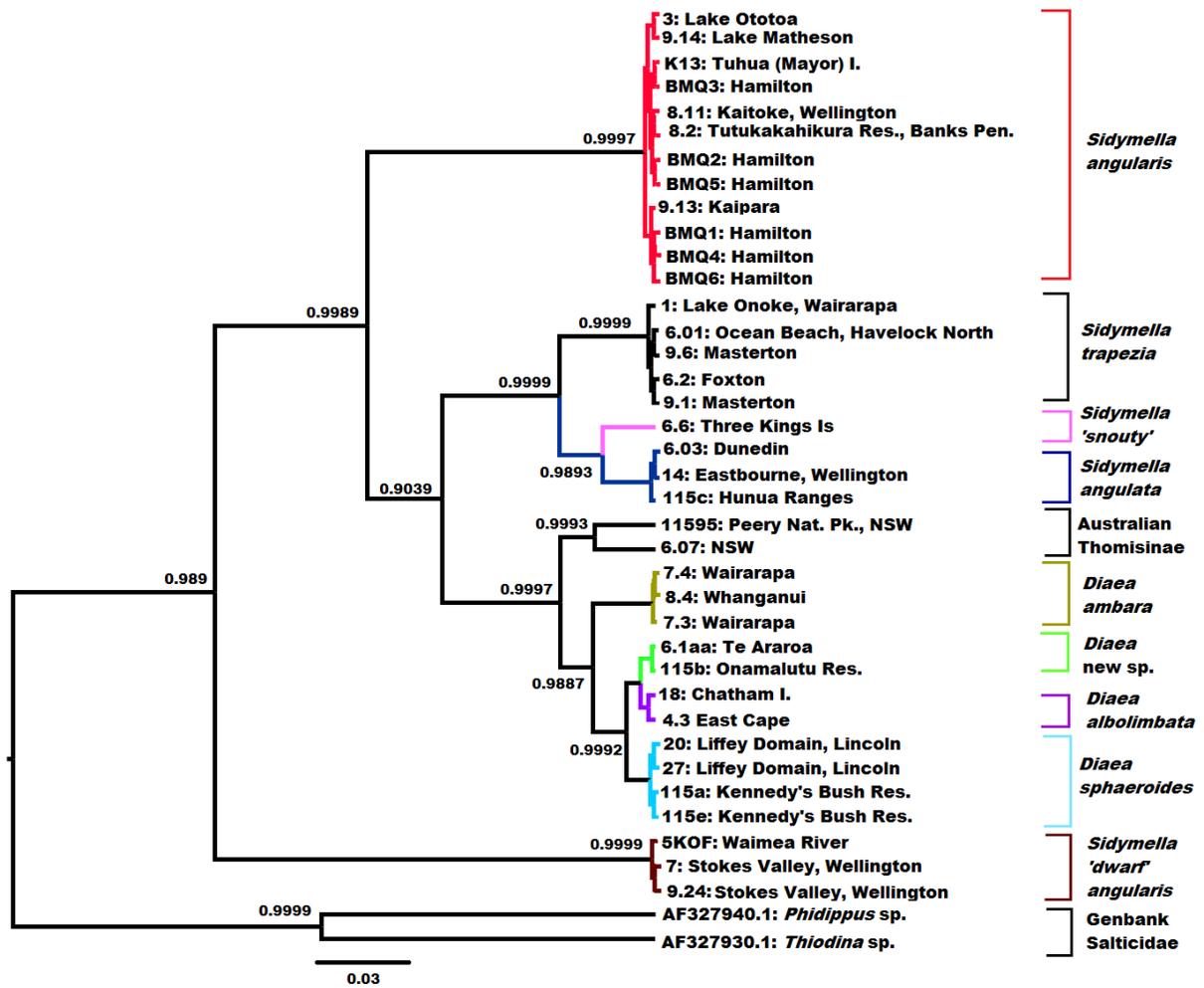


Fig. S2. Bayesian tree based on 28S sequence data. Posterior probability values are given above branches. Branches representing non-New Zealand endemic taxa are in black.

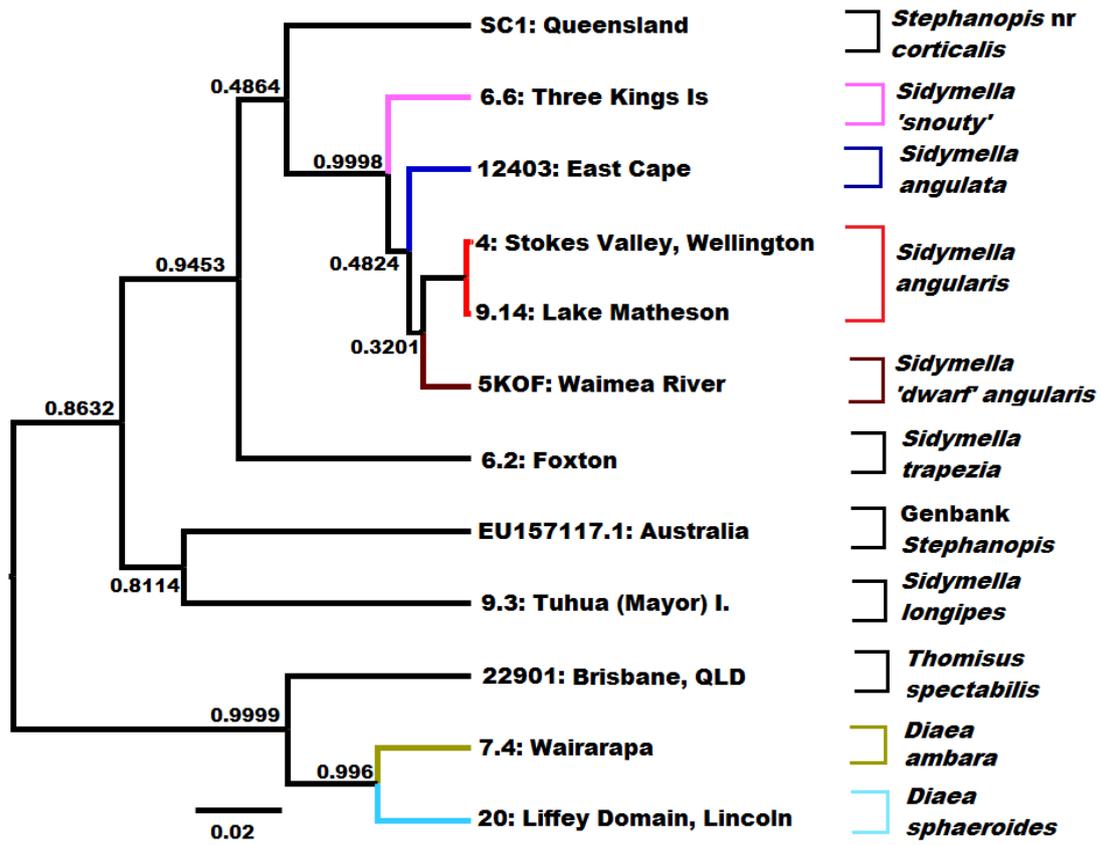


Fig. S3. Bayesian tree based on H3 sequence data. Posterior probability values are given above branches. Branches representing non-New Zealand endemic taxa are in black.

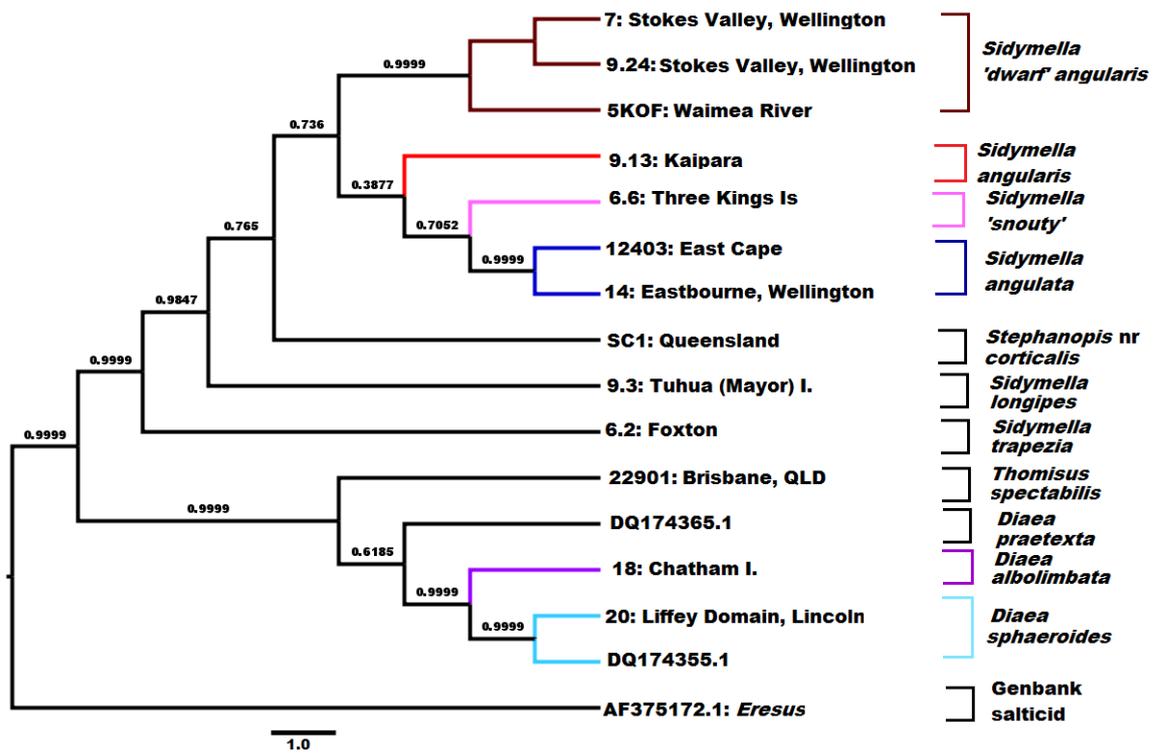


Fig. S4. Bayesian tree based on ND1 sequence data. Posterior probability values are given above branches. Branches representing non-New Zealand endemic taxa are in black.

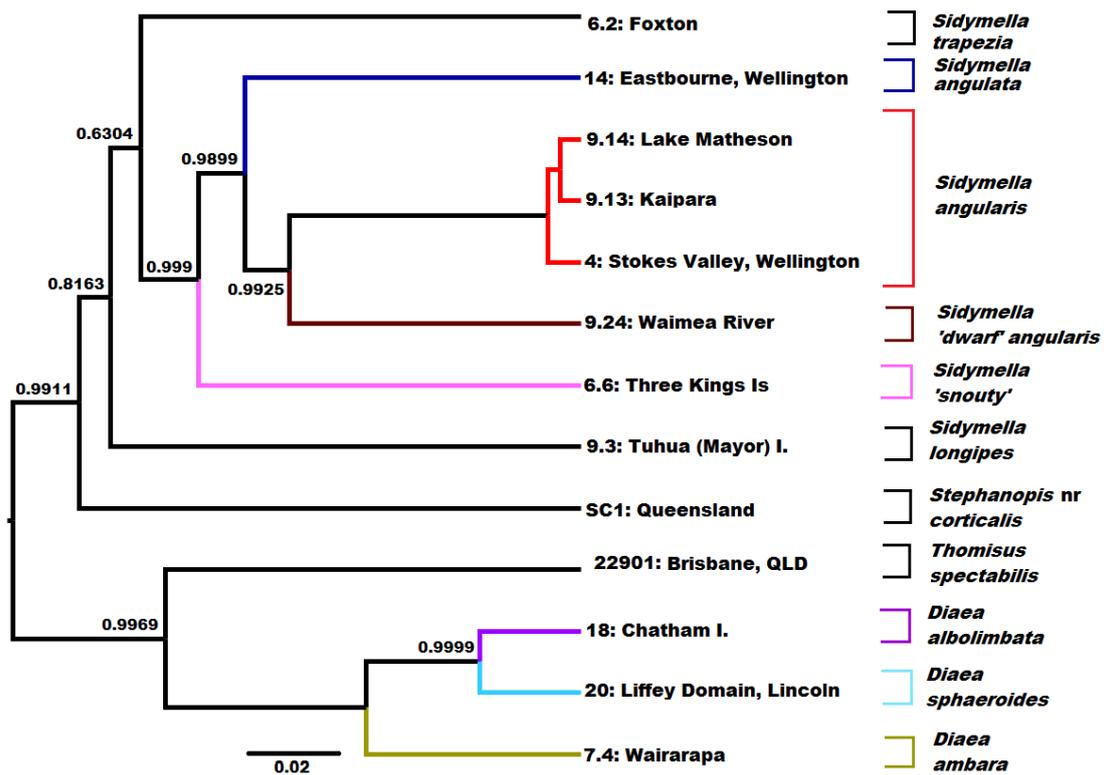


Fig S5. Bayesian tree based on combined data (CO1, 28S, H3 and ND1). Posterior probability values are given above branches. Branches representing non-New Zealand endemic taxa are in black.

Chapter 4: STUDY FINDINGS, FUTURE RESEARCH AND FINAL REMARKS

STUDY FINDINGS

At the end of Chapter 1, two questions and a number of areas of exploration were highlighted. In this section, I summarise the research outcomes of this thesis as they relate to these. My evaluation of the overall success of the project is given in *Final Remarks* at the end of this chapter.

1) *What is the composition of the New Zealand Thomisidae? More specifically, how many species are there and what is their taxonomic status?*

We now know the extent of the New Zealand thomisid fauna. There are two subfamilies, Stephanopinae and Thomisinae, present in New Zealand. Molecular data based on COI, 28S, H3, ND1 and combined sequences (Chapter 3) combined with morphological data (Chapter 2) found there are eleven species in total, nine of which are endemic. The remaining two appear to be relatively recent colonists from Australia. Based on the survey of museum collections, it is unlikely there are new endemic species awaiting discovery. However, if two Australian species can successfully invade New Zealand, others may follow.

Analysis of molecular data (Chapter 3: Figs 2-6) shows that New Zealand species from each subfamily form separate clades from their Australian relatives. The molecular data produced in this study is the largest GenBank deposition of sequences for Thomisidae to date, and is also the largest deposition for a New Zealand spider study. Furthermore, molecular data has also resolved several taxonomic issues. Species previously described exclusively from morphological characters are monophyletic and confirmed as valid taxa (e.g. Chapter 3: Fig. 2). Three taxa identified as prospective new species based on morphological assessment are confirmed as genetically distinct from previously described species (Chapter 2: *New species*).

Individuals of widespread species such as *Bryantymella angularis* that have colour and minor somatic variations are confirmed as conspecific rather than as groups of cryptic species (Chapter 3: Fig. 2 and *Are cryptic species present?*). Only two adults of *Bryantymella brevirostris* sp. nov. are known, specifically a female from Te Pahi, Northland and a male from the Three Kings Islands. Morphological assessment cannot prove conspecificity in a case like this, but very small genetic distances for COI sequence data indicates spiders from these localities are highly likely to be conspecific. (Chapter 3: *New species*).

The taxonomic revision (Chapter 2) used morphological data supported by molecular data (Chapter 3) to provide an up to date account of the New Zealand Thomisidae. All previously described species were redescribed to a modern standard with keys, habitus and diagnostic genitalic photographs also provided (Chapter 2: *Biosystematics*). Species previously known from one sex now have both sexes described and the description previously thought to be of the male of *Bryantymella angulata* is now recognized as belonging to *B. angularis* (Chapter 2: *Biosystematics*). Two species, *Synema suteri* and *Sidymella benhami* are now considered as junior synonyms of *Cymbachina ambara* and *Bryantymella angulata* respectively (Chapter 2: *Biosystematics*). Three new species, *Bryantymella thorini*, *B. brevirostris* and *Cymbachina urquharti*, were described for the first time. (Chapter 2: *Biosystematics*). Previously described endemic species were transferred to more appropriate genera due to similarity with each other and dissimilarity with the genotypes of their former genera. In the thomisines, all species are now in *Cymbachina* Bryant, while endemic stephanopines are now transferred to the new endemic genus *Bryantymella*. Placement of two Australian stephanopines proved problematic in the absence of a revision of Australian species and they are provisionally retained in *Sidymella*. Nomenclatorial changes are summarised in Table 1 from Chapter 2 (reproduced below). Updated biological and distributional information is presented for the family in general and individual species in particular. (Chapter 2: *Introduction* and individual species descriptions in *Biosystematics*).

	Previous Name	Current Name
Stephanopinae	<i>Sidymella angularis</i> (Urquhart, 1885)	<i>Bryantymella angularis</i> (Urquhart, 1885) comb. nov.
	<i>Sidymella angulata</i> (Urquhart, 1885)	<i>Bryantymella angulata</i> (Urquhart, 1885) comb. nov.
	-	<i>Bryantymella brevisrostris</i> sp. nov.
	-	<i>Bryantymella thorini</i> sp. nov.
	<i>Sidymella benhami</i> (Hogg, 1910)	<i>Bryantymella angulata</i> (Urquhart, 1885) new synonymy
	<i>Sidymella longipes</i> (L. Koch, 1874)* <i>Sidymella trapezia</i> (L. Koch, 1874)*	<i>Sidymella longipes</i> (L. Koch, 1874)* <i>Sidymella trapezia</i> (L. Koch, 1874)*
Thomisinae	<i>Cymbachina albobrunnea</i> (Urquhart, 1893)	<i>Cymbachina albobrunnea</i> (Urquhart, 1893)
	<i>Diaea albolimbata</i> L. Koch 1875	<i>Cymbachina albolimbata</i> (L. Koch 1875) comb. nov.
	<i>Diaea ambara</i> (Urquhart, 1885)	<i>Cymbachina ambara</i> (Urquhart, 1885) comb. nov.
	<i>Diaea sphaeroides</i> (Urquhart, 1885)	<i>Cymbachina sphaeroides</i> (Urquhart, 1885) comb. nov.
	-	<i>Cymbachina urquharti</i> sp. nov.
	<i>Synema suteri</i> Dahl, 1907	<i>Cymbachina ambara</i> (Urquhart, 1885) new synonymy

Table 1. Summary of taxonomic changes to the New Zealand Thomisidae made in this revision. *denotes Australian species established in New Zealand.

2) Does the modern New Zealand thomisid fauna support the Gondwanan vicariance model, or alternatively, are its' origins better explained by more recent colonization and subsequent radiation events? If the latter, can it be estimated when such events may have occurred?

Endemic New Zealand members of both subfamilies (Stephanopinae and Thomisinae) form distinct New Zealand clades compared to sampled Australian relatives (Chapter 3: Figs 2-6). However, based on genetic distances for COI data (Chapter 3: Tables 5a and 5b) it is clear that the New Zealand species began their divergence approximately five million years ago.

This figure is similar to that observed previously for the New Zealand wolf spiders (Vink & Paterson 2003).

Thus, the Gondwanan vicariance model is not supported for this family. An initial assumption of this study was that stephanopine spiders were poor dispersers as they are found on large, historically Gondwanan landmasses such as Australia, New Zealand and South America but appear to be absent from Pacific islands. In contrast, thomisines range across the Pacific. This initial assumption is not borne out by two novel findings. First, two species of Australian *Sidymella* are now recorded for New Zealand. Their presence on offshore islands, some of which are ordinarily uninhabited, is circumstantial evidence for long range dispersal, probably via ballooning. Second, as might be expected for a common and widely distributed species like *Bryantymella angularis* there is some haplotype diversity, yet specimens from quite disjunct localities are present in the same subclades (Chapter 3: Fig 2).

FUTURE RESEARCH

Biogeographic History of New Zealand Spiders

At the outset of this study, modern distributions suggested some New Zealand Thomisidae might be a good fit for the Gondwanan vicariance model (*sensu* Forster), but results indicate they are of relatively recent origin. The oldest known thomisid fossils are less than 60 million years old (Selden & Penney 2010), while New Zealand began drifting away from Gondwana about 80-85 million years ago. However, the assumption of a Gondwanan history in the absence of fossils is not without precedent. The “Gondwanan” monographs of Forster and co-workers (see Chapter 1: Table 3) also include several families where the oldest known fossils post-date the separation of New Zealand from Gondawana. Beauliey *et al.* (2013) observe that studies of southern hemisphere disjunctions in plants have found that groups were often too young to have been influenced by the Gondwanan break up. That appears to be a realistic possibility for the New Zealand Thomisidae., although the absence of older fossils is not conclusive proof that we know the true antiquity of this family. Testing groups with a much longer fossil history should greatly reduce such uncertainty.

Are there other spider groups that might demonstrate older and deeper divergences? While there are a many interesting possibilities, the mygalomorph spider family Hexathelidae may be a particularly good prospect for several reasons. First, the family has an ancient history, with fossils from some 230 million years ago (Seldon & Penney 2010). Second, Muriene *et al.* (2013) suggest high vagility may blur historic biogeographic signals to the point where inference of historical scenarios is impossible. Hexathelids are poor dispersers (Raven 1980), and it may not be coincidental that a number of New Zealand species are known from very few specimens or very few localities. Third, unlike the Thomisidae, the taxonomy of the hexathelids is well known and out of 112 species worldwide, 47 are from Australia and 25 are from New Zealand (Platnick 2013). Thus, the family appears to be very old, of low vagility and well documented, making them excellent candidates that might demonstrate divergence tied to the breakup of New Zealand and Australia. A multi-locus approach supported by morphological data based on the methods employed in this thesis could be used to explore divergence patterns for this and other families.

Taxonomy and Systematics

The taxonomic status of the New Zealand Thomisidae has been greatly clarified by this study. However, the same cannot yet be said for their Australian relatives. The molecular sampling of Australian taxa for comparative purposes in this thesis was limited and that fauna remains taxonomically unrevised. It is possible that Australian endemic species may be congeneric with the New Zealand genera *Cymbachina* and *Bryantymella*, or that these genera require some redefinition based on a more comprehensive Australian morphological data set. Currently, Pawel Szymkowiak (Adam Mickiewicz University, Poland) is reviewing the Australian Thomisinae, while Suresh Benjamin (Institute of Fundamental Studies, Sri Lanka) is studying the Australasian Stephanopinae. Both are using a combined morphological-molecular approach but neither study is complete. I am in communication with both workers and data from this thesis will support their studies with the goal of building a clear and taxonomically consistent overview of the thomisids of the Australasian sub-region.

The methods used in this thesis may be helpful in resolving taxonomic issues in other New Zealand spiders. For example, boundaries for some families are not clearly defined and Paquin *et al.* (2010) state that “differentiating Amaurobiidae from Agelenidae, Desidae and Amphinectidae is difficult/impossible”. Indeed, despite revising the New Zealand Agelenidae Forster and Wilton (1973) suggest their own taxonomic arrangement is at least in part polyphyletic. Additionally, Forster and Forster (1999) suggest that some New Zealand agelenids and amphinectids may ultimately belong in as yet unknown families. Molecular data allied to morphological characters may be of great utility in uncovering the true relationships and correct taxonomic position of these spiders.

Molecular Phylogenetics

Despite increasing usage, it is fair to say molecular-based phylogenetics has yet to fully realise its potential with respect to spiders. The number of reliable gene targets available to spider researchers is so limited compared to that available for other arthropod groups such as insects that they are described as “the usual suspects” (Agnarsson *et al.* 2013). A variety of gene targets, all of which had at least a partial track record of success with spiders, were used in this thesis, but results were mixed and some targets were problematic. For example, multiple copies of ITS1-ITS2 were amplified, and it appears paralogues of 28S may also be present in some species. Other targets such as 18S produced very little data. A limited range of gene targets and the reliability of the few that are available are not the only difficulties facing workers in the field of spider molecular phylogenetics. Agnarsson *et al.* (2013) also point out different studies may use the same gene targets but variation in primer choice means sequenced regions don’t always share much overlap, making comparison and compilation of phylogenetic data difficult.

Next generation sequencing (NGS) may prove useful in overcoming these limitations. In the medium to long term, sequencing of whole genomes may become commonplace, but as spiders have a genome size in the order of three billion base pairs (Goodacre 2013), the cost is currently prohibitive. In

the short to medium term, NGS is more likely to have an impact on spider phylogenetics in other ways. It has the potential to expand the limited set of genetic markers enormously and may have some utility in resolving issues such as amplification of multiple gene copies as observed in Chapter 3. As NGS requires very small amounts of starting material, it has the potential to enable sampling from museum specimens with DNA too degraded for conventional PCR (Goodacre 2013). This would dramatically increase the amount of potential study material, and, as many spider species (including several documented in this study) are known from very few specimens, may permit the inclusion of otherwise unobtainable taxa. Ultimately, NGS holds much promise for increasing the scope of spider molecular phylogenetic studies, but the potential for a continuation of the sometimes piecemeal and uncoordinated effort we see now remains. Consistency in the usage of novel markers with support from additional datasets (e.g. morphological, ecological or behavioural) could mean spider phylogenetics finally fulfils its potential.

Alternative Approaches for Species delimitation:

The approach to delimiting species using molecular data used in this thesis (trees plus p -distances) can be very effective (e.g. Hebert *et al.* 2003). In Chapter 3, molecular data was in agreement with species delimitation based on morphological data. However, not all studies involve easily recognizable morpho-taxa and a variety of analytical methods have been developed to delimit species based on molecular data alone. Hamilton *et al.* (2013) studied *Aphonopelma* spiders, a group they described as “*largely reliant upon sparse and sometimes poorly defined morphological data*”. In addition to tree-based and p -distance methods, they also used the Generalised Mixed Yule Coalescent (GMYC) approach. This method assumes independent evolution will produce distinct genetic clusters separated by longer internal branches. These clusters are delimited by optimizing the set of nodes that define the transitions between intraspecific and interspecific processes (Fujisawa & Barraclough 2013). GMYC is implemented in software such as BEAST (used in Chapter 3) – and see below.

A new and potentially superior species delimitation algorithm is the Poisson tree process model (PTP) of Zhang *et al.* (2013). The authors claim PTP outperforms GMYC and sequence similarity based methods where interspecific evolutionary distances are small, does not require an ultrametric tree nor a sequence similarity threshold as inputs and is far more efficient in processing large datasets. The R module 'Spider' (Brown *et al.* 2012) can also be used to delimit species but has the advantage of being able to analyse molecular or morphological data.

The molecular dataset used in this study is unlikely to be re-analysed in the short term. However, additional molecular-based species delimitation techniques may later prove to be extremely useful in untangling some of the more taxonomically challenging groups noted in the Taxonomy and Systematics section above and as new DNA sequences are added.

Estimation of divergence times

This study used a simple approach to the estimation of divergence times, specifically Brower's (1994) estimate of 2.3% genetic difference equating to one million years of divergence. As Fig. 1 below shows, this approach is still widely used in arthropod phylogenetic studies.

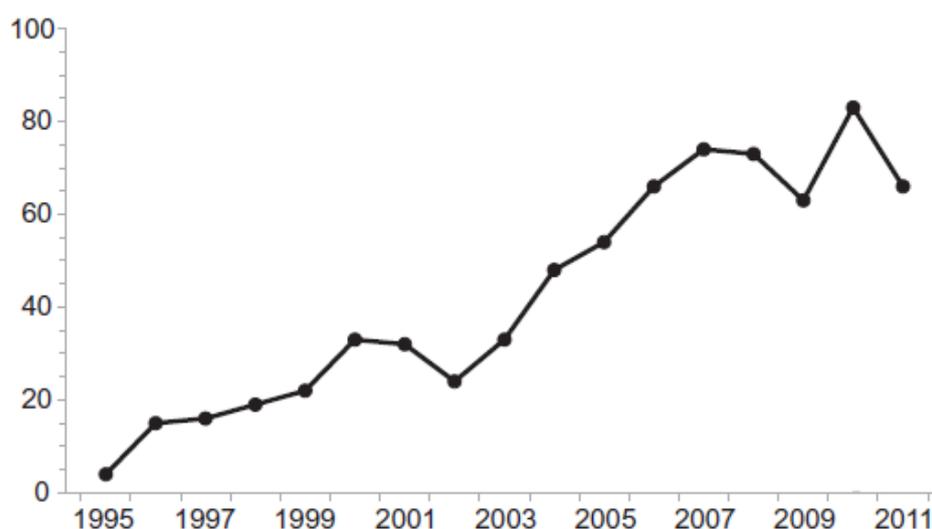


Fig. 1. Annual citations of Brower (1994). The data were obtained from Web of Science (accessed 26 December 2012). Figure adapted from Ho and Lo (2013).

This method is also prevalent in molecular studies of New Zealand spiders (e.g. Vink & Dupérré 2010). In the absence of useful fossil or ancient DNA information for many arthropod groups, calibration can be problematic. Geological and biogeographic events can potentially be used as calibration points, but these may be of questionable worth when dealing with highly vagile taxa. However, while using a general fixed rate such as Brower's (1994) has the advantage of being straightforward, it is not without potential problems. For example, it is assumed this rate is consistently applicable across a wide variety of arthropod lineages yet it is known that rates may vary between some lineages and/or over different time scales (Ho & Lo 2013). Ho and Lo (2013) note that there is fairly widespread evidence of rate variation among insect lineages, so it is advisable to test for a molecular clock. Relaxed-clock methods should be used if a strict clock is rejected. Although not explicitly stated in Chapter 3, CO I data for were subjected to a molecular clock test in MEGA 5.0 and the clock was not rejected.

Furthermore, the The Bayesian analysis using BEAST conducted in Chapter 3 could have been improved by incorporation of Brower's rate in the analysis itself rather than the post-hoc application that followed, as this would at least allow errors in dating estimates to be calculated (R. Cruickshank, Lincoln University, Pers. comm). The study of Hamilton *et al.* (2011) of *Aphonopelma* phylogeny offers a model approach for the application of this method in future work.

FINAL REMARKS

The 'total evidence' approach used in this thesis means we now have clear overview of the New Zealand Thomisidae with a well-resolved taxonomy supported by a clear phylogeny. Molecular data was instrumental in resolving several taxonomic issues that could not easily be determined on morphological criteria alone, while at the same time, we can have more confidence in the clades generated by the molecular analysis because of their coincidence with morphological characters. This study indicates that the New

Zealand Thomisidae, while distinct, is nonetheless a younger group than assumptions based on modern distributions implied. However, this does not necessarily mean the New Zealand spider fauna is entirely composed of young lineages. The methods in this thesis can be applied to other spider families to further explore questions relating to their taxonomy and biogeographic relationships.

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