

Phylogenetic placement of *Echinotheridion* (Araneae: Theridiidae) – do male sexual organ removal, emasculation, and sexual cannibalism in *Echinotheridion* and *Tidarren* represent evolutionary replicas?

Ingi Agnarsson

The University of British Columbia, Departments of Botany and Zoology,
#3529-6270 University Blvd., Vancouver, BC V6T 1Z4, Canada.
Department of Entomology, Smithsonian Institution, NHB-105,
PO Box 37012, Washington, DC 20013-7012, USA.
Email: ingi@zoology.ubc.ca, ingi@theridiidae.com

Abstract. Uniquely among spiders, males of two cobweb spider (Theridiidae) genera, *Tidarren* Chamberlin & Ivie, 1934 and *Echinotheridion* Levi, 1963, voluntarily amputate one of their secondary sexual organs (the pedipalpi, modified as sperm transfer organs) before their last molt and thus have only one palp as adults. This is the first step in a fascinating sexual biology observed in both genera, which is marked by sexual dimorphism – males are tiny compared with females – and usually involves both emasculation and sexual cannibalism. To study the evolution of these striking traits it is essential to understand the phylogenetic relationship of these genera. Both morphological and molecular data place *Tidarren* in the subfamily Theridiinae. However, *Echinotheridion* has not been placed phylogenetically to date owing to rarity of specimens, and difficulty of interpreting the highly autapomorphic palpal organ, the main source of morphological characters. Here, the phylogenetic position of *Echinotheridion* is inferred using fragments of three nuclear (*Histone 3*, *18S* rDNA, and *28S* rDNA) and two mitochondrial (*16S* rDNA and *COI*) loci. Each matrix separately, and a combined matrix, were analysed using parsimony with gaps either treated as missing data, or as 5th state, and with Bayesian methods. Although all genes agree that *Tidarren* and *Echinotheridion* are closely related, perhaps surprisingly, none of the analyses supported their sister relationship. The sister relationship was ambiguously supported in a preliminary morphological analysis, whereas combined molecular and morphological data refuted it. This implies a more complex evolutionary history of male sexual organ removal and other bizarre sexual biology of *Tidarren* and *Echinotheridion* than previously envisioned. Many of the analyses are equally consistent with two hypotheses: a single origin, followed by a secondary loss; or independent evolution of this behaviour in the two genera. However, based on the combined molecular Bayesian phylogeny, and some of the preliminary ‘total evidence’ analyses, the latter hypothesis is better supported.

Additional keywords: cobweb spiders, palpal amputation, theridiid phylogeny.

Introduction

The sexual biology of the theridiid genera *Echinotheridion* Levi, 1963 and *Tidarren* Chamberlin & Ivie, 1934 is unique among spiders. In both genera, sexual size dimorphism is marked, with the male only approximately one hundredth of the female body mass (Hormiga *et al.* 2000; Ramos *et al.* 2004). Prior to the ultimate molt, the male of all studied species affixes one palp (the right or left palp seemingly at random) in the silk lines of his webs and then circles around until the palp twists off (Branch 1942; Knoflach and van Harten 2000, 2001; Knoflach 2002; Knoflach and Benjamin 2003). The male then feeds on the detached palp. During the copulation sequence, the male first charges the remaining palp, and then seeks and courts a female. The male dies,

seemingly from fatigue, at the instance or soon after copulation is achieved (Knoflach 2002), but remains attached to the female via the palp. After a few minutes, or in some species instantly, the female entangles the male in the threads of her web, and turns around in circles until the palp twists off (emasculation). The female then feeds on the body of the male (except in *T. sisyphoides*, see Knoflach and Benjamin 2003), and the palp remains attached to the epigynum, forming a ‘mating plug’ until the female removes it after a few hours.

In at least *Tidarren*, sexual size dimorphism is apparently the result of both female size increase and male size decrease (Hormiga *et al.* 2000). However, the palpal organs have not reduced much, if at all, in size; they are as large as in most

related genera and in *Tidarren* represent ~10% of the male body mass (Ramos *et al.* 2004). The retention of palpal size may result from a constraint: a large palp is required for mechanical coupling with the reproductive organ of the relatively large female (Vollrath 1998). However, these relatively huge organs have been shown to limit the locomotive potential of males, thus reducing their ability to find, and compete for females (Ramos *et al.* 2004). The novel behaviour of palpal amputation is thus believed to have evolved as a result of conflict between body size and palp size evolution (Ramos *et al.* 2004). While improving locomotive potential, loss of one palp would not reduce reproductive potential, because the male dies immediately after achieving copulation; a second copulatory organ would only result in loss of gametes.

Tidarren and *Echinotheridion* share this bizarre sexual biology, and it would seem unexpected to have such striking characteristics evolve in parallel: ‘could palp-amputation of the subadult male and emasculation behaviour have evolved convergently in both genera? It appears that such peculiar traits are unlikely to have evolved twice...’ (Knoflach 2002: 144). Consequently, the two genera have been presumed to be sister genera (Wunderlich 1992, Knoflach 2002; Ramos *et al.* 2004), a hypothesis (hence the ‘homology hypothesis’) supported to some degree by similarities in their somatic morphology – both are believed to belong to the subfamily Theridiinae (see Agnarsson 2004; Arnedo *et al.* 2004). However, although *Tidarren* has been included in phylogenetic analyses of Theridiidae, both based on morphological (Agnarsson 2003, 2004, 2006a) and molecular (Arnedo *et al.* 2004) data, rarity of specimens has hitherto prevented the inclusion of *Echinotheridion* in a phylogenetic study.

The purpose of this paper is to estimate the phylogenetic position of *Echinotheridion* and thus test if palpal amputation and other unusual sexual traits evolved convergently in the two genera, or – as has always been presumed – once in their common ancestor.

Materials and methods

A female identified using Levi’s (1963) revision as *E. otlum* Levi, 1963 was collected in Jatun Sacha National Park (Estación Biológica Jatun Sacha), Napo, Ecuador (1°4′1.20″S 77° 37′1.20″W), 21–24.vii.2004, 400 m, forest understory, (I. Agnarsson *et al.*, voucher will be deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA). Genomic DNA was isolated with the DNAs QIAGEN DNeasy extraction kit (QIAGEN Inc., Ontario, Canada). Fragments of three nuclear (*Histone 3*, *18S* rDNA and *28S* rDNA) and two mitochondrial (*16S* rDNA and *COI*) genes were amplified (for primers and PCR settings, see Arnedo *et al.* 2004), and the PCR products were sequenced using the MacroGen Inc. (Seoul, Korea, model ABI 3730) sequencer. The sequences were submitted to GenBank (www.ncbi.nlm.nih.gov/Genbank/index.html, verified July 2006; GenBank accession numbers: DQ842140–DQ842144).

The sequences were added to the matrix of Arnedo *et al.* (2004). As the purpose here was not to test theridiid monophyly, some of the more distant theridiid outgroups were removed to facilitate the alignment.

Only the two taxa believed to be most closely related to theridiids, *Synotaxus* and *Nesticus* (see Griswold *et al.* 1998; Agnarsson 2003, 2004), were retained. Matrices were constructed for each gene separately, and these were aligned using ClustalX (Thompson *et al.* 1997), with gap cost set at 24 and gap extension at 6. A second set of matrices was made by manually adjusting each alignment containing gap regions (*16S*, *18S*, *28S*). Despite the obvious appeal of purely automated alignments, in particular in terms of repeatability (e.g. Giribet and Wheeler 1999), it is evident from molecular phylogenetic literature that manual alignments (or manual adjustments to Clustal alignments) continue to be popular. And in at least some test cases, manual alignments have outperformed Clustal alignments (e.g. Laamanen *et al.* 2005). The single-gene matrices were then concatenated into the ‘combined molecular’ matrices (Clustal and Clustal plus manual alignments). All matrices in NEXUS format (labelled transparently as: Morphology, 16SManual, 16SClustal, 18SManual, 18SClustal, 28SManual, 28SClustal, COIManual, COIClustal, H3Manual, H3Clustal, MoleculesCombined Manual, MoleculesCombinedClustal, MorphologyPlusMolecules Manual, MorphologyPlusMoleculesClustal) can be downloaded as Accessory Material from the *Invertebrate Systematics* website, and will be made available at <http://theridiidae.com/cladogramsi.html> (verified July 2006). The combined molecular and morphological matrices will also be submitted to TreeBase (www.treebase.org/treebase/, verified July 2006). The *Echinotheridion* sequences were also added to the preferred alignment (implied by POY, see Gladstein and Wheeler 1997) of Arnedo *et al.* (2004) by pairwise alignment with the *Tidarren* sequences in MacClade (Maddison and Maddison 2005), which uses the Needleman–Wunsch algorithm. This was done in an attempt to bias the results in favour of a sister relationship of the two, to provide a stronger test of the convergence hypothesis. Each of these matrices was analysed using equally weighted parsimony, treating gaps either as missing data, or as a 5th state, and with Bayesian methods.

Parsimony analyses were done in PAUP* (Swofford 2002). In each of the analyses, heuristic searches were done with 1000 random stepwise additions, and the subtree-pruning and regrafting branch swapping algorithm. For nodal support, Bootstrap percentages (Felsenstein 1985) were calculated in NONA, with 1000 Bootstrap replicates.

Bayesian analysis was performed using MrBayes V3.0 (Huelsenbeck and Ronquist 2001). The best fitting model for each matrix was chosen using Modeltest 3.6 (Posada and Crandall 1998). The preferred model for *16S*, *28S*, and *COI* was the general time reversible (GTR) + gamma distribution (Γ) + proportion of invariable sites (I) (Rodríguez *et al.* 1990; Yang 1994), for *18S* the Tamura–Nei with equal base frequencies (TrNef) + Γ + I model (Tamura and Nei 1993, GTR-type model with equal base frequencies), and for *Histone 3* the TrN + Γ + I model (Tamura and Nei 1993, GTR-type model where parameters controlling the rates of the different types of transitions are equal; this model is not available in MrBayes and hence the GTR + Γ + I model was used). For the protein-coding genes, the Bayesian analyses were partitioned by codon. For the combined molecular matrix the analysis was partitioned by loci, using the same model for each partition as in the single-gene analyses, and estimating all parameters independently for each partition (‘unlink statefreq = (all) revmat = (all) shape = (all) pinvar = (all)’). The model employed six substitution types (‘nst = 6’), with rates and proportion of invariable sites estimated (‘rates = invgamma’), and for the GTR analyses, base frequencies estimated from the data. For each analysis, the Markov chain Monte Carlo search was run with four chains for 5000000 generations, sampling the Markov chain every 1000 generations, and the sample points of the first 500000 generations were discarded as ‘burn-in’, after which the chain reached stationarity.

Parsimony continues to be the favoured method for analysing morphological data, and is here preferred. However, there are reasons to believe that methods that are best able to incorporate models of

sequence evolution in the phylogenetic inference are least likely to be misled by that complex process (e.g. Huelsenbeck and Crandall 1997). Furthermore, in analyses where many genes are combined, a homogeneous model estimated for the entire dataset is a compromise among the partitions – each partition may have evolved under a different model – and may lead to systematic error (e.g. Wilgenbusch and de Queiroz 2000; Brandley *et al.* 2005). Thus, it is important to be able to partition combined analyses so that models can be estimated, for example, independently for each gene. In light of that, the Bayesian approach offers much promise because it allows the incorporation of the best fitting available model and independent model estimations for data partitions, while simultaneously estimating the uncertainty associated with any parameter from the phylogenetic model (topology, branch lengths, and substitution model). The Bayesian results might therefore be preferred, *a priori*, to those of the parsimony analyses. A comparison with the parsimony results is, however, important not only to understand the sensitivity of the results to the method chosen, but it is also easier to assess the importance of information from gaps in a parsimony framework (a standard Bayesian analysis treats gaps as missing data).

For an independent – although preliminary – test of the molecular results, *Echinotheridion gibberosum* was scored for morphological characters, to the extent possible, based on descriptions and drawings of Knoflach (2002) and added to the growing genus-level theridiid phylogeny of (Agnarsson 2003, 2004, 2006a, 2006b; Agnarsson and Kuntner 2005). Appendix 1 lists the morphological characters and scoring for all taxa is shown in Appendix 2. This matrix can be downloaded as Accessory Material from the *Invertebrate Systematics* website and will be made available at <http://theridiidae.com/cladograms.html> (verified July 2006). The morphological matrix was analysed using parsimony with the same settings as described above (see Agnarsson 2004 for

further details). This matrix includes the character under study (male palpal amputation) and can thus be considered to be somewhat biased towards the homology hypothesis. Finally, the combined molecular matrices were fused with the morphological matrix (as described in Agnarsson 2003), and the fused matrix analysed using parsimony, and a partitioned Bayesian analysis. Fusing molecular and morphological matrices and analysing the combined data involves many considerations and it is beyond the scope of this study to explore them all, especially considering the preliminary nature of the morphological data. The main point here is simply evaluating the evidence for the relative placement of two taxa, not to produce a novel hypothesis of deeper theridiid phylogeny; a much more detailed ‘total evidence’ analysis is underway (M. Arnedo *et al.* unpublished). Here, for simplicity, congeners were fused even if not represented by the same species in the two datasets, which amounts to assuming monophyly of genera. The Bayesian analyses of the combined data specified morphological (using ‘parsmodel = yes’ or ‘standard’) and molecular partitions, in addition to sub-partitioning the molecular data according to gene, as done for the combined molecular matrix.

Results

A summary of results for each of the molecular analyses can be found in Table 1. Whether analysed separately or combined, no analysis supports the sister relationship of *Echinotheridion* and *Tidarren*. The Bayesian analyses of the combined molecular data, regardless of alignment, placed *Echinotheridion* sister to *Nesticodes*, and *Tidarren* as sister

Table 1. Summary of the results (strict consensus in the parsimony analyses) of each of the single-gene and combined molecular analyses, in regards to the relative placement of *Echinotheridion* and *Tidarren*

Each gene name, or combined data (= all), is followed by ‘c’ indicating Clustal alignment or ‘m’ indicating Clustal plus manual alignment (e.g. H3c = Histone 3, Clustal alignment). All of the hypothesis require two steps in the evolution of male sexual organ removal, or are silent about it (unresolved)

Gene	MP gaps ignored	MP gaps 5th state	Bayesian
16Sc	<i>Echinotheridion</i> + <i>Nesticodes</i> sister to <i>Tidarren</i> + <i>Achaearana</i>	<i>Tidarren</i> + <i>Achaearana</i> in a trichotomy with <i>Echinotheridion</i> and <i>Nesticodes</i>	<i>Tidarren</i> + <i>Achaearana</i> in a trichotomy with <i>Echinotheridion</i> and <i>Nesticodes</i>
16Sm	<i>Echinotheridion</i> + <i>Nesticodes</i> sister to <i>Tidarren</i> + <i>Achaearana</i>	<i>Echinotheridion</i> + <i>Nesticodes</i> sister to <i>Tidarren</i>	<i>Echinotheridion</i> + <i>Nesticodes</i> sister to <i>Tidarren</i> + <i>Achaearana</i>
18Sc	Pentachotomy including <i>Theridion longipedatum</i> , <i>Neottiura</i> , <i>Echinotheridion</i> , <i>Tidarren</i> , and <i>Rugathodes</i>	Pentachotomy including <i>Theridion longipedatum</i> , <i>Neottiura</i> , <i>Echinotheridion</i> , <i>Tidarren</i> , and <i>Rugathodes</i>	Pentachotomy including <i>Theridion longipedatum</i> , <i>Neottiura</i> , <i>Echinotheridion</i> , <i>Tidarren</i> , and <i>Rugathodes</i>
18Sm	Pentachotomy including <i>Theridion longipedatum</i> , <i>Neottiura</i> , <i>Echinotheridion</i> , <i>Tidarren</i> , and <i>Achaearana</i>	Pentachotomy including <i>Theridion longipedatum</i> , <i>Neottiura</i> , <i>Echinotheridion</i> , <i>Tidarren</i> , and <i>Achaearana</i>	Pentachotomy including <i>Theridion longipedatum</i> , <i>Neottiura</i> , <i>Echinotheridion</i> , <i>Tidarren</i> , and <i>Rugathodes</i>
28Sc	<i>Tidarren</i> + <i>Achaearana</i> sister to <i>Echinotheridion</i>	<i>Tidarren</i> + <i>Achaearana</i> sister to <i>Echinotheridion</i>	Nonachotomy including <i>Tidarren</i> + <i>Achaearana</i> , and <i>Echinotheridion</i>
28Sm	<i>Tidarren</i> + <i>Achaearana</i> with <i>Echinotheridion</i> in a large polytomy	<i>Tidarren</i> + <i>Achaearana</i> , unrelated to <i>Echinotheridion</i> + <i>Thymoites</i>	Nonachotomy including <i>Tidarren</i> + <i>Achaearana</i> , and <i>Echinotheridion</i>
COIc	<i>Echinotheridion</i> + <i>Nesticodes</i> unrelated to <i>Tidarren</i> + <i>Coleosoma</i>	No informative gaps in alignment	unresolved
H3c	Nonachotomy including <i>Ameridion</i> , <i>Theridion grallator</i> , <i>T. varians</i> , <i>Rugathodes</i> , <i>Thymoites</i> , <i>Coleosoma</i> , <i>Achaearana</i> , <i>Tidarren</i> , and <i>Echinotheridion</i>	No informative gaps in alignment	Hendecachotomy (11-tomy) including <i>Synotaxus</i> , <i>Neottiura</i> , <i>Ameridion</i> , <i>Theridion grallator</i> , <i>T. varians</i> , <i>Rugathodes</i> , <i>Thymoites</i> , <i>Coleosoma</i> , <i>Achaearana</i> , <i>Tidarren</i> , and <i>Echinotheridion</i>
Allc	<i>Tidarren</i> + <i>Achaearana</i> sister to <i>Echinotheridion</i>	<i>Tidarren</i> + <i>Achaearana</i> sister to <i>Echinotheridion</i>	<i>Echinotheridion</i> + <i>Nesticodes</i> sister to <i>Tidarren</i> + <i>Achaearana</i>
Allm	<i>Tidarren</i> + <i>Achaearana</i> sister to <i>Echinotheridion</i>	<i>Echinotheridion</i> + <i>Nesticodes</i> sister to <i>Tidarren</i> + <i>Achaearana</i>	see Fig. 1

to *Achaeearanea*, and the two pairs together form a clade (Fig. 1). Posterior probability support for this particular arrangement is generally high (89–100). The same result was obtained when *Echinotheridion* was added to the alignment preferred by Arnedo *et al.* (2004). Under parsimony, the combined molecular data suggest the relationship (*Echinotheridion* (*Tidarren*, *Achaeearanea*)) except in the Clustal plus manual alignment treating gaps as a 5th state, which agreed with the Bayesian analysis (Table 1). The morphological analysis found four most parsimonious trees, in two of which *Echinotheridion* and *Tidarren* were sisters. Most of the preliminary ‘total evidence’ analyses (Fig. 2) agree with the Bayesian analysis of the combined molecular data.

Discussion

Some of the striking features of the sexual biology of *Echinotheridion* and *Tidarren* are also seen in some other spiders. For example, in the widow spiders (*Latrodectus*,

Theridiidae), sexual cannibalism commonly occurs (e.g. Andrade 1996). In *Latrodectus*, as well as in some Nephilidae genera, sexual size dimorphism is marked, and copulation terminates in the male breaking off a part of his sexual organ (e.g. Andrade and Banta 2002; Kuntner 2005). The broken-off piece stays attached to the female genitalia and is presumed to serve as a mating plug (although, in many cases, the female mates again). Hence, there is evidence that unusual sexual biology has evolved convergently in different spider lineages. However, among spiders, and to my knowledge animals in general, voluntary sexual organ removal before mating is a unique behaviour of *Echinotheridion* and *Tidarren*. Is it possible that this extraordinary behaviour, observed in two related genera, is also convergent?

The addition of further molecular loci, and a careful morphological study of *Echinotheridion* (upon availability of further specimens) may, of course, lead to unambiguous support for a sister relationship of *Echinotheridion* and

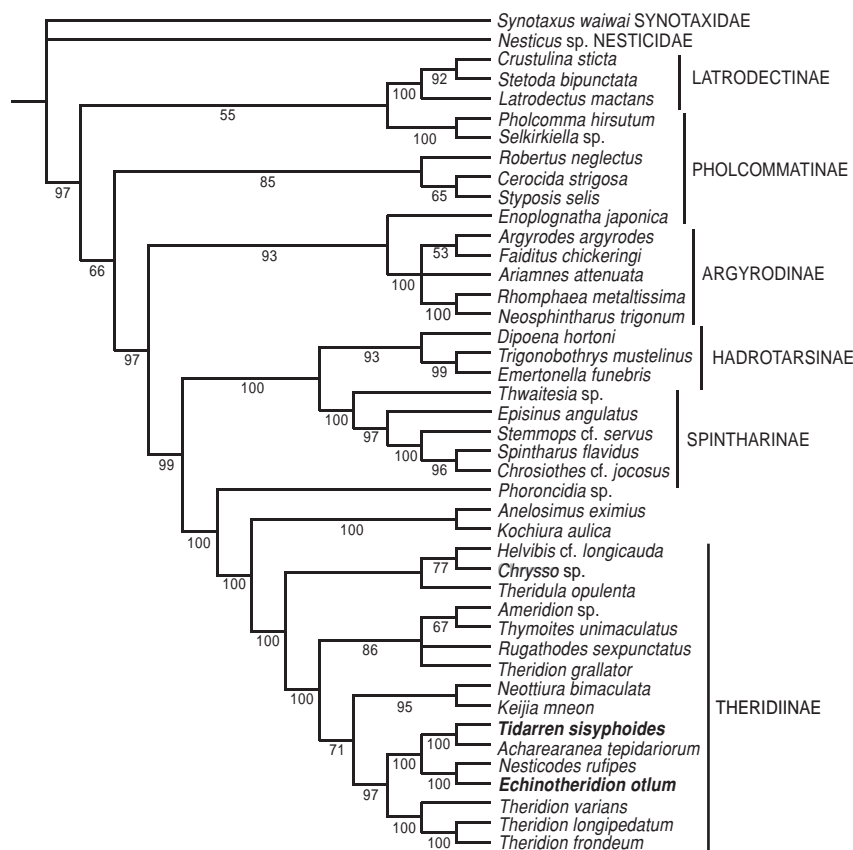


Fig. 1. Results of the Bayesian analysis of the combined molecular data (Clustal + manual alignment), numbers below branches are posterior probabilities (clades with 50 or less are collapsed). Subfamilies are labelled according to Agnarsson (2004) and Arnedo *et al.* (2004). Here, the simplest (most parsimonious) inference is that sexual organ removal and other unusual sexual behaviour in *Echinotheridion* and *Tidarren* (genera shown in bold font) evolved in parallel in the two genera. The placement of *Echinotheridion* and *Tidarren* is identical in the other combined Bayesian analysis (Clustal alignment), as well as when *Echinotheridion* is added to the preferred alignment of Arnedo *et al.* (2004, see methods).

Tidarren and thus for the intuitive hypothesis of a monophyletic origin of palpal amputation. However, the current results are based on relatively large independent datasets, analysed under a range of conditions, and none of the genes, morphology, or combined analyses unambiguously supports that sister relationship. These results force us to at least consider the alternative: that voluntary removal of a sexual organ and other unique or unusual sexual biology evolved convergently in *Tidarren* and *Echinotheridion*, or perhaps have been secondarily lost in related genera. On the trees resulting from Bayesian analyses of the combined molecular data (Fig. 1) and the analyses when all data are combined, (Figs 2) parallel origin of sexual organ removal is the most parsimonious explanation. Although such a result may sound surprising, parallel evolution of ‘complex’ behaviour is certainly not unheard of in theridiid spiders. For example, permanent non-territorial sociality, and the range of behaviours it encompasses, has evolved in parallel approxi-

mately seven times in closely related species within a single theridiid genus, *Anelosimus* (Agnarsson 2005, 2006b; I. Agnarsson, L. Avilés, J. A. Coddington and W. P. Maddison, unpublished data), and some additional three times in other closely related genera (*Theridion* and *Achaeareanea*).

In many of the analyses, secondary reversal to retaining both palps as an adult is an equally parsimonious explanation as a parallel origin of palpal removal, and this hypothesis costs only a single extra ‘step’ on trees in Figs 1–2. A ‘loss’ of such a behaviour as palpal emasculation may be a relatively simple evolutionary event and this hypothesis cannot be ruled out here. This would imply that the ancestor of one of the most diverse theridiid genera, *Achaeareanea*, amputated its palp. However, apart from ambiguous optimisation, there is no direct evidence for reversal in this behaviour (all *Echinotheridion* and *Tidarren* species have only one palp as adults); the same phylogenetic pattern could be explained without inferring behavioural reversal

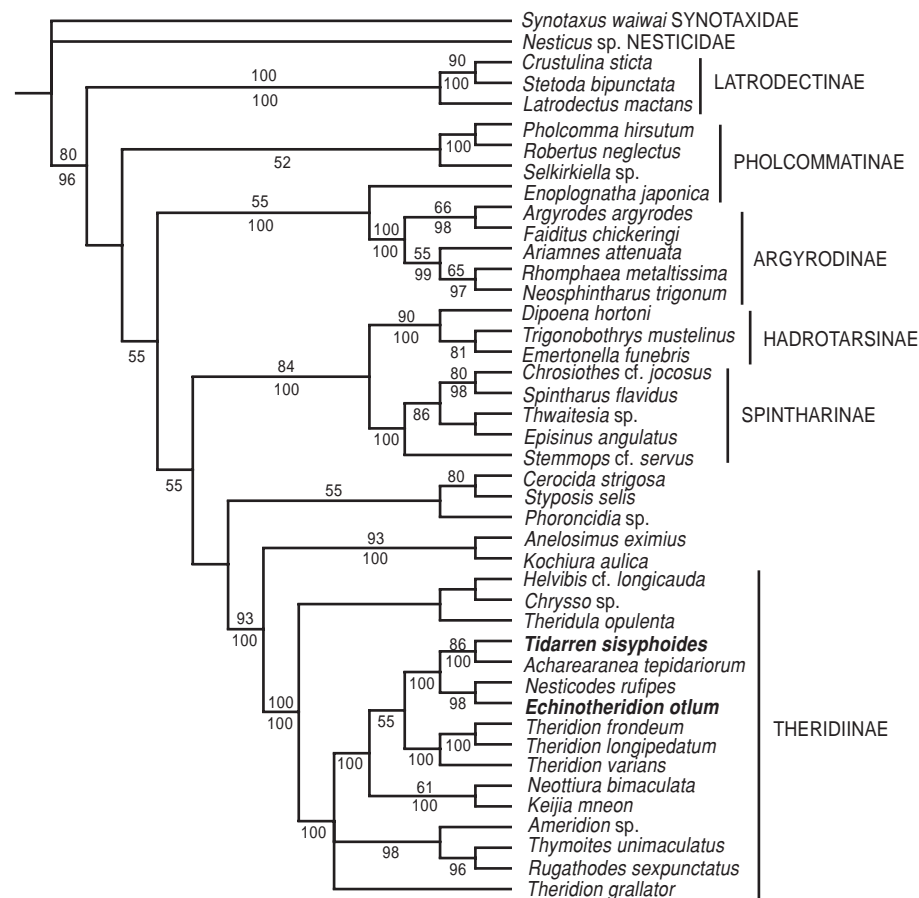


Fig. 2. Preliminary parsimony analysis of combined molecular (Clustal plus manual alignment) and morphological data. The results of Bayesian analysis of the same data are very similar, and suggest an identical relationship of *Echinotheridion* and *Tidarren*. Numbers above lines are bootstrap supports; numbers below lines show Bayesian posterior probabilities for clades also supported in the Bayesian analysis. Subfamilies are labelled according to Agnarsson (2004) and Arnedo *et al.* (2004). As for the parsimony analysis of the combined molecular data alone, the resulting tree also rejects the homology hypothesis.

by an ancestral polymorphism for this trait that was fixed to palpal amputation in *Echinotheridion* and *Tidarren*, but to palpal retention in *Achaearanea*.

As noted by Knoflach (2002), there are several conspicuous morphological, and some behavioural, differences between *Tidarren* and *Echinotheridion*, and all of the morphological characters that they share to the exclusion of most other theridiids are also shared by *Achaearanea* and/or *Nesticodes*. Likewise, their molecular sequences differ considerably and nearly all analyses agree that *Tidarren* is more closely related to *Achaearanea* than to *Echinotheridion*. Hence, behaviour apart, there is currently little to favour the homology hypothesis. Clearly, future studies should not only add further phylogenetic data, but also focus on detailed behavioural comparisons between the two genera, and other related genera, specifically *Achaearanea* and *Nesticodes*. For example, based on currently available data (Knoflach 2004) the putative placement of *Nesticodes* as sister to *Echinotheridion* is surprising as their sexual biology is very different.

In summary, the current results refute the sister relationship of *Tidarren* and *Echinotheridion* – two genera with sexual organ removal, emasculation and sexual cannibalism. This implies that these behaviours have either been secondarily lost in related taxa, or these behaviours represent rare evolutionary replicas of a suite of complex sexual behaviours.

Acknowledgments

Thanks to Matjaž Kuntner, Jun-Xia Zhang, Laura May-Collado, Camilla Myers and two anonymous reviewers for helpful comments on a version of the manuscript. Research and collecting permits in Ecuador were obtained through the Instituto Ecuatoriano de Areas Protegidas y Vida Silvestre, with the sponsorship of the Museo Ecuatoriano de Ciencias Naturales and the Department of Biology of the Pontificia Universidad Católica del Ecuador. Support for this research came from NSERC grants to Leticia Avilés and Wayne P. Maddison, and a Killam Postdoctoral Fellowship to I. Agnarsson.

References

- Agnarsson, I. (2003). The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae: Synotaxidae) with a description of a new species from Guyana, and notes on theridioid phylogeny. *Invertebrate Systematics* **17**, 719–734. doi:10.1071/IS03002
- Agnarsson, I. (2004). Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneioidea, Theridiidae). *Zoological Journal of the Linnean Society* **141**, 447–626. doi:10.1111/j.1096-3642.2004.00120.x
- Agnarsson, I. (2005). A revision and phylogenetic analysis of the American *ethicus* and *rupununi* groups of *Anelosimus* (Araneae, Theridiidae). *Zoologica Scripta* **34**, 389–413. doi:10.1111/j.1463-6409.2005.00189.x
- Agnarsson, I. (2006a). Asymmetric female genitalia and other remarkable morphology in a new genus of cobweb spiders (Theridiidae, Araneae) from Madagascar. *Biological Journal of the Linnean Society* **87**, 211–232. doi:10.1111/j.1095-8312.2006.00569.x
- Agnarsson, I. (2006b). A revision of the New World *eximius* group of *Anelosimus* (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. *Zoological Journal of the Linnean Society* **146**, 453–593. doi:10.1111/j.1096-3642.2006.00213.x
- Agnarsson, I., and Kuntner, M. (2005). Madagascar: an unexpected hotspot of social *Anelosimus* spider diversity (Araneae: Theridiidae). *Systematic Entomology* **30**, 575–592. doi:10.1111/j.1365-3113.2005.00289.x
- Andrade, M. C. B. (1996). Sexual selection for male sacrifice in the Australian redback spider. *Science* **271**, 70–72.
- Andrade, M. C. B., and Banta, E. M. (2002). Value of male remating and functional sterility in redback spiders. *Animal Behaviour* **63**, 857–870. doi:10.1006/anbe.2002.2003
- Arnedo, M. A., Coddington, J., Agnarsson, I., and Gillespie, R. G. (2004). From a comb to a tree: Phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* **31**, 225–245. doi:10.1016/S1055-7903(03)00261-6
- Branch, J. H. (1942). A spider which amputates one of its palpi. *Bulletin of the South California Academy of Science* **41**, 139–140.
- Brandley, M. C., Schmitz, A., and Reeder, T. W. (2005). Partitioned Bayesian analyses, partition choice, and the phylogenetic relationship of scincid lizards. *Systematic Biology* **54**, 373–390. doi:10.1080/10635150590946808
- Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist* **125**, 1–15. doi:10.1086/284325
- Gladstein, D. S., and Wheeler, W. C. (1997). 'POY: the Optimization of Alignment Characters.' (American Museum of Natural History: New York.)
- Giribet, G., and Wheeler, W. C. (1999). On gaps. *Molecular Phylogenetics and Evolution* **13**, 132–143. doi:10.1006/mpev.1999.0643
- Griswold, C. E., Coddington, J. A., Hormiga, G., and Scharff, N. (1998). Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneioidea). *Zoological Journal of the Linnean Society* **123**, 1–99. doi:10.1006/zjls.1997.0125
- Hormiga, G., Coddington, J. A., and Scharff, N. (2000). The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology* **49**, 435–462. doi:10.1080/10635159950127330
- Huelsenbeck, J. P., and Crandall, K. A. (1997). Phylogeny estimation and hypothesis testing using maximum likelihood. *Annual Review of Ecology and Systematics* **28**, 437–466. doi:10.1146/annurev.ecolsys.28.1.437
- Huelsenbeck, J. P., and Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics (Oxford, England)* **17**, 754–755. doi:10.1093/bioinformatics/17.8.754
- Knoflach, B. (2002). Copulation and emasculation in *Echinotheridion gibberosum* (Kulczynski, 1899) (Araneae, Theridiidae). In 'European Arachnology 2000'. (Eds S. Toft and N. Scharff.) pp. 139–144. (Aarhus University Press: Aarhus.)
- Knoflach, B. (2004). Diversity in the copulatory behaviour of comb-footed spiders (Araneae, Theridiidae). *Denisia* **12**, 161–256.
- Knoflach, B., and Benjamin, S. (2003). Mating without sexual cannibalism in *Tidarren sisyphoides* (Araneae, Theridiidae). *The Journal of Arachnology* **31**, 445–448.
- Knoflach, B., and van-Harten, A. (2000). Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). *Journal of Natural History* **34**, 1639–1659. doi:10.1080/00222930050117530
- Knoflach, B., and van-Harten, A. (2001). *Tidarren argo* sp. nov. (Araneae: Theridiidae) and its exceptional copulatory behaviour: Emasculation, male palpal organ as a mating plug and sexual cannibalism. *Journal of Zoology* **254**, 449–459. doi:10.1017/S0952836901000954

- Kuntner, M. (2005). A revision of *Herennia* (Araneae, Nephilidae, Nephilinae), the Australasian 'coin spiders'. *Invertebrate Systematics* **19**, 391–436. doi:10.1071/IS05024
- Laamanen, T. R., Meier, R., Miller, M. A., Hille, A., and Wiegmann, B. M. (2005). Phylogenetic analysis of *Themira* (Sepsidae: Diptera): sensitivity analysis, alignment, and indel treatment in a multigene study. *Cladistics* **21**, 258–271. doi:10.1111/j.1096-0031.2005.00066.x
- Levi, H. W. (1963). American spiders of the genus *Achaearanea* and the new genus *Echinotheridion* (Araneae, Theridiidae). *Bulletin of the Museum of Comparative Zoology, Harvard* **129**, 187–240.
- Maddison, D. R., and Maddison, W. P. (2005). 'MacClade: Analysis of Phylogeny and Character Evolution. Version 4.08.' (Sinauer Associates: Sunderland, MA.)
- Posada, D., and Crandall, K. A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics (Oxford, England)* **14**, 817–818. doi:10.1093/bioinformatics/14.9.817
- Ramos, M., Irschick, D. J., and Christenson, T. E. (2004). Overcoming an evolutionary conflict: Removal of a reproductive organ greatly increases locomotor performance. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 4883–4887. doi:10.1073/pnas.0400324101
- Rodríguez, F., Oliver, J. F., Marín, A., and Medina, J. R. (1990). The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* **142**, 485–501.
- Swofford, D. L. (2002). 'PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0.' (Sinauer Associates: Sunderland, Massachusetts.)
- Tamura, K., and Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* **10**, 512–526.
- Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F., and Higgins, D. G. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**, 4876–4882. doi:10.1093/nar/25.24.4876
- Vollrath, F. (1998). Dwarf males. *Trends in Ecology & Evolution* **13**, 159–163. doi:10.1016/S0169-5347(97)01283-4
- Wilgenbusch, J., and de Queiroz, K. (2000). Phylogenetic relationships among the phrynosomatid sand lizards inferred from mitochondrial DNA sequences generated by heterogeneous evolutionary processes. *Systematic Biology* **49**, 592–612. doi:10.1080/10635159950127411
- Wunderlich, J. (1992). 'Die Spinnen-Fauna der makaronesischen Inseln.' (Verlag J. Wunderlich: Straubenhardt.)
- Yang, Z. (1994). Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Journal of Molecular Evolution* **39**, 306–314. doi:10.1007/BF00160154

Manuscript received 26 September 2005, revised and accepted 2 June 2006.

Appendix 1. List of the morphological characters (see Agnarsson 2004 for detailed descriptions)*Female genitalia*

- (1) *Epigynal ventral margin*: entire (0); with scape (1).
 (2) *Epigynal dorsal plate*: absent (0); present (1).
 (3) *Epigynal plate surface*: smooth (0); ridged (1).
 (4) *Copulatory pore position*: caudal (0); ventral (1).
 (5) *Copulatory pore shape*: wide (0); narrow slits (1).
 (6) *Copulatory bursa anterior margin*: entire (0); medially acute (1).
 (7) *Copulatory duct placement relative to spermathecae*: posterior (0); lateral or anterior (1).
 (8) *Copulatory duct*: simple loop (0); two or more loops (1).
 (9) *Copulatory duct relative to spermathecae*: apart (0); encircling (1).
 (10) *Spermathecal number*: two (0); four (1).
 (11) *Spermathecal shape*: ovoid; elongate (0); dumbbell (1).
 (12) *Spermathecal accessory lobes*: absent (0); present (1).
 (13) *Fertilisation duct sclerotisation*: light (0); heavy (1).

Male genitalia

- (14) *Tibial distal end*: subequal to base (0); broadened (1).
 (15) *Tibial rim*: slightly asymmetric (0); scoop-shaped (1).
 (16) *Tibial rim setae*: irregular (0); regular, strong setae (1).
 (17) *Tibial rim protrusion*: dorsal to cymbium (0); faces bulb (1).
 (18) *Tibial retrolateral trichobothria*: three or more (0); two (1); one or none (2).
 (19) *Tibial prolateral trichobothria*: two or more (0); one (1); none (2).
 (20) *Patellal spur*: absent (0); present (1).
 (21) *Cymbium*: entire (0); expanded retrolaterally (1).
 (22) *Cymbial retromargin*: entire (0); with apophysis (1); grooved (2).
 (23) *Cymbial dorsobasal margin*: entire (0); incised (1); ridged (2).
 (24) *Cymbial distal promargin*: entire (0); with apophysis (1); *Latrodectus* (2).
 (25) *Cymbial mesal margin*: entire (0); incised (1).
 (26) *Cymbial tip sclerotisation*: normal (0); light (1).
 (27) *Cymbial tip setae*: normal (0); thick and curved (1).
 (28) *Cymbial sheath*: absent (0); present (1).
 (29) *Paracymbium*: present (0); absent (1).
 (30) *Paracymbium shape*: *Argiope* (0); *Tetragnatha* (1); *Pimoa* (2); *Linyphia* (3); cup (4); *Nesticid* (5).
 (31) *Bulb-cymbium lock mechanism*: absent (0); present (1).
 (32) *Lock placement*: basal (0); distal; central (1).
 (33) *Lock mechanism*: hook (0); hood; *Theridula* (1).
 (34) *Cymbial hook orientation*: downwards (0); upwards (1).
 (35) *Cymbial hook*: inside cymbium (0); ectal margin (1).
 (36) *Cymbial hook inferior groove*: absent (0); present (1).
 (37) *Cymbial hook tip*: blunt (0); strongly tapering (1).
 (38) *Cymbial hood size*: narrow (0); broad; *Spintharus* (1).
 (39) *Cymbial hood region*: translucent (0); opaque (1).
 (40) *Bulbal sclerite of lock mechanism*: median apophysis (0); embolus base (1).
 (41) *Alveolus placement*: ectal (0); central; mesal (1).
 (42) *Alveolar cavity*: simple (0); with alveolar sclerite (1).
 (43) *Alveolus shape*: suboval (0); mesal extension (1).
 (44) *Subtegular retrolateral margin*: entire (0); lobed (1).
 (45) *Tegulum size*: normal (0); huge (1).
 (46) *Tegulum ectal margin*: entire (0); protruded (1).
 (47) *Tegular groove*: absent (0); present (1).
 (48) *Tegular arch*: absent (0); present (1).
 (49) *Tegular pit*: absent (0); present (1).
 (50) *Tegular pit-embolus interaction*: embolus base (0); embolic apophysis (1).
 (51) *Sperm duct trajectory switchbacks I and II*: present (0); absent (1).
 (52) *Sperm duct trajectory switchback I*: separate (0); touching (1).
 (53) *Sperm duct trajectory switchback II*: entirely in tegulum (0); terminates in embolus (1).
 (54) *Sperm duct trajectory post-switchbacks II turn*: absent (0); present (1).

- (55) *Sperm duct trajectory switchbacks I and II segment alignment*: divergent (0); parallel (1).
 (56) *Sperm duct trajectory switchbacks I and II orientation*: in plane (0); out of plane (1).
 (57) *Sperm duct trajectory reverse switchbacks I and II*: absent (0); present (1).
 (58) *Sperm duct trajectory switchback III*: absent (0); present (1).
 (59) *Sperm duct trajectory switchback IV*: absent (0); present (1).
 (60) *Sperm duct entering embolus*: clockwise (0); counter-clockwise (1).
 (61) *Sperm duct constriction*: gradual (0); abrupt before switchback I (1).
 (62) *Conductor*: present (0); absent (1).
 (63) *Conductor tip width*: subequal to base (0); enlarged (1).
 (64) *Conductor form*: with a groove for embolus (0); entire (1).
 (65) *Conductor surface*: smooth (0); heavily ridged (1).
 (66) *Conductor folding*: entire (0); complex (1); *Helvibis* (2).
 (67) *Conductor tip sclerotisation*: like base (0); more than base (1).
 (68) *Conductor base*: entire (0); grooved (1).
 (69) *Conductor origin*: tegular margin (0); apical to tegular margin (1).
 (70) *Subconductor*: absent (0); present (1).
 (71) *Median apophysis*: present (0); absent (1).
 (72) *Median apophysis and sperm duct*: not in median apophysis (0); inside median apophysis (1).
 (73) *Median apophysis-tegulum attachment*: membranous (0); fused (1).
 (74) *Median apophysis-tegular connection*: broad (0); narrow (1).
 (75) *Median apophysis form*: unbranched (0); two branches (1).
 (76) *Median apophysis central region*: entire (0); with apophysis (1).
 (77) *Median apophysis II*: absent (0); present (1).
 (78) *Median apophysis distal tip*: entire (0); hooded (1).
 (79) *Median apophysis hood form*: narrow, pit-like (0); scoop-shaped (1).
 (80) *Theridioid tegular apophysis*: absent (0); present (1).
 (81) *Theridioid tegular apophysis branches*: unbranched (0); two branches (1).
 (82) *Theridioid tegular apophysis apex*: entire (0); with a small apophysis (1).
 (83) *Theridioid tegular apophysis form*: entire (0); grooved (1); excavate (2).
 (84) *Theridioid tegular apophysis basal portion*: bulky (0); huge, membranous (1).
 (85) *Theridioid tegular apophysis distal tip*: entire (0); hooked (1).
 (86) *Theridioid tegular apophysis surface*: smooth (0); ridged (1).
 (87) *Embolus and theridioid tegular apophysis*: loosely associated (0); embolus enclosed in apophysis (1).
 (88) *Embolus tip*: entire (0); bifid (1).
 (89) *Embolus origin*: retroventral on tegulum (0); retrolateral (1).
 (90) *Embolus surface*: smooth (0); ridged (1).
 (91) *Embolus shape*: short to moderate (0); extremely long (1).
 (92) *Embolus spiral*: normal (0); thick, much broader than tip (1).
 (93) *Embolus spiral*: suboval or round (0); distinctly flattened (1).
 (94) *Embolus form*: entire (0); with transverse suture (1).
 (95) *Embolus distal rim*: entire (0); deeply grooved (1).
 (96) *Embolus terminus*: abrupt (0); with a distal apophysis (1).
 (97) *Embolus-tegulum junction*: fixed (0); membranous (1).
 (98) *Embolus base*: entire (0); lobed (1).
 (99) *Embolus division b*: absent (0); present (1).
 (100) *Embolus spiral insertive piece*: entire (0); break-off point (1).
 (101) *Extra tegular sclerite*: absent (0); present (1).

Somatic morphology

- (102) *Lateral eyes (male)*: juxtaposed (0); separate (1).
 (103) *Median eyes (male)*: normal (0); on tubercle (1); eye region raised (2).
 (104) *Anterior median eye size v. anterior lateral eye (male)*: subequal (0); smaller (1).
 (105) *Anterior median- lateral eye separation (female)*: over 1 diameter (0); 1 diameter or less (1).

(continued next page)

Appendix 1. (continued)

- (106) *Cheliceral promargin*: toothed (0); smooth (1).
 (107) *Cheliceral anterior tooth shape*: blunt (0); pointed (1).
 (108) *Cheliceral anterior tooth number*: four or more (0); three (1); two (2); one (3).
 (109) *Cheliceral proximal tooth size*: as big or smaller than adjacent (0); larger than adjacent (1).
 (110) *Cheliceral posterior margin*: toothed (0); smooth (1).
 (111) *Cheliceral posterior tooth number*: four or more (0); three (1); two (2); one (3).
 (112) *Cheliceral furrow*: smooth (0); denticulate (1).
 (113) *Cheliceral sexual dimorphism*: subequal (0); male larger (1).
 (114) *Cheliceral ectal surface (male)*: smooth (0); stridulatory (1).
 (115) *Cheliceral anterior base*: rounded (0); with a distinct knob (1).
 (116) *Cheliceral apophysis (male)*: absent (0); present (1).
 (117) *Cheliceral paturon length*: normal (0); short (1).
 (118) *Cheliceral paturon width*: normal (0); thin (1).
 (119) *Cheliceral fang length (male)*: normal (0); huge (1).
 (120) *Cheliceral fang shape*: cylindrical (0); sickle-shaped (1).
 (121) *Cheliceral hairs*: weakly serrate (0); strongly serrate (1).
 (122) *Cheliceral boss*: present (0); absent (1).
 (123) *Carapace*: smooth (0); rugose (1); scaly (2); rippled (3); bumpy (4).
 (124) *Carapace height (male)*: normal (0); raised (hadrotarsid) (1).
 (125) *Carapace color*: uniform (0); longitudinal dark band (1).
 (126) *Carapace shape*: longer than wide (0); subequal (1).
 (127) *Carapace hairiness*: sparse or patchy (0); uniform (1).
 (128) *Carapace pars stridens*: irregular (0); regular ridges (1).
 (129) *Regular pars stridens*: separate (0); continuous (1).
 (130) *Interocular area*: flush with clypeus (0); projecting (1).
 (131) *Clypeus*: concave or flat (0); projected (1).
 (132) *Ocular area setae (male)*: sparse (0); in a dense field (1).
 (133) *Clypeal setae (male)*: normal (0); modified (1).
 (134) *Labium distal margin*: rebordered (0); not rebordered (1).
 (135) *Labium-sternum connection*: seam (0); fused (1).
 (136) *Labium shape*: subrectangular (0); triangular (1).
 (137) *Sternum*: elongate (0); subequal or wider than long (1).
 (138) *Sternocoxal tubercles*: present (0); absent (1).
 (139) *Sternum setal bases*: unmodified (0); raised (1).
 (140) *Pedicel location*: anterior (0); medial (1).
 (141) *Pedicel lyriform organs*: narrow (0); broad (1).
 (142) *Abdomen*: w/paired humps (0); ellipsoid, smooth (1).
 (143) *Abdomen colour pattern*: folium; (0) uniform or unpigmented (1).
 (144) *Abdomen folium*: spots or blotches (0); central band (1).
 (145) *Dorsal band*: edge light (0); edge dark (1); *Ameridion* (2).
 (146) *Abdomen dot pigment*: silver (0); non-reflective, dull (1).
 (147) *Abdomen pedicel area (male)*: smooth (0); sclerotised (1).
 (148) *Abdomen pedicel area sclerotisation*: continuous (0); separate (1).
 (149) *Abdomen supra-pedicellate nubbins*: absent (0); present (1).
 (150) *Stridulatory pick row*: absent (0); present (1).
 (151) *Stridulatory pick row form*: weakly keeled (0); strongly keeled (1).
 (152) *Stridulatory pick row pick number*: three or less (0); four or more (1).
 (153) *Stridulatory pick row ectally-oriented picks*: present (0); absent (1).
 (154) *Stridulatory pick row insertion*: flush with abdomen surface (0); on ridge (1).
 (155) *Stridulatory pick row region*: smooth (0); grooved (1).
 (156) *Stridulatory pick row mesal pointing picks*: absent (0); present (1).
 (157) *Stridulatory pick row mesally oriented picks angle*: dorsal (0); perpendicular or ventral (1).
 (158) *Stridulatory pick row setal bases*: low, gently ridged (0); acute (1).
 (159) *Stridulatory pick row*: straight (0); distinctly curved; argyrodine (1).
 (160) *Stridulatory pick row dorsal pick spacing*: normal (0); compressed (1).
 (161) *Stridulatory pick row relative to pedicel*: lateral (0); dorsal (1).
 (162) *Additional stridulatory picks*: absent (0); present (1).
 (163) *Suprapedicellate dorsal proprioceptors*: absent (0); present (1).
 (164) *Suprapedicellate ventrolateral proprioceptors*: absent (0); present (1).
 (165) *Abdominal suprapedicellate apodemes*: rugose (0); smooth (1).
 (166) *Abdomen surface*: smooth (0); with scuta (1).
 (167) *Sigilla*: conspicuous (0); inconspicuous, unicolorous (1).
 (168) *Epiandrous fusules*: present (0); absent (1).
 (169) *Epiandrous fusule*: in pair of sockets (0); in a row (1).
 (170) *Epiandrous fusule pair number*: more than ten (0); eight or less (1).
 (171) *Male seminal vesicula*: small (0); large and dark (1).
 (172) *Colulus*: present (0); absent; invaginated (1).
 (173) *Colulus size*: large (0); small (1).
 (174) *Colular setae*: present (0); absent (1).
 (175) *Colular setae number (female)*: three or more (0); two (1).
 (176) *Palpal claw (female)*: present (0); absent (1).
 (177) *Palpal claw*: attenuate (0); palmate (1); semi-palmate (2).
 (178) *Palpal claw dentition (female)*: dense (0); sparse (1).
 (179) *Palpal tibial trichobothria (female)*: over six (0); three to five (1); one to two (2).
 (180) *Palpal tarsal setae (female)*: smooth (0); serrated (1).
 (181) *Palpal tarsus dorsal setae (female)*: present (0); absent (1).
 (182) *Femur I relative to II*: subequal (0); robust, larger (1).
 (183) *Femoral macrosetae*: present (0); absent (1).
 (184) *Leg IV relative length (male)*: third; second (0); longest (1).
 (185) *Leg IV relative length (female)*: third (0); second (1); longest (2).
 (186) *Femur v. metatarsus*: metatarsus longer (0); metatarsus shorter (1).
 (187) *Metatarsus v. tibia*: metatarsus longer (0); metatarsus shorter (1).
 (188) *Metatarsal ventral macrosetae*: normal (0); thick (1).
 (189) *Metatarsus I trichobothria position*: proximal (0); distal (1); submedian (2).
 (190) *Metatarsus III trichobothrium*: present (0); absent (1).
 (191) *Metatarsus IV trichobothrium*: absent (0); present (1).
 (192) *Patella-tibia autospasy*: absent (0); present (1).
 (193) *Tarsus IV setae*: smooth (0); serrate (tarsal comb) (1).
 (194) *Tarsus IV comb*: smooth (0); theridiid grooves (1).
 (195) *Tarsus IV comb*: simple, straight (0); curved hooks (1).
 (196) *Tarsus IV comb dorsal margin*: straight (0); notched (1).
 (197) *Tarsus I ventral setae*: ungrouped (0); grouped (1).
 (198) *Tarsal organ size*: small (normal) (0); enlarged (1).
 (199) *Tarsus IV central claw v. lateral (male)*: short (0); longer (1).
 (200) *Tarsus IV central claw (female)*: normal (0); long; minute (1).
Spinnerets
 (201) *Spinneret insertion*: normal (0); abdomen extending beyond (1).
 (202) *Spinneret sclerotised ring*: absent (0); present (1).
 (203) *Anterior lateral spinneret median surface*: normal (0); with parallel ridges (1).
 (204) *Anterior lateral spinneret piriform spigot bases*: normal (0); reduced (1).
 (205) *Anterior lateral spinneret piriform field size*: large (0); small (1).
 (206) *Posterior lateral spinneret flagelliform spigot*: similar to cylindrical (0); longer than cylindrical (1).
 (207) *Posterior lateral spinneret post cylindrical spigot base*: normal (0); enlarged (1).
 (208) *Cylindrical spigot bases*: equal to or smaller than ampullates (0); huge (1).
 (209) *Cylindrical shaft surface*: smooth (0); grooved (1).
 (210) *Posterior lateral spinneret cylindrical spigot number*: two (0); one (1).
 (211) *Posterior lateral spinneret aciniform spigot number*: five or more (0); four or less (1).
 (212) *Posterior lateral spinneret flagelliform spigot*: present (0); absent (1).

(continued next page)

Appendix 1. (continued)

(213) <i>Posterior lateral spinneret aggregate spigot number (female):</i> two (0); one (1).	<i>Behaviour and web building</i>
(214) <i>Posterior lateral spinneret aggregate spigot size v. cylindrical:</i> equal or smaller (0); larger (1).	(224) <i>Prey-catching web:</i> present (0); absent (1).
(215) <i>Posterior lateral spinneret anterior aggregate spigot shape:</i> normal (0); flat (1).	(225) <i>Web:</i> orb (0); sheet (1); rectangular orb (2); cobweb (3); H (4); mesh (5); line (6); <i>Phoroncidia</i> (7).
(216) <i>Posterior lateral spinneret posterior aggregate spigot shape:</i> normal (0); flat (1).	(226) <i>Sticky silk in web:</i> present (0); absent (1).
(217) <i>Posterior lateral spinneret aggregate gland form:</i> entire (0); lobed (1).	(227) <i>Sticky silk placement:</i> sheet (0); on gumfoot lines (1).
(218) <i>Posterior lateral spinneret aggregate position:</i> parallel (0); end to end (1).	(228) <i>Wrap-bite attack:</i> present (0); absent (1).
(219) <i>Posterior lateral spinneret aggregate and flagelliform spigots (male):</i> absent (0); present (1).	(229) <i>Sticky silk wrap attack:</i> absent (0); present (1).
(220) <i>Posterior lateral spinneret minor ampullate spigot nubbins:</i> present (0); absent (1).	(230) <i>Egg sac:</i> spherical to lenticular (0); stalked (1).
(221) <i>Posterior lateral spinneret cylindrical spigot base:</i> distinct (0); indistinct or absent (1).	(231) <i>Egg case:</i> round (0); knob (1); rhomboid (2); elongate (1); spiky (1).
(222) <i>Posterior lateral spinneret aciniform spigot number:</i> five or more (0); 4 (1); 3 (2); 2 (3); 1 (4); 0 (5).	(232) <i>Egg sac outermost fibres:</i> fine (0); thick, loose (1).
(223) <i>Posterior lateral spinneret minor ampullate spigot shaft:</i> short (0); longer than cylindrical shafts (1).	(233) <i>Egg sac fibre ultrastructure:</i> smooth (0); spiny (1).
	(234) <i>Web construction:</i> solitary (0); communal (1).
	(235) <i>Sex ratio:</i> subequal (0); more than three times female-biased (1).
	(236) <i>Male palp amputation:</i> absent (0); present (1).
	(237) <i>First palpal insertion:</i> transfer sperm (0); pseudocopulation (1).
	(238) <i>Palpal insertions:</i> ipsilateral (0); contralateral (1).
	(239) <i>Sperm induction:</i> independent (0); during copulation (1).
	(240) <i>Mating thread:</i> present (0); absent (1).
	(241) <i>Bulbal movements:</i> no (0); rhythmic haematodocha (1).
	(242) <i>Male position during sperm deposition:</i> below (0); above (1).

Appendix 2. The morphological character matrix

Taxa	Characters							
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	
<i>Argiophe</i>	000000?0-0	0000000000	0000000000	0-----0---	000000000-	00000000-0	0000000000	
<i>Tetragnatha</i>	000-0000-1	0001000000	0000000001	0-----0---	100000000-	00000000-0	0000000000	
<i>Pimoa</i>	01000000-0	0000000000	1000000002	0-----0---	200000000-	00000000-0	0001000000	
<i>Linyphia</i>	1100000100	1000000010	0000000003	0-----0---	100000000-	00000000-0	01-----	
<i>Synotaxus waiwai</i>	0000000100	0010000111	0200000004	0-----0---	100000000-	1--0--00-0	01-----	
<i>Synotaxus monoceros</i>	0000000100	0010000111	0200000004	0-----0---	100000000-	1--0--00-0	01-----	
<i>Eidmanella</i>	00010000-0	0100000110	0000000005	0-----0---	100100000-	0000100110	01-----	
<i>Nesticus</i>	00010000-0	0100000110	0000000005	0-----0---	100100000-	0000100110	0001000000	
<i>Dipoena nigra</i>	00000010-1	0001000110	0000000001-	1100010--0	200010000-	0000000101	0001000000	
<i>Emertonella funebris</i>	00011010-1	0001000210	0000000001-	1100010--0	200000000-	0000000101	01-----	
<i>Euryopsis gertschi</i>	00011010-1	0001000220	0000000001-	1100010--0	200000000-	0000000101	01-----	
<i>Thwaitesia margaritifera</i>	00010000-0	0001011110	0000000001-	1100010--0	210000000-	1-----0100	0010011000	
<i>Episinus amoenus</i>	0001101100	0001011110	0000000001-	1100010--0	200000000-	0000000110	0010111000	
<i>Spintharus flavidus</i>	0001000100	0001011110	0000000001-	111--1-210	200000000-	0000000100	0010111000	
<i>Latrodectus geometricus</i>	0001011110	2001111110	000200011-	1100010--0	200000000-	00000000-0	1001000100	
<i>Latrodectus mactans</i>	0001011110	2001111110	000200011-	1100010--0	200000000-	00000000-0	1001000100	
<i>Crustulina sticta</i>	00010010-0	0001111220	0001000001-	1100010--0	200000000-	00000000-0	1001000100	
<i>Steatoda grossa</i>	00011010-0	0001111110	0000000001-	1100010--0	200000000-	00000000-0	1001000100	
<i>Carniella siam</i>	0001000100	0001111220	0000000001-	1001101--0	200000000-	0000000100	0?????????	
<i>Robertus frontatus</i>	00011010-0	2001111220	0000000001-	1101101--0	200000000-	0000000100	0001000000	
<i>Pholcomma hirsutum</i>	0001101100	0001111220	0000000001-	1101101--0	200000000-	00000100-0	0001000000	
<i>Enoplognatha latimana</i>	00010000-0	0001011110	0000000001-	1101100--0	200000000-	1-----0100	0000101000	
<i>Enoplognatha ovata</i>	00010000-0	0001011110	0000000001-	1101100--0	200000000-	1-----0100	0000101000	
<i>Selkirkiella magallanes</i>	0001100100	0001011210	0000000001-	1101101--0	200000000-	0000000100	0010101000	
<i>Selkirkiella alboguttata</i>	0001100100	0001011210	0000000001-	1101101--0	200000000-	0000000100	0010101000	
<i>Phoroncidia</i> sp.	0001100110	0001000220	0000000001-	1101100--0	200000000-	0000001100	01-----	
<i>Cerocida strigosa</i>	000110?110	2001011220	0000000001-	1101100--0	200000000-	1-----00-0	01-----	
<i>Stemmops</i> cf. <i>servus</i>	0001100110	0001011210	0000100001-	1101000--0	200000000-	00000000-0	0000000000	
<i>Argyrodes argyrodes</i>	00010000-0	0001111110	0001000001-	1100000--0	200000000-	0000011110	0000000000	
<i>Argyrodes elevatus</i>	00010000-0	0001111110	0001000001-	1100000--0	200000000-	0000011110	0000000000	
<i>Neospintharus trigonus</i>	00010000-0	0001111110	0000000001-	1100000--0	200000000-	0000011110	0001000000	
<i>Rhomphaea metaltissima</i>	00010000-0	0001011220	0000000001-	1100000--0	200000000-	0000011110	0000000000	
<i>Ariannes</i> cf. <i>attenuatus</i>	00010010-0	1001111220	0001000001-	1100000--0	200000000-	0000011110	0000000000	
<i>Faiditus</i> cf. <i>chickeringi</i>	00010110-0	0001111110	0000000001-	1100000--0	200000000-	0000011110	0000000000	
<i>Kochiura aulica</i>	0001000110	0001111110	0000000111-	1101010--0	200000000-	00000100-0	0010000000	
<i>Kochiura rosea</i>	0001000110	0001111110	0000000111-	1101010--0	200000000-	00000100-0	0010000000	
<i>Anelosimus lorenzo</i>	00110110-0	0001111110	000010011-	111----110	201000000-	00000100-0	0001000000	
<i>Anelosimus rupununi</i>	00110110-0	0001111110	000010011-	111----110	201000000-	00000100-0	0001000000	
<i>Anelosimus pulchellus</i>	10110000-0	0001111110	0000000001-	121----010	200000000-	01000100-0	0001000001	
<i>Anelosimus vittatus</i>	10110000-0	0001111110	0000000001-	121----010	200000000-	01000100-0	0001000001	
<i>Anelosimus dude</i>	00010000-0	0001111110	0000110001-	111----000	200010100-	00001100-0	0000000000	
<i>Anelosimus biglebowski</i>	00010000-0	0001111110	0000110001-	111----000	200010100-	00001100-0	0000000000	
<i>Anelosimus analyticus</i>	00110000-0	0001111110	0000110001-	111----000	200000000-	00011100-0	0001000001	
<i>Anelosimus eximius</i>	00110000-0	0001111110	0000110001-	111----000	200000000-	00011100-0	0001000001	
<i>Anelosimus baeza</i>	00110000-0	0001111110	0000110001-	111----000	200001000-	00011100-0	0001000001	
<i>Anelosimus studiosus</i>	00110000-0	0001111110	0000110001-	111----000	200000000-	00011100-0	0001000001	
<i>Chrysso</i> cf. <i>nigriceps</i>	00010100-0	0001111220	0000000001-	111----110	2000000010	00000100-0	0001000001	
<i>Nesticodes rufipes</i>	00010010-0	0001111120	0000000001-	111----010	200000000-	00000100-0	0001100000	
<i>Theridion frondeum</i>	00010000-0	0001111120	0000000001-	111----110	2000000011	0000010110	0000000010	
<i>Theridion longipedatum</i>	00010000-0	0001111120	0000000001-	111----110	2000000011	0000010110	0000000010	
<i>Theridion varians</i>	00010000-0	0001111220	0000000001-	111----010	2000000011	0000010100	0000001010	
<i>Theridion pictum</i>	00010000-0	0001111220	0000000001-	111----010	2000000011	0000010100	0000001010	
<i>Coleosoma floridanum</i>	00010000-0	0001111220	0000000001-	111----010	1000000011	0000010110	0000001010	
<i>Theridula emertoni</i>	00010000-0	0001111220	0020000001-	1100100--0	2000100010	1-----00-0	0001000000	
<i>Helvibis</i> cf. <i>longicaudatus</i>	0001001100	0001111220	0000000001-	111----010	1000000010	0000110110	0010021000	
<i>Tidarren sisyphoides</i>	10010000-0	0001111220	0000000001-	111----010	2000000010	00000100-0	0000001010	
<i>Ameridion</i> sp.	00000000-0	0001111220	0100000001-	111----010	2000000000-	1-----00-0	0001000010	
<i>Ameridion</i> cf. <i>petrum</i>	00000000-0	0001111220	0100000001-	111----010	2000000000-	1-----00-0	0001000010	

(continued next page)

Appendix 2. (continued)

Taxa	Characters						
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Thymoites unimaculatus</i>	00010000-0	0001111220	000000001-	112-----	200000000-	00000000-0	01-----
<i>Achaearana tepidariorum</i>	00010000-0	0001111120	001000001-	111----011	100000010-	00100100-0	0000101000
<i>Achaearana vervoorti</i>	00010000-0	0001111120	001000001-	111----011	100000010-	00100100-0	0000101000
<i>Achaearana wau</i>	00010000-0	0001111120	001000001-	111----011	100000000-	00100100-0	0000101000
<i>Echinotheridion gibberosum</i>	00000000-0	0001111220	000000001-	111----??0	????0000??	??????????	?00?100000
Taxa	Characters						
	7777777778	8888888889	9999999990	0000000001	1111111111	1111111111	1111111111
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Argiope</i>	00000000-0	-----000	0000001000	0000000000	1100000000	000000?0-0	0000000000
<i>Tetragnatha</i>	1-----0-0	-----000	0000001000	0100000000	0010000010	000000?0-0	0000000100
<i>Pimoa</i>	001-000--0	-----000	000000000?	0000100100	2001000000	01000000-0	000000010?
<i>Linyphia</i>	1-----0-0	-----000	0000001000	0001100000	0011000010	00000000-0	0000100100
<i>Synotaxus waiwai</i>	1-----1	0020001000	0000000000	0000100100	0000000000	11000000-0	0001001100
<i>Synotaxus monoceros</i>	001-000--1	0020001000	0000000000	0000100100	0000000000	11000000-0	1001001100
<i>Eidmanella</i>	001-0000-1	0000001000	0000000000	0001100100	0000000000	11000000-0	0000101100
<i>Nesticus</i>	001-0000-1	0000001000	0000000000	0001100100	0000000000	11000000-0	0000101100
<i>Dipoena nigra</i>	01010000-1	0000000000	0000001000	000011---1	-000001101	11010100-0	0001011101
<i>Emertonella funebris</i>	0101000101	0000010000	0000001000	000011---1	-000001101	11010100-0	0001011101
<i>Euryopis gertschi</i>	0101000101	0000010000	0000001000	000011---1	-000001101	11010100-0	0001011101
<i>Thwaitesia margaritifera</i>	0101000101	0000100000	0000001000	1000101101	-000000100	01000000-0	0001100100
<i>Episinus amoenus</i>	0101000101	0000100000	0000001000	1000101201	-000000100	01000000-0	0001100100
<i>Spintharus flavidus</i>	0101000101	0000000000	0000001000	00011003-1	-000000100	01000000-0	0001000100
<i>Latrodectus geometricus</i>	01010000-1	0000010000	1010001101	010011---1	-000000000	01000010-0	0001000100
<i>Latrodectus mactans</i>	0101000101	0000010000	1010001101	010011---1	-000000000	01000010-0	0001000100
<i>Crustulina sticta</i>	0101000101	0000100001	0000011100	00001003-1	-000000000	0110001100	0001100111
<i>Steatoda grossa</i>	0101000101	0000100000	0000011100	00001003-1	-000000000	0110001100	0001000110
<i>Carniella siam</i>	0101000100	-----000	0000001000	0001100110	2000000000	0100000110	1101101101
<i>Robertus frontatus</i>	0101000111	0000000000	0000001100	1001100100	2000000000	0100000110	0001101101
<i>Pholcomma hirsutum</i>	0001000111	0010000010	0000001000	1001100100	0000000000	0120000110	0001101101
<i>Enoplognatha latimana</i>	0101000111	0010001010	0000001000	1001100110	3010010010	0100000100	0001000100
<i>Enoplognatha ovata</i>	0101000101	0010001010	0000001000	1001100110	3010010010	0100000100	0001100100
<i>Selkirkiella magallanes</i>	0101000101	0111001010	0000001000	1001100100	1000000000	0100000110	0001000101
<i>Selkirkiella alboguttata</i>	010?000111	0111001010	0000001000	1001100100	1000000000	0100000110	0001000101
<i>Phoroncidia</i> sp.	000?000111	0011001010	0000001100	00201003-1	-000001100	?1000000-1	0001001101
<i>Ceroctida strigosa</i>	00010000-1	0011001010	0000001000	0001100010	0100000000	11300000-0	0001100101
<i>Stemmops</i> cf. <i>servus</i>	0001000111	0000000000	1000001100	00201003-1	-000001100	01000000-0	0001100101
<i>Argyrodes argyrodes</i>	0101000111	0000010001	0000011100	0010100110	3100000000	0100000101	1111100000
<i>Argyrodes elevatus</i>	0101000101	0000010001	0000011100	0010100110	3100000000	0100000101	11?1100000
<i>Neospintharus trigonus</i>	0101000101	0000010000	0000001100	0000100110	3100000000	0100000101	1111000000
<i>Rhomphaea metaltissima</i>	0101000101	0000010001	0000001100	0000100110	3100000000	0100100101	0111100000
<i>Ariamnes</i> cf. <i>attenuatus</i>	0101000101	0000010001	0000011100	0000100110	3100000000	01000000-1	0111100100
<i>Faiditus</i> cf. <i>chickeringi</i>	0101000101	0000100000	0000001100	0000100110	1100000000	0100000100	1101100000
<i>Kochiura aulica</i>	000?000101	0010110000	1000001100	0000100110	1000000000	0100000100	0001000100
<i>Kochiura rosea</i>	0001000111	1010010000	1000001100	0000100110	0000000000	0100000100	0001000100
<i>Anelosimus lorenzo</i>	0000100111	0000100000	0000101100	0000100110	1000000000	01000000-0	0001000100
<i>Anelosimus rupununi</i>	00001000-1	0000100000	0000101100	0000100110	1000000000	01000000-0	0001000100
<i>Anelosimus pulchellus</i>	00000000-1	000000000?	0000001?0	0000100110	1000000000	01000000-0	0001000101
<i>Anelosimus vittatus</i>	00000000-1	0000000001	0000001110	0000100110	1000000000	01000000-0	0001000101
<i>Anelosimus dude</i>	00000000-1	0000100000	0000001100	0000100110	1000000000	01000000-0	0001000101
<i>Anelosimus biglebowski</i>	00000000-1	0000100000	0000001100	0000100110	1000000000	01000000-0	0001000101
<i>Anelosimus analyticus</i>	00000000-1	0000110000	0000001110	0000100110	1000000000	01000000-0	0001000100
<i>Anelosimus eximius</i>	00000000-1	0000110100	0100001100	0000100110	1000000000	01000010-0	0001000100
<i>Anelosimus baeza</i>	00000000-1	0000110101	0100001110	0000100110	1000000000	01000010-0	0001000100
<i>Anelosimus studiosus</i>	00000000-1	0000110101	0100001110	0000100110	1000000000	01000010-0	0001000100
<i>Chryso</i> cf. <i>nigriceps</i>	00000100-1	0000000000	0000001100	0000100110	1000000000	01000000-0	0001100100

(continued next page)

Appendix 2. (continued)

Taxa	Characters						
	0000000001	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
	7777777778	8888888889	9999999990	0000000001	1111111112	2222222223	3333333334
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Nesticodes rufipes</i>	00000000-1	0000000000	0000001100	0000100211	-000000000	0100000100	0001000101
<i>Theridion frondeum</i>	00000110-1	0000000000	0000001100	0001100?01	-000100000	0100000100	0001000100
<i>Theridion longipedatum</i>	00000110-1	0000000000	0000001100	0001100?0	3000100000	0100000100	0001000101
<i>Theridion varians</i>	00000100-1	0000110000	0000001100	0000100211	-000000000	0100100100	0001000100
<i>Theridion pictum</i>	00000100-1	0000110000	0000001100	0000100211	-000000000	01001?0100	000100?1??
<i>Coleosoma floridanum</i>	00000000-1	0000000000	0000001100	0001100201	-000100000	0100000100	0001100100
<i>Theridula emertoni</i>	00000000-1	0000010000	0000001100	0000100211	-000000000	0100000110	0001000101
<i>Helvibis cf. longicaudatus</i>	0000010111	0000000000	1000001000	0000100201	-000000000	0140000100	0001100100
<i>Tidarren sisypoides</i>	00000000-1	0000000000	0000001000	0000100201	-000000000	0100000100	0001101101
<i>Ameridion sp.</i>	00000100-1	0000000000	0000001000	0000100?11	-000100000	0100000100	0001100101
<i>Ameridion cf. petrum</i>	00000100-1	0000000000	0000001000	0000100?11	-000100000	0100000100	0001100101
<i>Thymoites unimaculatus</i>	00?0000-0	-----000	0000000000	0000100211	-000000000	0100100100	0001100101
<i>Achaearanea tepidariorum</i>	1-----0	-----000	0000001100	0000100211	-000000000	0100000100	0001100101
<i>Achaearanea verwoorti</i>	1-----0	-----000	0000001100	0000100211	-000000000	0100000100	0001100101
<i>Achaearanea wau</i>	1-----0	-----000	0001001100	0000100111	-000000000	0100000100	0001100101
<i>Echinotheridion gibberosum</i>	000?000--?	??????000	0000001?00	000011---1	-000001?0	01001?0?0	0001000001
Taxa	Characters						
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111112	2222222222
	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Argiope</i>	0000-00-10	---00-----	--00000001	?00000000?	0000000000	0000--0000	0000000000
<i>Tetragnatha</i>	0101100-10	---00-----	--00000000	?000000000	0000?0000?	0000--00?0	0000000010
<i>Pimosa</i>	0100-10-10	---00-----	--01001010	?000000100	00011?1010	1100-0002	0001001000
<i>Linyphia</i>	0101010-10	---00-----	--01001010	?000000010	0001111000	0100-0000	0001001000
<i>Synotaxus waiwai</i>	0100-10-10	---00-----	--01001010	?000000111	1010000010	0010000010	1001100000
<i>Synotaxus monoceros</i>	0100-10-10	---00-----	--01001010	?000000111	1010000010	0010000010	1001100000
<i>Eidmanella</i>	011-10-10	---00-----	--01001011	?000100011	1011111010	1010000000	0001100000
<i>Nesticus</i>	011-10-10	---00-----	--110010?1	?000100011	1011111010	1010000000	0001100000
<i>Dipoena nigra</i>	0100-10-10	---00-----	--11100001	?000101011	1011100010	0010001000	1001100000
<i>Emertonella funebris</i>	0100-10-10	---00-----	--011001--	?2-0101021	1012200010	0010001002	0011100000
<i>Euryopsis gertschi</i>	0100-10-10	---00-----	--011001--	?2-1-01021	1012200010	0010001002	0011100000
<i>Thwaitesia margaritifera</i>	0000-00-11	000000--00	10111010?1	?010100011	1011100010	0011110100	00011-0000
<i>Episinus amoenus</i>	0000-10-11	000000--00	1011101001	?010100011	1011100010	0011110100	0001100000
<i>Spintharus flavidus</i>	0000-10-11	000000--00	10111011--	?010100021	101110001?	0011110100	0001100000
<i>Latrodectus geometricus</i>	0100-10-11	000000--00	1011100011	0000000010	1011100000	0011100000	0001100000
<i>Latrodectus mactans</i>	0100-10-11	000000--00	1011100011	?000000010	1011100000	0011100000	0001100000
<i>Crustulina sticta</i>	0100-11011	1101010000	0011100011	?000000121	1011111000	0011100000	0001100000
<i>Seiatoda grossa</i>	0100-11011	1101010000	1011100001	?000000011	1011110010	0011100000	0001100000
<i>Carniella siam</i>	011--11011	1001010000	10101011--	?00010012?	1011211001	001?000102	00011?0???
<i>Robertus frontatus</i>	011--11011	110100--00	1010100001	?000100121	1011111000	0011000102	0001100000
<i>Pholcomma hirsutum</i>	011--11011	10010100-0	1010110001	?000100121	1011111000	0011000102	0001100000
<i>Enoplognatha latimana</i>	0101111011	1101010000	0111101000	?000100011	1011100010	0011000100	0001000000
<i>Enoplognatha ovata</i>	0101111011	1101010000	0111101000	0000100011	1011100010	0011000100	0001000000
<i>Selkirkia magallanes</i>	0101110-11	001011-0--	1-11101001	?000100121	1011111000	0011000100	0001110000
<i>Selkirkia alboguttata</i>	011--10-11	001011-0--	1-11101001	?000100121	1011111000	0011000100	0001110000
<i>Phoroncidia sp.</i>	0000-10-00	----0-----	--10100001	?2-011--21	1111211000	001?000100	0101100000
<i>Cerocida strigosa</i>	011--11010	----0-----	--001011--	?010100121	1011111001	0011000100	0001100001
<i>Stemmops cf. servus</i>	011--10-11	00000100-0	1010101001	?000100121	1012211000	0011000102	0101100000
<i>Argyrodes argyrodes</i>	0100-01011	1101010020	0010101001	?000100111	1010011000	0011000111	10011-0110
<i>Argyrodes elevatus</i>	0100-01011	1101010020	0010101001	?000100111	1010011000	0011000111	10011-0110
<i>Neospintharus trigonus</i>	1000-01011	110100-20	0010101001	?000100111	1011111000	0011100111	10011-0110
<i>Rhomphaea metallissima</i>	1100-01111	010100-20	00101011-	?000100121	1011111000	0011000111	1001100110
<i>Ariamnes cf. attenuatus</i>	1100-01111	010100-20	0010101011	?000100121	1011111000	0011100111	1001100110
<i>Faiditus cf. chickeringi</i>	0000-01011	1101010000	0010101001	?000100111	101001100?	0011000111	10011-0110
<i>Kochiura aulica</i>	0101011011	1100010000	1011101001	0010100?21	1010111000	0011000110	0001110000

(continued next page)

Appendix 2. (continued)

Taxa	Characters						
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111112	2222222222
	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Kochiura rosea</i>	0101011011	1100010000	1011101001	?010100021	1010111000	0011000110	0001110000
<i>Anelosimus lorenzo</i>	0101011111	0100010-00	0011101001	?1-0100011	1010100000	0011000110	0001110000
<i>Anelosimus rupununi</i>	0101011111	0100010-00	0011101001	?1-0100011	1010100000	0011000110	0001110000
<i>Anelosimus pulchellus</i>	0101011011	1?000?????	??111010?0	?1-0100011	1110111100	0011000110	0001110000
<i>Anelosimus vittatus</i>	0101011011	110000-00	1011101000	?1-0100011	1110111100	0011000110	0001110000
<i>Anelosimus dude</i>	0101011011	1100010010	1011101001	?1-0100011	1110111000	0011000110	0001110000
<i>Anelosimus biglebowski</i>	0101011011	1100010010	1011101001	?1-0100011	1110111000	0011000110	0001110000
<i>Anelosimus analyticus</i>	0101011011	1100011011	1011101001	?1-0100011	1010111100	0011000110	0001100000
<i>Anelosimus eximius</i>	0101011011	1100011011	1011101001	?1-0100011	1010111000	0011000110	0001100000
<i>Anelosimus baeza</i>	0101011011	1100011011	1011101000	?1-0100011	1010111000	0011000110	00011000?0
<i>Anelosimus studiosus</i>	0101011011	1100011011	1011101001	?1-0100011	1010111?00	0011000110	0001100000
<i>Chryso cf. nigriceps</i>	0100-11111	0?00010000	1011101011	?1-1-00111	1011111000	0011000110	1001010000
<i>Nesticodes rufipes</i>	0100-11011	1100010000	0111101011	?1-1-00011	1011100010	0011100110	0001010000
<i>Theridion frondeum</i>	0101111011	1101010000	1111101011	?1-1-00021	1011110000	0011100110	0001110000
<i>Theridion longipedatum</i>	0101-11011	1101010000	1111101011	?1-1-00021	1011110000	0011100110	000111000?
<i>Theridion varians</i>	0101110-11	1100010000	0011101011	11-1-00021	1011110000	0011100110	0001110000
<i>Theridion pictum</i>	0?011???11	11?0? ??????	??111??01?	11-1??002?	1??1?100?0	0011100110	?001110000
<i>Coleosoma floridanum</i>	0101111011	1001010000	1011101011	?1-1-00?21	1011110000	0011?00110	00011??000
<i>Theridula emertoni</i>	0100-10-11	00000100-0	1011101011	?1-1-02011	1011100000	00111001?0	0001010000
<i>Helvibis cf. longicaudatus</i>	0100-11011	1001010000	1011101011	?1-1-00?21	1011111000	0011000100	1001110000
<i>Tidarren sisyphoides</i>	011--11011	1100010000	1011101011	?1-1-00121	1011111001	0011000110	00011?000?
<i>Ameridion sp.</i>	0101210-11	1100010100	1011101011	?1-1-00021	1011111020	0011000110	0001100000
<i>Ameridion cf. petrum</i>	0101210-11	1100010100	1011101011	?1-1-00021	1011111020	0011000110	0001100000
<i>Thymoites unimaculatus</i>	0100-10-11	1000010100	1011101011	?1-1-00121	1011111000	0011000110	0001110000
<i>Achaearanea tepidarium</i>	0100-11111	1100010000	1111101011	?1-1-02011	101?100000	0011100110	0001010000
<i>Achaearanea verwoorti</i>	0100-11111	1100010000	1111101011	?1-1-02011	101?100000	0011100110	0001010000
<i>Achaearanea wau</i>	0100-11111	1100010000	1111101011	01-1-02011	101?100000	0011100110	0001010000
<i>Echinotheridion gibberosum</i>	??00-1? ????	???????????	?????01???	?1-1-020??	101???????	?01???????	00?????????
Taxa	Characters						
	2222222222	2222222222	2222222222				
	1111111112	2222222223	3333333344				
	1234567890	1234567890	123456789012				
<i>Argiope</i>	000000?-00	0000000000	00?000??00?				
<i>Tetragnatha</i>	0000000-00	020001-1-0	00?000010?10				
<i>Pimoa</i>	100100?-01	05-01??1-?	???000??????				
<i>Linyphia</i>	0000000-01	02101001-0	00?000101?01				
<i>Synotaxus waiwai</i>	000100?-00	1200200010	0??000??????				
<i>Synotaxus monoceros</i>	000100?-00	1200200010	0??000??????				
<i>Eidmanella</i>	100100?-00	02?0301010	0??000??????				
<i>Nesticus</i>	1001001-00	02?0301010	0??000000?0				
<i>Dipoena nigra</i>	010?10?-11	030? ??????	???0000?0???				
<i>Emertonella funebris</i>	110111?111	0301---01?	???000??0???				
<i>Euryopis gertschi</i>	1101111111	0301--???	???000??0???				
<i>Thwaitesia margaritifera</i>	010111?101	030061-???	?11000??????				
<i>Episinus amoenus</i>	0001111101	030040101?	?1?000??????				
<i>Spintharus flavidus</i>	000111?101	0300401???	???000??????				
<i>Latrodectus geometricus</i>	0001111001	0100301010	400000??????				
<i>Latrodectus mactans</i>	0001111001	0100301010	0??00000011?				
<i>Crustulina sticta</i>	0001111001	01003?????	???0000?01??				
<i>Steatoda grossa</i>	0001111001	011030101?	???000??001?				
<i>Carniella siam</i>	100100?-11	?50???????	???000??????				
<i>Robertus frontatus</i>	100110?-01	030???????	???000??????				
<i>Pholcomma hirsutum</i>	100110?-11	040???????	0??000??????				
<i>Enoplognatha latimana</i>	0001111001	03103?????	???000??????				
<i>Enoplognatha ovata</i>	0001111001	03103??010	0??0000?0000				

(continued next page)

Appendix 2. (continued)

Taxa	Characters		
	2222222222	2222222222	222222222222
	1111111112	2222222223	333333333444
	1234567890	1234567890	123456789012
<i>Selkirkiella magallanes</i>	000110?-01	030031-??0	0??000??????
<i>Selkirkiella alboguttata</i>	000110?-01	030031-??0	0??000??????
<i>Phoroncidia</i> sp.	100111?011	0300601???	??000??????
<i>Cerocida strigosa</i>	100110?-11	030???????	??00??????
<i>Stemmops</i> cf. <i>servus</i>	100111?0?1	030???????	??000??????
<i>Argyrodes argyrodes</i>	0101111101	03006????1	1?0-0000?0?
<i>Argyrodes elevatus</i>	0101111101	03006????1	1?0-00??????
<i>Neospinitharus trigonus</i>	010111?011	03006????1	1??-00??????
<i>Rhomphaea metaltissima</i>	00111-?-11	030061?011	2??000??????
<i>Ariamnes</i> cf. <i>attenuatus</i>	00111-?-11	030061?011	3??000??????
<i>Faiditus</i> cf. <i>chickeringi</i>	010111?111	03006??11	1??000??????
<i>Kochiura aulica</i>	000111?101	03103?????	??0000?00??
<i>Kochiura rosea</i>	000111?101	03103?????	??0?0???????
<i>Anelosimus lorenzo</i>	000111?101	03105????0	0??110??????
<i>Anelosimus rupununi</i>	000111?101	03105????0	0??110??????
<i>Anelosimus pulchellus</i>	000111?101	031???????	?????0???????
<i>Anelosimus vittatus</i>	000111?101	03103????0	0??000??????
<i>Anelosimus dude</i>	000111?101	031???????	????00???????
<i>Anelosimus biglebowski</i>	000111?101	031???????	????00???????
<i>Anelosimus analyticus</i>	000111?101	031011-010	0??1?0???????
<i>Anelosimus eximius</i>	000111?101	031011-010	00?110???????
<i>Anelosimus baeza</i>	000111?101	031011-010	0??110???????
<i>Anelosimus studiosus</i>	000111?101	031011-010	0??110???????
<i>Chryso</i> cf. <i>nigriceps</i>	000111?101	031???????	??000???????
<i>Nesticodes rufipes</i>	000111?101	0310301010	0??000???????
<i>Theridion frondeum</i>	000111?101	03103????0	0??000???????
<i>Theridion longipedatum</i>	000111?101	03103?????	??000???????
<i>Theridion varians</i>	0001111101	0310300??0	0?0000111100
<i>Theridion pictum</i>	0001111101	03103?0010	0?0??01111??
<i>Coleosoma floridanum</i>	0?0111??01	?31030??0	0??0001111??
<i>Theridula emertoni</i>	000111?101	031031-010	0??0010?00??
<i>Helvibis</i> cf. <i>longicaudatus</i>	000111?101	031???????	??000???????
<i>Tidarren sisypoides</i>	000111?101	03103????0	0??000???????
<i>Ameridion</i> sp.	000111?101	031???????	??000???????
<i>Ameridion</i> cf. <i>petrum</i>	000111?101	031???????	??000???????
<i>Thymoites unimaculatus</i>	000111?001	030???????	??000???????
<i>Achaearanea tepidariorum</i>	000111?101	03105?????	??110???????
<i>Achaearanea vervoortii</i>	000111?101	03105????0	0??1100??????
<i>Achaearanea wau</i>	000111?101	0310301010	0??00000010?
<i>Echinotheridion gibberosum</i>	???????????	???031?????	??0010?00??