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A molecular phylogenetic approach to the New Zealand species of Enantiobuninae (Opiliones : Eupnoi : Neopilionidae)

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Running title: Phylogenetics of the New Zealand Enantiobuninae

Abstract. We report the first phylogeny based on molecular data for the New Zealand species in the genera *Forsteropsalis*, *Pantopsalis*, and *Mangatangi*, and comment on the taxonomic implications of our results, including the diagnostic viability of important morphological characters. Members of the New Zealand Enantiobuninae constitute some of the most charismatic soil arthropods of the archipelago, and a striking example of sexual dimorphism, with nondescript females but colourful males boasting exaggerated chelicerae many times longer than their bodies. The genera *Forsteropsalis* and *Pantopsalis* recently underwent revision, but many questions remained about the validity of many species designations, due to issues of characters of dubious taxonomic value, female specimens designated as holotypes despite the males holding all the diagnostic characters, and the suspected presence of more than one male form within some species. We present the first molecular phylogenetic study of the group, including extensive sampling of fresh material across New Zealand. Our results reject the controversial monophyly of Neopilionidae and comment on the taxonomic implications of the results, including the diagnostic validity of morphological characters traditionally used on the groups.

The following taxonomic action is taken: *Forsteropsalis nigra* is considered a junior synonym of *Forsteropsalis inconstans* (**new synonymy**).

Additional keywords: Monoscutidae, Australia, biogeography, phylogeny

Introduction

The order Opiliones consists of 6,539 described species (Kury 2013), divided into four suborders, 45 families and about 1,500 genera (Machado, Pinto-da-Rocha *et al.* 2007; Sharma and Giribet 2011; Sharma, Prieto *et al.* 2011; Pinto-da-Rocha, Bragagnolo *et al.* 2014), with many new species being described every year. Within Opiliones, the suborder Eupnoi includes the superfamilies Caddoidea and Phalangioidea (Shear 1982). The first group, Phalangioidea, forms a monophyletic assemblage of those eupnoids with long legs and smooth palps (Shultz 1998; Giribet, Rambla *et al.* 1999; Shultz and Regier 2001; Giribet, Edgecombe *et al.* 2002; e.g., Giribet, Vogt *et al.* 2010). Phalangioidea is divided into the families (1) Phalangiidae Latreille, 1802, of nearly world-wide distribution, and which includes the cosmopolitan “daddy-longleg” or common harvestman, *Phalangium opilio* Linnaeus, 1758; (2) Sclerosomatidae Simon, 1879, a speciose family with more than 1,300 species and many more to be described in dense subtropical forests (Machado, Pinto-da-Rocha *et al.* 2007); (3) Protolophidae Banks, 1893 (Cokendolpher 2007b); (4) Monoscutidae Forster, 1948, as prior to Taylor (2011) and as discussed below, from New Zealand and Australia; and (5) Neopilionidae Lawrence, 1931 with a temperate Gondwanan distribution: New Zealand, Australia, South Africa and South America, and diagnosed by the penis morphology (Hunt and Cokendolpher 1991b). The current work is concerned with the last two, Monoscutidae and Neopilionidae.

Prior to Taylor (2011) work on Neopilionidae included, among others, the families (1) Neopilionidae, with 8 genera and 15 species from South Africa (including *Neopilio australis*), Australia and South America, and (2) Monoscutidae Forster, 1948 with 5 genera and 32 species found in Australia and New Zealand (Fig. 1). The 8 genera within Neopilionidae were divided into three subfamilies: (1) Neopilioninae Lawrence, 1931, with a single species from South Africa; (2) Enantiobuninae Mello-Leitão, 1931 with four South American species; and (3) the larger group Ballarrinae Hunt & Cokendolpher, 1991, which included mostly species from Australia, one from Chile, and one from South America. Monoscutidae was divided into: (1) Monoscutinae Forster, 1948, from New Zealand and having heavy sclerotization and small ozopores; and (2) Megalopsalidinae Forster, 1949, characterized by a smooth carapace, except for small spines in some, e.g., *Forsteropsalis nigra* (Forster, 1944) and *F. inconstans* (Forster, 1944), and by the presence of visible ozopores, and which contained *Megalopsalis* (Australia and New Zealand), *Pantopsalis* Simon, 1879, (New Zealand endemic), and *Spinicrus* Forster, 1949 (Australia) (Cokendolpher 2007a; Cokendolpher and Taylor 2007b).

The New Zealander and Australian species of Eupnoi also show a striking sexual polymorphism with conspicuously enlarged male chelicerae, and nondescript females (Fig. 2). The long chelicerae in the males can reach up to 10 times the length of the body, comically extending high above the individual, and which in some cases also have grossly enlarged second segments that rival the girth of the main body of the animal, e.g., *Forsteropsalis fabulosa* (Phillips & Grimmett, 1932) and *Megalopsalis turneri* Marples, 1944 (Forster 1944b; Marples 1944; Forster 1949b; Forster and Wilton 1968; Forster and Forster 1999; Taylor 2004a; Taylor 2011). This presence of sexual dimorphism, and the dearth of characters in the female chelicerae in *Pantopsalis*, *Forsteropsalis*, and *Megalopsalis* are largely responsible for the taxonomic instability of the species in each genus (Figs. 3, 4) . Females in both *Pantopsalis* and *Forsteropsalis* have a uniform brown colour, with almost identical markings, so most species descriptions have been based on males, and females have been assigned to species when they are collected in close proximity to an identifiable male, which is not free of error, as it is common to collect specimens of different species in close proximity (see also Fernández et al. submitted). As an example of the confusion this has caused, in 1949 Forster corrected Pocock's (1902a) purported *Megalopsalis hoggi* female as the male of *Spinicrus camelus*, although a few years earlier, Forster himself had described *Megalopsalis luna* from a specimen which Taylor later assigned to a *Pantopsalis* female (Forster 1944b; Taylor 2004a), something that Forster must have noticed in his original description of the female of *Pantopsalis mila*, which matches his own description of the *Megalopsalis luna* male (Forster 1964b). Taylor (2004) also reported that Pocock described a male of *Pantopsalis jenningsi* as a female of *Pantopsalis nigripalpis*, something that Pocock himself corrected a year later (Pocock 1903a; Taylor 2011). In addition to sexual dimorphism, male dimorphism has also been reported, with some species purportedly having distinct broad-chelicerae and a long-chelicerae male forms, which have been dubbed the 'normal' and 'effeminate' forms (Forster 1964b; Taylor 2004a). In light of this, and in apparent frustration, Forster (1965) spelled out the rampant taxonomic confusion brought by sexual dimorphism, with what he saw as different authors describing species independently from males and females, and ended the description of several new species with a note that he would not attempt a key for Monoscutidae of New Zealand until the issue of assigning males to females had been resolved (Forster 1962b). Lacking breeding experiments or molecular studies (but see Fernández et al. submitted), it is unknown if the forms belong to the same species, and if they do, how many species have either or both forms, or if the forms are in discrete categories or occupy a range of sizes and variants, as reported by Kauri (1954) for *Spinicrus minimus*. If true, this could mean that the current designations are just an artefact from poor sampling from a highly polymorphic population.

Although the phylogeny of the order Opiliones has received substantial attention in the past decades (Giribet, Rambla *et al.* 1999; Giribet and Wheeler 1999; Shultz and Regier 2001; Giribet, Edgecombe *et al.* 2002; Giribet and Kury 2007; Giribet, Vogt *et al.* 2010), only recently Giribet *et al.* (2010) published the first molecular sequences that included members of the new Enantiobuninae (former Monoscutidae), although the sampling and analysis was only in the context of the broader phylogenetic relationships of the whole order Opiliones. Here we report the first comprehensive molecular systematics study of the New Zealand species currently assigned to Enantiobuninae, based on freshly collected material from New Zealand, Australia and South Africa, and in context with previously published molecular data for South American Enantiobuninae, Sclerosomatidae, Phalangiidae, and Caddidae. We examine the congruence between our molecular results against the current and historical species designations based on morphology, including the assignment of females to species based on molecular data. Additional population-level work is presented in an accompanying paper dealing with species delimitation (Fernández et al., submitted). We also analyse our data and comment on the monophyly of the current genera and the validity of historical diagnostic characters.

Materials and methods

Specimen sampling

Our sampling included 92 fresh specimens, 11 from Australia, 2 from South Africa and 79 from New Zealand, collected from 2002 to 2014 (Table 1 and Fig. 5). Specimens were collected by hand and preserved in 96% ethanol and stored at -80 ºC for long-term preservation of DNA. Sequences from GenBank belonging to the family Caddidae were used to root the trees (Table 1). A specimen of *Phalangium opilio*, also collected in New Zealand, was used along GenBank sequences from other studies including Phalangiidae, Sclerosomatidae, *Vibone*, *Thrasychirus*, *Hesperopilio*, *Ballara* and other Neopilionidae to test the monophyly of Enantiobuninae, Neopilionidae, and Monoscutidae as presently defined (Giribet, Vogt *et al.* 2010; Hedin, Tsurusaki *et al.* 2012; Groh and Giribet 2014). Most specimens were collected from the vegetation, walking about, or from the underside of fallen logs and rocks, and were most abundant during night time. Specimens were deposited at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ) the Zoological Museum, Natural History Museum of Denmark (NHMD), and the Museum of New Zealand/Te Papa Tongarewa, Wellington, New Zealand (TPT). All DNA isolates from new material were deposited at the MCZ except for *Pantopsalis snarensis*, which was deposited at TPT.

Molecular sequences

Total genomic DNA was isolated from one leg from each specimen with the DNeasy® Tissue Kit (QIAGEN, Valencia, California, USA). We sequenced the a 540 fragment of the 18S rRNA gene and a 2.2 kb fragment of 28S rRNA nuclear ribosomal genes, and a

745 bp fragment of the protein-encoding mitochondrial gene cytochrome *c* oxidase subunit I (COI), all which have been recently used for the estimation of phylogenetic relationships within arthropods, particularly the order Opiliones (Edgecombe, Wilson *et al.* 2000; Giribet, Edgecombe *et al.* 2001; Prendini, Crowe *et al.* 2003; Boyer and Giribet 2004; Prendini, Weygoldt *et al.* 2005; Boyer, Baker *et al.* 2007; Boyer, Clouse *et al.* 2007; Boyer and Giribet 2007; Sharma and Giribet 2009; Murienne, Edgecombe *et al.* 2011)

COI was PCR amplified using the primer pair LCO1490 (Folmer, Black *et al.* 1994) and HCOoutout (Prendini, Weygoldt *et al.* 2005; Schwendinger and Giribet 2005); 18S rRNA using primer sets 1F-4R, 4F-18Sbi, and 18Sa2.0-9R (Giribet, Carranza *et al.* 1996; Whiting, Carpenter *et al.* 1997) and 28S rRNA with primer sets 28S1F-28Srd4b, 28Sa-28sb, and 28Srd4.8a-28Srd7b1 (Park and Ó Foighil 2000; Schwendinger and Giribet 2005; Edgecombe and Giribet 2006). PCR products were visualized in 1% agarose gel electrophoresis, and purified PCR products with the Millipore MultiScreen PCRµ96 filter plate system (Millipore, Waltham, MA). For the sequencing reaction we used the BigDye (Applied Biosystems) and cleaned unincorporated primers and dye with Performa DTR Plates (Edge Biosystems; Gaithersburg, MD). We analysed the labelled fragments with an ABI Prism 3730xl Genetic Analyzer (Applied Biosystems), and edited the resulting .ab1 files using SEQUENCHER 4.7 (Gene Codes Corporation 2007; Ann Arbor, MI). We visually inspected all fragments, sequenced using both primers, to ascertain ambiguous base calls or detect possible contamination. All sequences were deposited in GenBank and accession numbers are provided (Table 1).

Phylogenetic analysis

All file format manipulations were performed with Mesquite (Maddison and Maddison 2010), and sequence alignments for the maximum likelihood analyses were performed with MUSCLE 3.7 (Edgar 2004). For the maximum likelihood estimation of phylogenetic trees we used RAxML (Stamatakis 2006). jModeltest (Posada 2009) was used to select the best-fit evolutionary model under the Akaike information criterion (AIC) (Akaike 1974): GTR + gamma + invariant sites (Yang 1993). Bootstrap support values were calculated from 100 replicates. The direct optimization method (Wheeler 1996; Wheeler, Aagesen *et al.* 2006) as implemented in POY (Wheeler, Lucaroni *et al.* 2014) was used to evaluate trees under the parsimony criterion. The data were partitioned in *a priori* segments to avoid clustering of sequences with missing ends. One of the equally-parsimonious trees was selected for measuring nodal support, and jackknife support was calculated by resampling the data 100 times with a 0.36 probability of deletion. Consensus trees were calculated with the Consense program in the PHYLIP package (Felsenstein 1989), and trees reorganized in FigTree (Rambaut 2011).

Results and discussion

Monophyly of Neopilionidae

Our results from both the parsimony and the maximum likelihood criteria (Figs. 6, 7) reject Neopilionidae *sensu* Šilhavý (1970) and *sensu* Taylor (Taylor 2011; Taylor 2013b), as it includes the two representatives of the genus *Hesperopilio* Shear, 1996, formerly in Caddidae (Shear 1996) but recently transferred to Phalangioidea (Groh and Giribet 2014).

These results are relevant as they are the first molecular evidence of the paraphyly of Neopilionidae in the long and complicated history of the family.

The family Neopilionidae (*sensu* Ballarinae + Enantiobuninae + Neopilioninae, see Fig. 1) has had an interesting, if also very unstable history. In 1931, Lawrence erected the subfamily Neopilioninae Lawrence, 1931 for a new South African species, *Neopilio australis* Lawrence, 1931. Also in 1931, Mello-Leitão described the subfamily Enantiobuninae Mello-Leitão, 1931 using material from South America, but later in that same year he synonymized it with Neopilioninae (Mello-Leitão 1931). In 1948 Forster created the subfamily Monoscutinae Forster, 1948 for two New Zealand species: *Acihasta salebrosa* Forster, 1948 and *Monoscutum titirangiensis* Forster, 1948. Forster characterized this New Zealander group of Eupnoi by not having dorsal opisthosomal segmentation (Forster 1948b). A year later, Forster erected Megalopsalinae Forster, 1949 to accommodate *Megalopsalis* Roewer, 1923, *Spinicrus* Forster, 1949 and *Nodala* Forster, 1949, all from Australia (Forster 1949a). Kauri (1961) described the genus *Vibone* Kauri, 1961 and elevated Neopilioninae to family, as Neopilionidae Kauri, 1961. By this time, even as the classification of the family matured, in 1962 Forster still considered the New Zealand genera *Megalopsalis* and *Pantopsalis* part of Phalangiinae (Forster 1962a), unrelated to his other material designated as Monoscutinae, and even still in 1964 still listed *Pantopsalis* under Phalangiidae (Forster 1964a). Šilhavý (1970) provided a historical account of Neopilionidae and divided the family into geographical groups, with Neopilioninae for the South African genera, with a reduced palpal tarsal claw, Megalopsalinae for the Australian and New Zealand genera (although not mentioning *Acihasta* Forster, 1948), recognizing variation in the palpal tarsal claw, and Enantiobuninae for the South American species in the genus *Thrasychirus* Simon, 1884.

Work continued in 1970 with the addition of Megalopsalidinae (Megalopsalinae [sic] which then included the genus *Monoscutum* Forster, 1948) (Martens 1976a), into an sextended Neopilionidae by Šilhavý (1970) (Fig. 1). Later Martens (1976b) raised Megalopsalinae to family level and corrected the name to Megalopsalididae. Two decades later, Hunt and Cokendolpher (1991a) erected the taxon Ballarrinae for *Vibone* Kauri, 1961 (from South Africa) with four new genera: *Ballarra* Hunt & Cokendolpher, 1991, *Plesioballarra* Hunt & Cokendolpher, 1991 and *Arrallaba* Hunt & Cokendolpher, 1991 (southern Australia), and *Americovibone* Hunt & Cokendolpher, 1991 (southern South America). However, their cladistic morphological analysis did not support monophyly of Neopilionidae (Fig. 1). Monoscutinae and Megalopsalidinae, however, continued to be recognized by subsequent authors, e.g., Hunt (1990b), Hunt and Cokendolpher (1991a), and Taylor (2004b), although the monophyly of Monoscutidae was still based on a single character, the presence of paired lateral bristle groups on the penis at the shaft or glans articulation (Hunt and Cokendolpher 1991a) (of importance is to note that Monoscutidae has previously been incorrectly referred to as Megalopsalididae, before Crawford (1992b) pointed out that the subfamily Monoscutinae had priority over Megalopsalidinae).

Up to this point, Monoscutidae thus contained two distinctive subfamilies, Monoscutinae and Megalopsalidinae, Monoscutinae containing three monotypic genera (1) *Monoscutum* Forster, 1948, (2) *Acihasta* Forster, 1948, and (3) *Templar* Taylor, 2008, the latter only recently added (Taylor 2008a), and an undescribed species of an uncertain genus from New South Wales, Australia (Hunt 1990b; Hunt and Cokendolpher 1991a). Megalopsalidinae contained three genera: (1) *Megalopsalis* (13 spp.), (2) *Pantopsalis* (11 spp.), and (3) *Spinicrus* (8 spp.) (see Taylor, 2004 for a checklist). In 2011 Taylor synonymised Monoscutidae with Neopilionidae using results from a morphological cladistic analysis that showed Monoscutidae to be nested within Neopilionidae (*Neopilio* + (*Ballara* + Monoscutidae)), and which positioned the Chilean *Thrasychirus* Simon, 1884 (Neopilionidae: Enantiobuninae) within Monoscutidae, which, as we have discussed, was up to then a group otherwise wholly constrained within New Zealand and Australia (Taylor 2011). This conclusion, based on a few morphological characters, was not supported in the unweighted parsimony tree, and thus awaited the inclusion of more samples from Neopilionidae and the addition to the analysis of more characters, molecular and morphological (see Taylor 2013 for another analysis with monophyly of Neopilionidae). However, regardless of the sister vs. nested relationship between Neopilionidae and Monoscutidae, the inclusion of *Thrasychirus* within Monoscutidae changed the name of the family or subfamily, wherever a final taxonomic revision lands the ranking, to Enantiobuninae, which has priority (Taylor 2011; Taylor 2013a).

This new Enantiobuninae (*sensu Thrasychiroides* + *Thrasychirus* + former Monoscutidae, see Fig. 1), lacks consistent synapomorphies and diagnostic characters, and in the field they are normally identified as being the only group of Opiliones within New Zealand and Australia with long legs, save for the synanthropic species *Phalangium opilio* (Phalangiidae) and *Nelima doriae* (Sclerosomatidae) and the endemic but small *Acropsopilio neozelandiae* (Acropsopilionidae) (Forster 1948a; Taylor 2011).

White (1849a) described the first member of what was to become the Eupnoi of New Zealand and Australia, *Phalangium listeri* from New Zealand, which would later be transferred to the genus *Pantopsalis* as its type species (Simon 1879a). The holotype, however, has been reported as lost (Taylor 2004a; Taylor 2013a), and the original description had no specific locality information as to where within New Zealand the specimen was collected, and lacked diagnostic characters (White 1849a; Simon 1879a; Taylor 2004a). Taylor (2004) first declared the species a *nomen dubium* and later reinstated it (Taylor 2013a) after examination of associated material purportedly used by Simon in the original description of the species. Neotypes were then assigned, however, while reporting variation within the specimen lot on the morphology of the enlarged chelicerae of the males, quite possibly the most important character for species identification in the family. Colenso (1882b) later described *Phalangium cheliferoides*, which was later transferred to *Pantopsalis* (Nicholls, Sirvid *et al.* 2000). Taylor (2004), however, reported a deteriorated type and no other specimens with good characters to distinguish it from other species, and declared it a *nomen dubium*. Although he later reestablished the species, the diagnostic characters remained unclear: e.g., although the presence of a medial stripe on the opisthosoma was presented as diagnostic, this character state is shared by other related species, and is missing in one of the specimens assigned to the species in the same study (Taylor 2013a).

Sørensen (1886) described the first Australian Eupnoi, *Macropsalis serritarsus*, which was later changed to *Megalopsalis* because *Macropsalis* was pre-occupied by a bird genus (Roewer 1923). The description of *Megalopsalis* included a first attempt at characters for inter-generic diagnosis: (1) spines on the ocularium, (2) abdomen shorter than cephalothorax, (3) tibia and patella of palpus of unequal length in *Pantopsalis*, (4) tibia II with pseudoarticulations, and (5) a ramous bifurcation in the patella of the palpus in *Megalopsalis*. All of these, except for the patella of the palpus, were considered plesiomorphic states by later authors (Taylor 2004a; Taylor and Hunt 2009) (but see below for further discussion on the cladistic value of the patella). Pocock (1902b) added *Macropsalis hoggi* Pocock, 1902, *Pantopsalis albipalpis* Pocock, 1902, *P. nigripalpis* Pocock, 1902, and *P. nigripalpis spiculosa* Pocock, 1902, and later (1903a) *P. coronata* Pocock, 1903, *Pantopsalis trippi* Pocock, 1903 and *Pantopsalis jenningsi* Pocock, 1903, followed by Hogg (1909) with *Macropsalis chiltoni* Hogg, 1909, and *Pantopsalis tasmanica* Hogg, 1909. Roewer (1911) attempted a first taxonomic grouping with other long-legged Opiliones by including *Megalopsalis* and *Pantopsalis* within the African and Holarctic Phalangiinae, a classification which was quickly discarded by subsequent authors. Species descriptions continued in that century with Hogg (1920) adding *Pantopsalis wattsi* Hogg, 1920, *P. pococki* Hogg, 1920, *P. grayi* Hogg, 1920 and *P. halli* Hogg, 1920. Roewer (1923) added *Pantopsalis continentalis* Roewer, 1923, and later *Macropsalis* (*Megalopsalis*) *fabulosa* Grimmett & Phillips, 1932 was also described. Forster (1944b) made the first attempt at a complete revision of the New Zealand and Australian Eupnoi genera, adding several species to *Megalopsalis* without apparently looking into the many species already described in *Pantopsalis*. Despite expressing doubts about the cladistic value of the only remaining diagnostic character separating the *Megalopsalis* from *Pantopsalis*, the ramous patella of the palp, Forster added *Megalopsalis chiltoni* Forster, 1944, *M. chiltoni nigra* Forster, 1944, *M. inconstans* Forster, 1944, *M. tumida* Forster, 1944, *M. triascuta* Forster, 1944, *M. luna* Forster, 1944, *M. marplesi* Forster, 1944, and *M. grimmetti* Forster, 1944. Forster also later made the first conjectures about phylogeographic relationships among the described species, and noted the probable close relationship between the New Zealand and Australia opilionid fauna (Forster 1947). A year later, Forster (1948c) also established Monoscutinae (although joined by plesiomorphies), and added two monotypic genera with *Acihasta salebrosa* Forster, 1948 and *Monoscutum titirangiensis* Forster, 1948. In the first comprehensive treatment of the Australian monoscutids, Forster (1949b) established Megalopsalinae (as per our historical overview above, later corrected for spelling and upgraded to the family level Megalopsalididae (Martens 1976a).) However, from a family status, Megalopsalididae was later downgraded again under Monoscutidae (Hunt 1990a; Hunt and Cokendolpher 1991b; Crawford 1992a). Forster subsequently raised the genus *Spinicrus* Forster, 1949 to distinguish the Australian and New Zealand species, adding *S. camellus* Forster, 1949, *S. stewarti* Forster, 1949, and transferring from *Pantopsalis* both *S. tasmanica* (Hogg 1909) and just based on the published description, *S. continentalis* (Rower 1923). Kauri (1954) and later Hickman (1957) added *S. minumus* Kauri, 1954, *S. porongorupensis* Kauri, 1954, *S. thrypticum* Hickman, 1957, and *S. nigricans* Hickman, 1957. Back in New Zealand, and again despite doubting the diagnostic value of the palpal patellar character on which the whole classification rested, Forster added *Pantopsalis johnsi* Forster, 1964, *P. mila* Forster, 1964, *P. distincta* Forster, 1964, *P. snaresensis* Forster, 1964 and *P. rennelli* Forster, 1964. In one of the last chapters or the taxonomic history of the group, Taylor revised *Pantopsalis*, adding *P. phocator* Taylor, 2004, synonymizing *P. nigripalpis* and *P. jenningsi* (with *P. albipalpis*), *P. trippi* (with *P. coronata*), *P. mila* (with *P. johnsi*), and making the following generic transfers: *Pantopsalis wattsi*, *P. grayi*, *P. distincta* to *Megalopsalis*, and *Megalopsalis luna* to *Pantopsalis*. In 2008 Taylor (2008b) added *Megalopsalis linaei* Taylor, 2008, which he later (Taylor 2011) transferred to a new genus, *Tercentenarium* Taylor, 2011. Taylor (2009) then went on to erect the new genus *Neopantopsalis* Taylor, 2009, in an attempt to reorganize *Spinicrus* from geography-based to cladistics, using the following characters for *Neopantopsalis*: raised bumps in the dorsal prosomal plate (only in 'major' males), the presence of hyperthophied spines on leg I ('major' males again), and oblong dorsoventrally flattened glans of the penis; kept *Megalopsalis* defined with the character of the patellar ramification, and added for *Spinicrus* the characters of dorsal margin of the prosoma horizontal rather than sloping, and flattened glans of the penis. Taylor (2009) also added *Neopantopsalis quasimodo* Taylor, 2009, *N. pentheter* Taylor, 2009, *N. psile* Taylor, 2009 and *N. thaumatopoios* Taylor, 2009, while noting that probably none of the Australian genera of Monosctutidae, as listed then, formed monophyletic groups. The same reorganization was done for the New Zealand *Megalopsalis*, and all species in the country where either declared *nomina dubia*, synonymized, or transferred to a new genus, *Forsteropsalis* Taylor, 2011, to which one species was subsequently added, *Forsteropsalis pureroa* Taylor, 2013 (Taylor 2011; Taylor 2013a). Left standing were thus: *Forsteropsalis chiltoni* (Hogg, 1910), *F. distincta* (Forster 1964), *F. fabulosa* (Phillipps & Grimmett, 1932), *F. grayi* (Hogg, 1920), *F. grimmetti* (Forster, 1944), *F. inconstans* (Forster, 1944), *F. marplesi* (Forster, 1944), *F. nigra* (Forster, 1944), *F. wattsi* (Hogg, 1920) and *F. pureroa* Taylor, 2013; with a new Australian species added to *Megalopsalis* based on the patellar character: *M. epizephyros* Taylor, 2011, *M. eremiotis* Taylor, 2011, *M. leptekes* Taylor, 2011, and *M. pilliga* Taylor, 2011.

Our results, thus, find no evidence to support either Monoscutidae *sensu* Crawford (1992b) or *sensu* Cokendolpher and Taylor (2007b) (Fig. 1). They also support the idea that *Hesperopilio* (Australia and Chile, formerly in Caddidae (Groh 2014)) is closely related to the now-entirely South American Enantiobuninae, here represented by *Thrasychirus gulosus* (Hedin, Tsurusaki *et al.* 2012). Although this represents the first large analysis of Neopilionidae and other related taxa using molecular data (see also Groh & Giribet, 2014), we refrain from proposing any taxonomic changes until a denser sampling, especially of the New Zealand genera *Acihasta, Monoscutum, and Australiscutum*, additional Australian fauna, the South American *Thrasychirus* and most important, the South African *Neopilio* are included in the analyses. However, it is comforting to see another large Opiliones clade with deep biogeographic structure, including a distribution similar to those of the families Pettalidae and Triaenonychidae (Giribet & Kury, 2007), and thus we centre our phylogenetic discussion on the New Zealand species of Enantiobuninae.

Taylor's (2011) morphological cladistic analysis found that none of the then-"neopilionid" genera formed monophyletic groups (although, it must be noted, they did form a clade under the weighted analysis) and based on these results, he synonymised Monoscutidae with Neopilionidae. Our sampling does not allow for a complete resolution of this long-standing controversy (e.g., Šilhavý 1970; Hunt and Cokendolpher 1991a; Taylor 2011), as many key genera were not sampled: e.g. *Neopilio*, some members of Monoscutinae, e.g. *Acihata*, *Monoscutum*, or *Australiscutum*, nor some key genera from Megalopsalidinae: e.g. *Tercentenarium*. However, our results do show that our clade of Australian/New Zealand species does not include the South African *Vibone*, originally described in Neopilionidae (Kauri 1961). Although Hunt and Cokendolpher (1991a) transferred *Vibone* from Neopilioninae to their new subfamily Ballarrinae, our analyses reject this relationship, as *Ballarra* groups with the Australasian clade that includes *Pantopsalis, Forsteropsalis, Spinicrus, Mangatangi*, etc., and does not group with its Neopilionidae clade (Hunt and Cokendolpher 1991a; their figure 4A) or with Ballarrinae (their figure 4B). Our results therefore agree with Taylor's (2011) unweighted morphological cladistic analysis, in that it separates *Ballarra* from the other Neopilionidae (although *Vibone* was not sampled in that study).

Broader relationships among the New Zealand + Australia native eupnoids

The internal relationships within the Megalopsalididae are not fully supported in our analysis, although *Ballarra* (Ballarrinae) shows as the sister group of the remaining genera. Within the New Zealand + Australian native eupnoids, the first division is between the clade with pectinate palpal claws and a clade with smooth palpal claws (Fig. 8). The pectinate-claw divides is divided into the New Zealand *Mangatangi* and the Australian species (probably *Megalopsalis*); the smooth-claw finds support for a clade of *Forsteropsalis*, a clade of *Pantopsalis* and a clade that includes *Forsteropsalis pureora*, *F. wattsi* and *Megalopsalis turneri*, but neither this clade nor its relationship to the other clades is well resolved. Additionally, two other undescribed species, here represented by specimens MCZ 29229 and MCZ 29239 have an unsupported position.

The Megalopsalidinae of New Zealand: a taxonomic overview of Pantopsalis and Forsteropsalis

The distinction among the genera within the former Monoscutidae has been problematic since the description of each genus (Cokendolpher and Taylor 2007a). For example, when Sørensen (1886) described *Macropsalis* (now *Megalopsalis*), he used as diagnostic characters the spines on the ocularium of *Megalopsalis* vs. smooth in *Pantopsalis*, but since then, many species that now belong in *Megalopsalis* have been described with a smooth ocularium, while some *Pantopsalis* continue to be described with spines (Taylor 2004a), and in any case, the character might be variable within species. Another character, that of the opisthosoma being longer than prosoma, has the problem that the opisthosoma is soft and prone to deformation during preservation (Taylor 2004a) and in our observation of freshly collected material from type localities, can vary between molts. The difference in size between the patella and the tibia in *Pantopsalis*, Sørensen's (1886) "*palporum partibus patellari et tibiali sibi longitudine sub aequalibus*", is also of doubtful validity since both characters can vary within species (Hickman 1957, see Taylor, 2004). The last remaining characters are the presence of a spiny process in the patella of the palp (between *Pantopsalis* vs. *Forsteropsalis* and between *Spinicrus* + *Neopantopsalis* and *Megalopsalis*), the number of brushes in the penis between *Forsteropsalis* and *Pantopsalis*, the bowing of the cheliceral claw between *Pantopsalis* vs. *Forsteropsalis*, and a 'triangular dorsolateral keel on the glans, with the apex of the triangle at the distal end of the glans' (Taylor 2011), also between *Forsteropsalis* and *Pantopsalis*. All of these characters are of suspect validity: for example, from Taylor's (2004) illustrations the scoring of abundance of penis bristles seems to be subjective. The palpal patellar structure, also described as a branch (Sørensen's (1886) "*parte patellari non ramosa*"), splitting, spur, process (Forster 1944b), or apophysis (Taylor 2004a;

Taylor and Hunt 2009), has been especially problematic, since it has been used as the sole basis in the erection of new genera and in the transfer species between genera. For example, using the patellar process as a character, Taylor (2004) transferred Forster's (1964b) *Pantopsalis distincta* to *Megalopsalis distincta* even though the purported female of the species does not have a patellar process, and the purported male only has a small, pointed one. In his key, Forster (1944b) used the apophysis to distinguish among the two genera, but then used this character to assign a female specimen of what otherwise seemed like a typical *Pantopsalis* female to *Megalosalis luna* (Taylor 2011). Two decades later, Forster again described a new species, *Pantopsalis distincta*, and included in the description a female with a "well developed process on the prodistal surface of the patella of the palp" (Forster 1964b), the exact then-synapomorphy for the sympatric *Megalopsalis* (now *Forsteropsalis* for the New Zealand species). Taylor (2004) continued to use this character throughout his revision of *Pantopsalis*, making adjustments as to its shape to assign specimens with a patellar process to *Pantopsalis*. Surprisingly, in Taylor's (2011) own morphology-based cladistic analysis, the patellar process comes as a plesiomorphy. Forster himself had also noted that it might vary within molts of the same individual (Forster 1964b). The distinctive shape of the keel of the glans, the last character state supporting *Pantopsalis* together, was reported as absent in the resurrection of *Pantopsalis cheliferoides* (Taylor 2013a).

The sequence similarity and subsequent clustering of males and females into well-supported clades confirms a wide range of morphological disparity among species, particularly in the shape, coloration, and size of the male chelicerae, and the presence of sexual dimorphism (Figs. 6, 7) is consistent with a reduced number of species for

Pantopsalis and *Forsteropsalis*. For these New Zealand species, identifications were made following Taylor's (2004a; Taylor and Hunt 2009; 2011; 2013a) recent revisions of *Pantopsalis*, *Megalopsalis* (now *Forsteropsalis* for the New Zealand species), and *Neopantopsalis*, as well as the original descriptions. This reduced number of species, in the context of our extensive sampling within New Zealand (Fig. 5), and the fact that most clades included at least one male, suggests that the same approach could lead to a reduced number of species also for the Australian genera of *Spinicrus*, *Megalopsalis*, and *Neopantopsalis*.

Mangatangi

The genus *Mangatangi* was recently described by Taylor (2013a) based on a male and a female specimens from Mangatangi, Hunua Ra., and a male from Cuvier Is. From this genus, we collected a male in Te Urewera N.P. The genus is easily identified by the pectinate pedipalpal tarsal claw, a character shared with the Australian species of Neopilionidae (Taylor 2004a) (Fig. 8). All the specimens belonging to this genus (n=5) clustered together in a clade. One specimen (MCZ 29239) was identified as *Mangatangi parvum,* while the other ones could not be identified at the species level based on the available literature. Our specimen from Te Urewera clusters with other specimens from Queen Charlotte Sound and Kaikoura (South Island), although they probably constitute more than one species. Interestingly, in our phylogenetic trees (Figs. 6, 7), *Mangatangi* forms a clade with the Australian species albeit with low bootstrap support, instead of the New Zealand species, which confirms the importance of the pectinate pediplapal tarsal claw in the higher systematics of the group.

The Forsteropsalis pureora*,* F. wattsi*, and* M. turneri *clade.*

This clade includes species originally described as *Pantopsalis* (*P. wattsi* Hogg, 1920), *Forsteropsalis* (*F. pureora* Taylor, 2013) and *Megalopsalis* (*M. turneri* Marples, 1944), but its relationship to the other *Pantopsalis* or *Forsteropsalis* remains unsupported. *Forsteropsalis pureora* Taylor, 2013 (Note: The species is referred to as *F. pureroa* in the abstract and figure captions of the original description) was described by Taylor (2013a) based on a single male specimen from Waipapa Reserve, Pureora, which matches our specimens from Te Urewera National Park (MCZ 29240), but this species also closely matches the description of another North Island species, *Forsteropsalis inconstans* (Forster 1944b), a species with a problematic history that starts with an original description that included specimens from three different species (Forster 1944b; Taylor 2011), and a striking similarity to *Forsteropsalis nigra* (Forster 1944) except for a few small red markings on the propeltidium (Taylor 2011). *Forsteropsalis inconstans* also has the same coloration pattern (the "white" markings in the preserved animals of Forster and Taylor are orange in living specimens), from which Taylor distinguished in "not having the posterior part of the propeltidium and the mesopeltidium heavily denticulate", while also mentioning how *F. pureora* can be confused with *F. distincta*, *F. chiltoni*, *F. marplesi* and *F. wattsi*.

In our analyses, the *F. pureora* specimens appear as the sister group to what we identified as *F. wattsi* (Hogg 1920), another North Island species with the "wide horseshoe belt of bright cream-colour", which was described based on a single specimen from Hawera. Our specimens from Mount Stokes and Hori Bay form a clade, although some specimens match the description of Hogg (1920), including how the horseshoe belt of bright cream-colour has "intervals into the lighter colour".

All of the cave-dwelling specimens collected formed a third cluster of specimens members of this larger clade, despite some being collected from opposite sides of the South Island. The majority of the specimens were, however, collected ca. 100 km from the type locality of the South Island endemic *Megalopsalis turneri* Marples, 1944, and formed a clade with a male that matches the original description of *M. turneri*, based on a single dried specimen collected near Lake Manapouri. This species was considered by Taylor (2011) as a probable member of *Forsteropsalis*, but not transferred. It also seems that this is the species discussed in Meyer-Rochow's (1988) work (see discussion below on *Forsteropsalis tumida* reported from the Waitomo Cave system), since Meyer-Rochow's specimens were adapted to living in caves with bioluminescent fungus gnats, and while repelled by sunlight are nevertheless particularly sensitive to the bioluminescent spectra emitted by the insects in these caves. All of the specimens included in this clade from the analysis were collected near bioluminescent fungus gnats.

Pantopsalis*: The* listeri *group*

The remaining samples of *Pantopsalis* constitute a clade including specimens from Southland to Te Urewera N.P. This clade includes dark species (black carapace) with a brown to reddish pigmented pedipalpal femur (from half to most of its length), not pink, the rest of the pediplap being white. It also includes specimens with black opisthosomas or with different degrees of a white-silver strip in the intercalary membrane of the opisthosomal tergites.

Our analyses identify two main clades of specimens similar to *P. listeri* (White, 1849). Taylor (2013b) provides a redescription and a discussion of this species, based on examination of a neotype from the MNHN, Paris, and uses Simon (1879b) concept of the species, adding the following to the description "Dorsum of opisthosoma with pale silvery, narrow, transverse stripes on posterior margins of segments", illustrated in a live specimen photographed by Simon Pollard (of unspecified precedence). We have observed such transverse stripes with a large degree of variation, from very broad in specimens from Kahurangi N.P. and Arthur's Pass N.P. to less conspicuous in Westland Tai Puitini N.P. and Te Urewera N.P., or totally absent in Mount Aspiring N.P. (see Fernández et al., submitted). Taylor (2013b) also illustrated *P. cheliferoides* (Colenso 1882a), the only *Pantopsalis* reported from the North Island, an animal similar in morphology to some of the "*listeri*" morphotypes with swollen chelicera, similar to some of our specimens from Kahurangi N.P. and Mount Aspiring N.P.. Many of these localities find astonishing disparity in cheliceral size and shape, or in the banding pattern of the opisthosoma, despite belonging to the same clade. Our two clades of "listeri" include (1) specimens from the North and South Islands: Te Urewera N.P., Wellington, Kahurangi N.P., Arthur's Pass N.P., and a female from Waimate, spanning almost the whole country, which we assign to *P. cheliferoides* following Taylor (2013b); and (2) specimens from Mt. Aspiring N.P., and Westland Tai Puitini N.P., of much more restricted geographical distribution, with smoother ocularium, which we assign to *P. listeri*. The original description of *P. listeri* is inaccurate, and no types or type locality exist, although the species was probably based on specimens from the North Island. However, Simon (1879b) designated a neotype from Westland-Tai Poutini, and we follow Taylor (2013b) with respect to the stability of the type of the genus.

White (1849b) succinctly described *Phalangium listeri* White, 1849, with New Zealand as its type locality, and Simon (1879b) redescribed the species. Taylor (2013b) interpreted that a possible locality for the species was the Bay of Islands, in the North Island, but designated as a neotype a MNHN specimen, presumably examined by Simon, from 'Ile du Milieu, Filhol', probably referring to its collector, Henri Filhol, who was a member of the 1874 French Transit of Venus expedition to Campbell Island. On his way back from Campbell Island, Filhol made stops at Stewart Island, Christchurch, Wellington and Auckland, and could have picked up the *P. listeri* specimens during his Christchurch stop. 'Ile de Milieu' is the French name for the South Island. Taylor (2013b) appealed to the criterion of stability to assign *P. listeri* to the MNHN specimens examined by Simon from Westland, and thus we use the name *P. listeri* for our restricted clade, including specimens from Westland-Tai Poutini and Mt. Aspiring N.P.

Pantopsalis albipalpis Pocock, 1903b is another dark species with the clear palps from the South Island, described based on specimens from near Dunedin (Pocock 1903b), including multiple synonymies, such as *Pantopsalis nigripalpis* Pocock, 1903b, *P. nigripalpis spiculosa* Pocock, 1903b and *P. jenningsi* Pocock, 1903a; all synonymised by Taylor (2004b). It is unlikely that *P. albipalpis* would remain as a valid species. name for the South Island. Taylor (2013b) appealed to the criterion of stability to assign *P. listeri* to the MNHN specimens examined by Simon from Westland, and thus we use the name *P. listeri* for our restricted clade, including specimens from Westland-Tai Poutini and Mt. Aspiring N.P.

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A discussion of the distinctions between Forsteropsalis *and* Pantopsalis

Although none of the specimens from the *Pantopsalis* clades had a large patellar process, it is not clear that this trait can be used as a diagnostic character. In his last published comment on *Pantopsalis*, Forster (1964b) referred to an unpublished study of the New Zealand species indicating that the patellar process is a secondary sexual character often present in the females but not the males, citing as an example *Pantopsalis rennelli*, where the males do not have the process but the females do. Furthermore, Forster noted that the patellar process is ‘extraordinarily well developed’ in early developmental stages but diminishes with every moult. Our data and phylogenetic analyses support this latter view

(Fig. 9). However, most females of *Pantopsalis* displayed an hourglass-like mark in their backs, while the *Forsteropsalis* females displayed a box-like mark typical of other Australian and New Zealander eupnoids, such as *Spinicrus* and *Mangatangi* (Fig. 10.)

Forsteropsalis

A single male individual from Te Urewera National Park with an unusual palp morphology was collected, MCZ 29239. This species displays the cream-colored prosomal horseshoe, smooth ocularium, but the opisthosoma is brown, with two longitudinal darker bands. Most conspicuous characteristics are the heavily denticulate chelicerae and the elongated palps of uniform brown color, unlike most other species that display shorter palps with the distal segments lightly pigmented. This species was collected together with *Mangatangi parvum*, *Forsteropsalis pureora*, and *F. Nigra.*

A member of *Forsteropsalis*, a single specimen (MCZ 29252) differs from all other members of the clade in having a palp mostly without conspicuous colour patterns, as opposed to its sympatric species *F. wattsi*. It does have “remnants” of the cream-colour horseshoe, but limited to two small marks.

Forsteropsalis fabulosa

We found another clade including just a few specimens, which includes a male and a female of *Forteropsalis fabulosa* (Phillipps and Grimmett, 1932) from Belmont Regional Park, Wellington (the type locality given by Phillipps and Grimmett, 1932 was also Wellington). *Forsteropsalis fabulosa* is the sister group to a clade that includes 1 female from Kaikoura, and 1 female and 1 small female-looking specimen with enlarged chelicers (probably a male of a species without markerd sexual dimorphism) from Hinewai, in Banks Peninsula. Additional collecting in the northeastern region of the South Island should help clarify these putative species.

Forsteropsalis chiltoni

Forsteropsalis chiltoni (Hogg, 1910) is the only *Forsteropsalis* species known from Stewart Island (Taylor, 2011) and very similar to *F. marplesi* (Forster, 1944). We identified a clade of Stewart Island *Forsteropsalis*, which is unfortunately only represented by females, a juvenile, and a single male, with female coloration, a large ocularium, and with smooth large chelicerae that does not correspond to the description of *F. chiltoni* either from Hogg (1910) or the redescription by Taylor (2011). However, a different female specimen from Stewart Island clusters with a series of females from Southland, the Catlins and Banks Peninsula. The sister group to this South Island/Stewart Island clade is a male from the Otago Peninsula, matching the description of *F. marplesi*. We thus suspect that the *chiltoni* group includes multiple species in the eastern-southeastern part of the South Island. We tentatively call the male from Otago *F.*

marplesi, its sister group including the specimen from Stewart Island *F. chiltoni*, and the other Stewart Island clade *Forsteropsalis* n.sp.

Forsteropsalis inconstans

One of the most widespread species of New Zealand monoscutids is *Forsteropsalis inconstans*. Geographically, specimens from this clade have been collected in the North Island: Tararua Forest Park, relatively near Feilding, the type locality of the species (Forster, 1944), in two localities near Wellington (Karori Wildlife Sanctuary and Wilton's Bush Nature Walk); and in the South Island: Kahurangi N.P., Paparoa N.P., Haast, Whakapohai Wildlife Refuge, Arthur's Pass N.P., Westland-Tai Poutini N.P., and Mount Aspiring N.P. This clade includes heavily denticulate specimens, including the recently molted female-colored specimens from Kahurangi N.P.

Originally *F. nigra* was described as a subspecies of *F. chiltoni,* which had the red markings on the carapace. Forster (1944a) described *Megalopsalis inconstans* Forster, 1944 based on a female specimen. In the same paper he described *Megalopsalis chiltoni nigra* Forster, 1944, based on two male specimens, a subspecies that was elevated to species by Taylor (2011). Our analyses clearly show that the red markings vary with specimens and thus we consider both names to be co-specific. Since *Megalopsalis inconstans* was published as a species and *M. chiltoni nigra* as a subspecies, the former name takes priority. We thus consider *Forsteropsalis nigra* a junior synonym of *Forsteropsalis inconstans* (**new synonymy**).

Forsteropsalis inconstans is the sister group to a species represented by a specimen (MCZ129520) from Roaring Billy Falls, in the Haast Pass in the West Coast of the South Island. The latter specimen + *Forsteropsalis inconstans* are sister to a female (MCZ 29253) from Mt. Stokes, in the Northernmost part of the South Island.

Conclusions

Our study is the first to use a molecular data set to study relationships within the New Zealand Neopilionidae. Although we were not able to fully test the monophyly of the New Zealand neopilionids, our data is consistent with the existence of a monophyletic clade of neopilionids from Australia and New Zealand. Our data largely support the current taxonomic revisions for *Pantopsalis* and *Forsteropsalis*, and suggest that a reduced number of species seems warranted. More data are however needed to solve the intrageneric relationships, as well as the relationships between the New Zealand genera and the rest of the Australian species of Neopilionidae.

Figure and table captions

Figure 1. (A) Current phylogenetic hypothesis of the internal relationships within Monoscutidae before Taylor's (2011) placement of Monoscutidae (defined as Megalopsalidinae + Monoscutinae) within the Enantiobuninae. **(B)** Šilhavý's (1970) classification of Neopilionidae, in which the general formed clades concordant with geography. **(C)** Hunt and Cokendolpher's (1991) competing hypotheses, neither of which found monophyly for Neopilionidae.

Figure 2. Examples of *Forsteropsalis*: (a) *Forsteropsalis fabulosa* female specimen, for which species determination was made by its proximity to a male of this species; (b) *Forsteropsalis fabulosa* male, with the most grossly enlarged chelicers of the genus; (c) *Forsteropsalis nigra*, characterized by sclerotization of the carapace; and (d) *Forsteropsalis inconstans*. Photos by Sebastián Vélez (a-b) and Gonzalo Giribet (b-d).

Figure 3. Variation of chelicerae among species of *Forsteropsalis*, *Pantopsalis*, and *Spinicrus*. (A) *Forsteropsalis fabulosa* male; (B) *Forsteropsalis fabulosa* female; (C) *Forsteropsalis turneri* male; (D) MCZ129520 male; (E) *Forsteropsalis nigra* male; (F) *Forsteropsalis nigra* male; (G) *Forsteropsalis nigra* female; (H) *Forsteropsalis marplesi* female; (I) *Forsteropsalis wattsi* male; (J, K) *Pantopsalis chiltoni* male; (L) *Pantopsalis listeri* male Type I; *Pantopsalis listeri* Type II; (O, P, Q) *Spinicrus* spp. males from Australia.

Figure 4. Morphological variation in dentition, claw length, and curvature of female chelicerae of (A) *Forsteropsalis turneri*, voucher MCZ129521; (B) *Mangatangi parvum*, voucher MCZ129565; (C) *Pantopsalis phocator*, voucher MCZ129586; and *Forsteropsalis inconstans*, voucher DNA129540.

Figure 5. Map of New Zealand with sampling points. Each dot represents a unique sampling locality. Some dots were slightly shifted to clarify the illustration, and all exact localities are listed on Table 1. Stars indicate type locality for each particular species.

Figure 6. Phylogenetic relationships based on a tree selected under the maximum likelihood criterion, with tree search strategy as implemented in RAxML. Numbers above branches indicate bootstrap support values after 100 replicates. Only bootstrap values >50% are presented.

Figure 7. Phylogenetic relationships based on a tree selected under the parsimony criterion, under parameter set 111 for a combined COI + 18S + 28S dataset, as implemented in POY under a dynamic-homology search strategy. Numbers above branches represent jackknife support fractions, 1000 repetitions with 0.36 resampling probability. Only jackknife fractions >0.50 are presented. Squares represent if monophyly was found (black) or not (white) for different indel and transversion:transition cost parameters: left to right 111, 121, 141, 211, and 3221. Parameter set names follow Boyer & Giribet (2007).

Figure 8. Comparison of pedipalpal tarsal claw from representative specimens of *Mangatangi*, *Pantopsalis*, and *Forsteropsalis*. (a) *Mangatangi parvum*. Note the tooth comb on the claw. (b) *Pantopsalis* sp. (c) *Forsteropsalis turneri*. (d) *Forsteropsalis wattsi*.

Figure 9. Palpi of representative species of *Forsteropsalis*, *Pantopsalis*, and *Mangatangi* showing the relative length of the tubercule of the patella (Pa), indicated by the arrows. Notice how the size does not correlate with the generic placement of each specimen. (a) *Forsteropsalis nigra* male. (b) *Forsteropsalis nigra* female. (c) *Forsteropsalis wattsi* female. (d) *Forsteropsalis chiltoni* female. (e) *Pantopsalis* sp. (f) *Pantopsalis* sp. (g) *Pantopsalis* sp. (h) *Forsteropsalis turneri* female. (I) *Forsteropsalis turneri* female. (j) *Mangatangi* sp. female.

Figure 10. Dorsal view of species of *Forsteropsalis*, *Pantopsalis*, *Mangatangi*, and an unidentified Australian species: (A) MCZ129517 *Forsteropsalis marplesi*; (B) MCZ129519 *Forsteropsalis nigra*; (C) MCZ129542 *Forsteropsalis wattsi*; (D) MCZ129587 *Pantopsalis listeri;* (E) MCZ136146 *Pantopsalis phocator*; (F) MCZ129549 Australian sp.; (G) MCZ129518 *Mangatangi* sp.

Table 1. Voucher, locality and GenBank accession numbers for the sequenced specimens.

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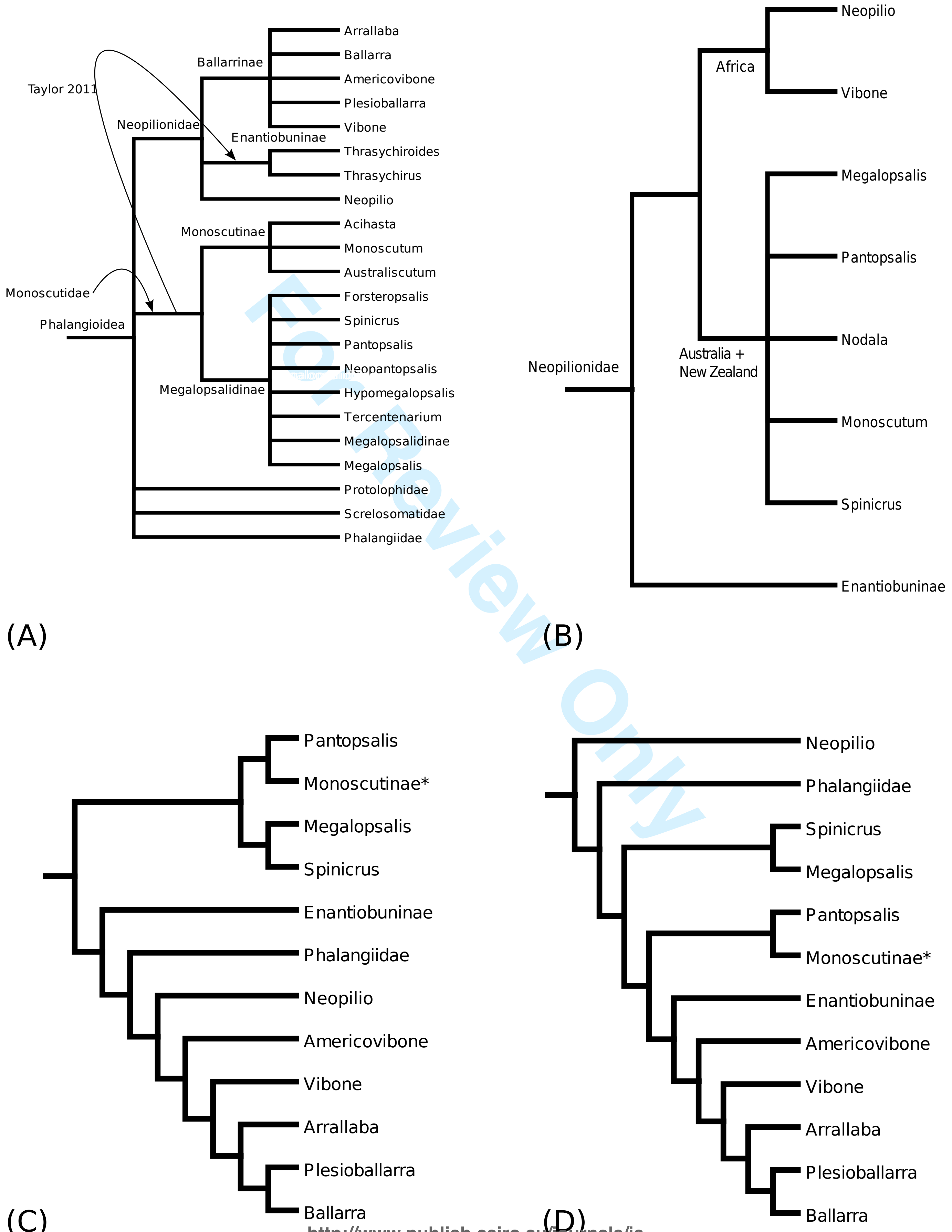
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Plesioballarra
Vibone
Thrasychiroides
Thrasychirus
Neopilio
Acihasta
Monoscutum
Australiscutum
Forsteropsalis
Spinicrus
Pantopsalis
Neopantopsalis
Hypomegalopsalis
Tercentenarium
Megalopsalidinae
Megalopsalis
Protolophidae
Screlosomatidae
Phalangiidae
(A)
Neopilio
Africa
Vibone
Megalopsalis
Pantopsalis
Nodala
Australia +
New Zealand
Neopilionidae
Monoscutum
Spinicrus
Enantiobuninae
(B)
Pantopsalis
Monoscutinae*
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Spinicrus
Enantiobuninae
Phalangiidae
Neopilio
Americovibone
Vibone
Arrallaba
Plesioballarra
Ballarra
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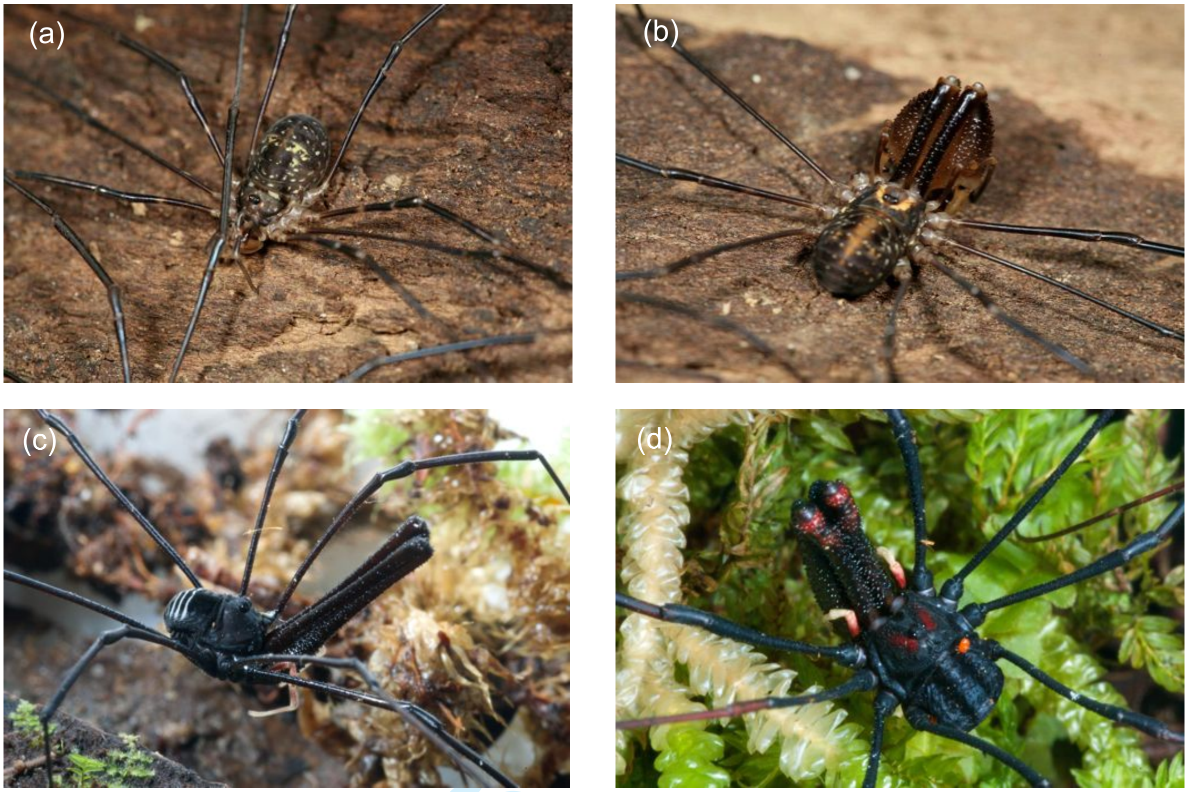
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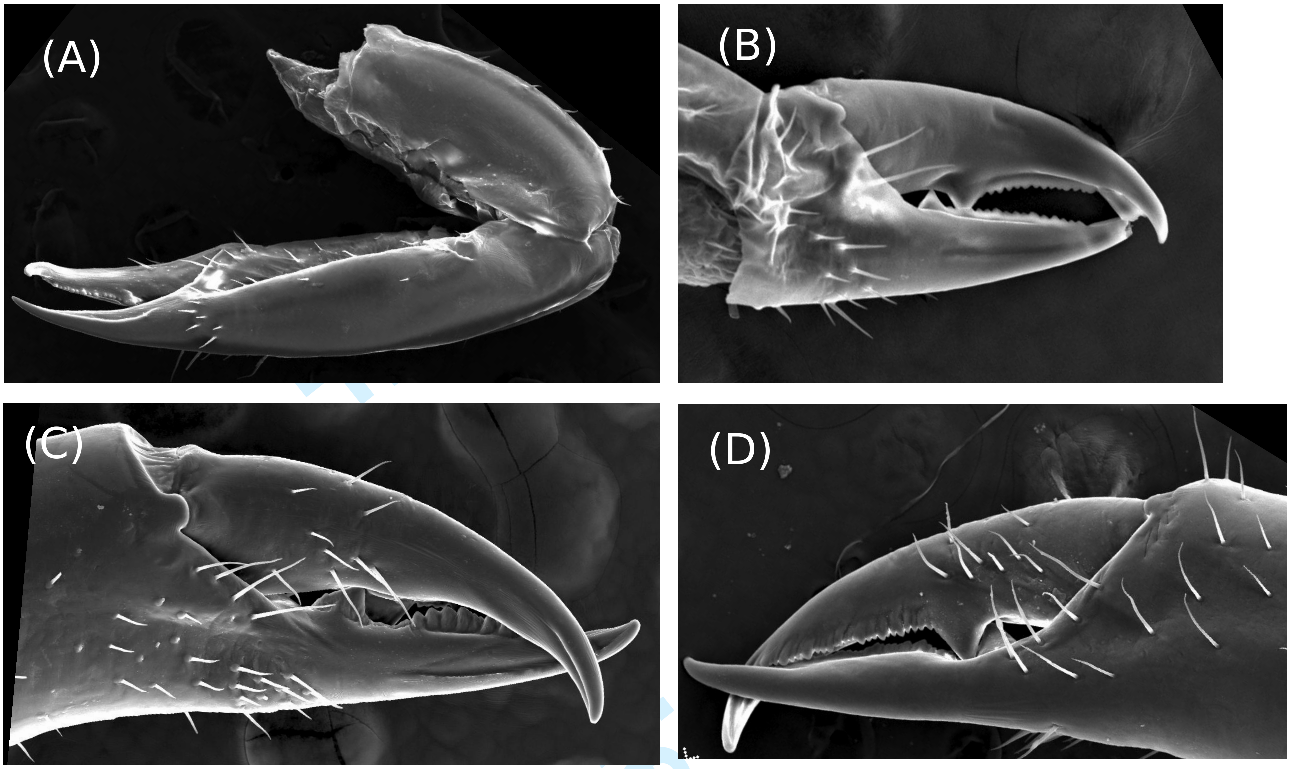
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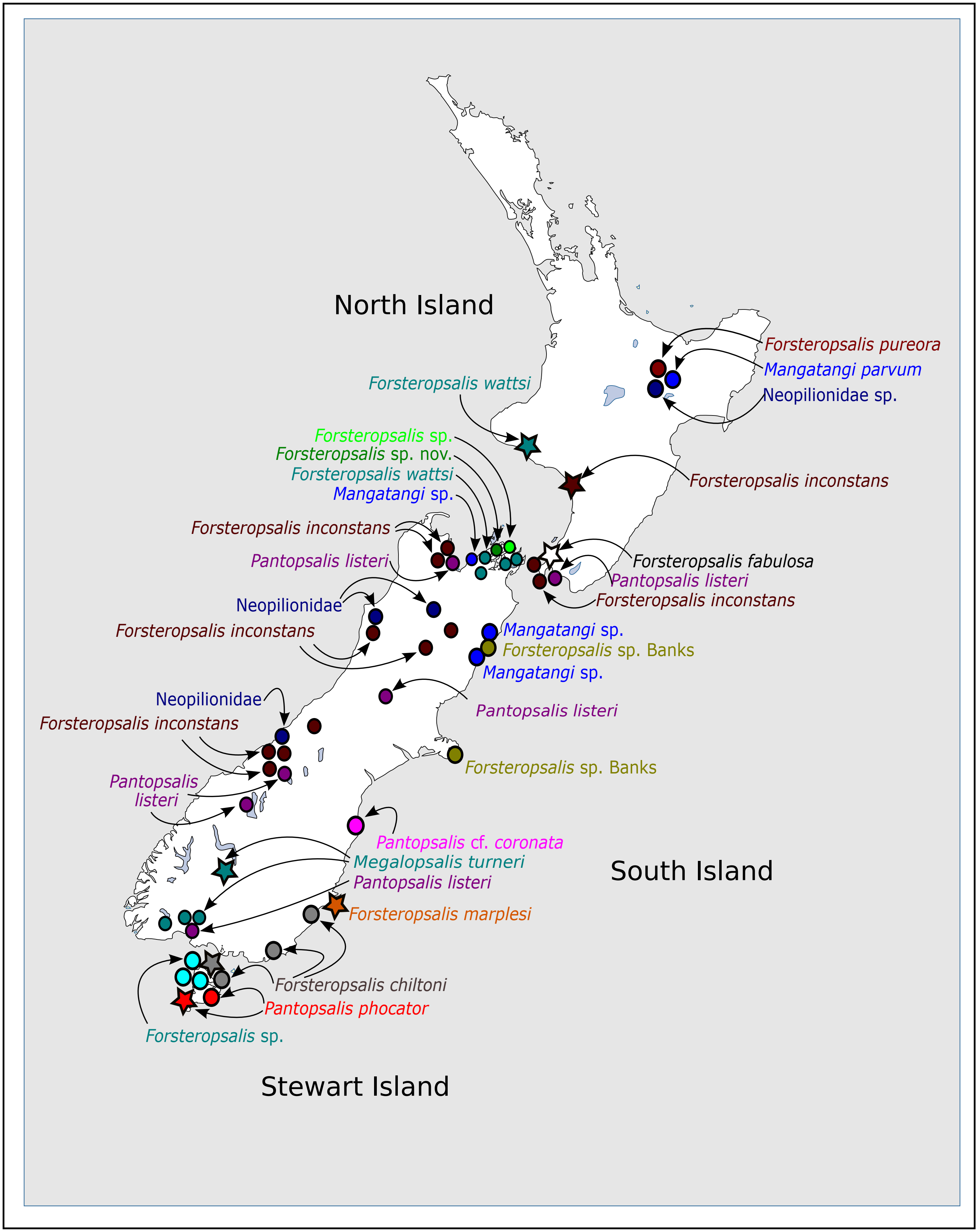
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Pantopsalis listeri
Neopilionidae
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Pantopsalis listeri
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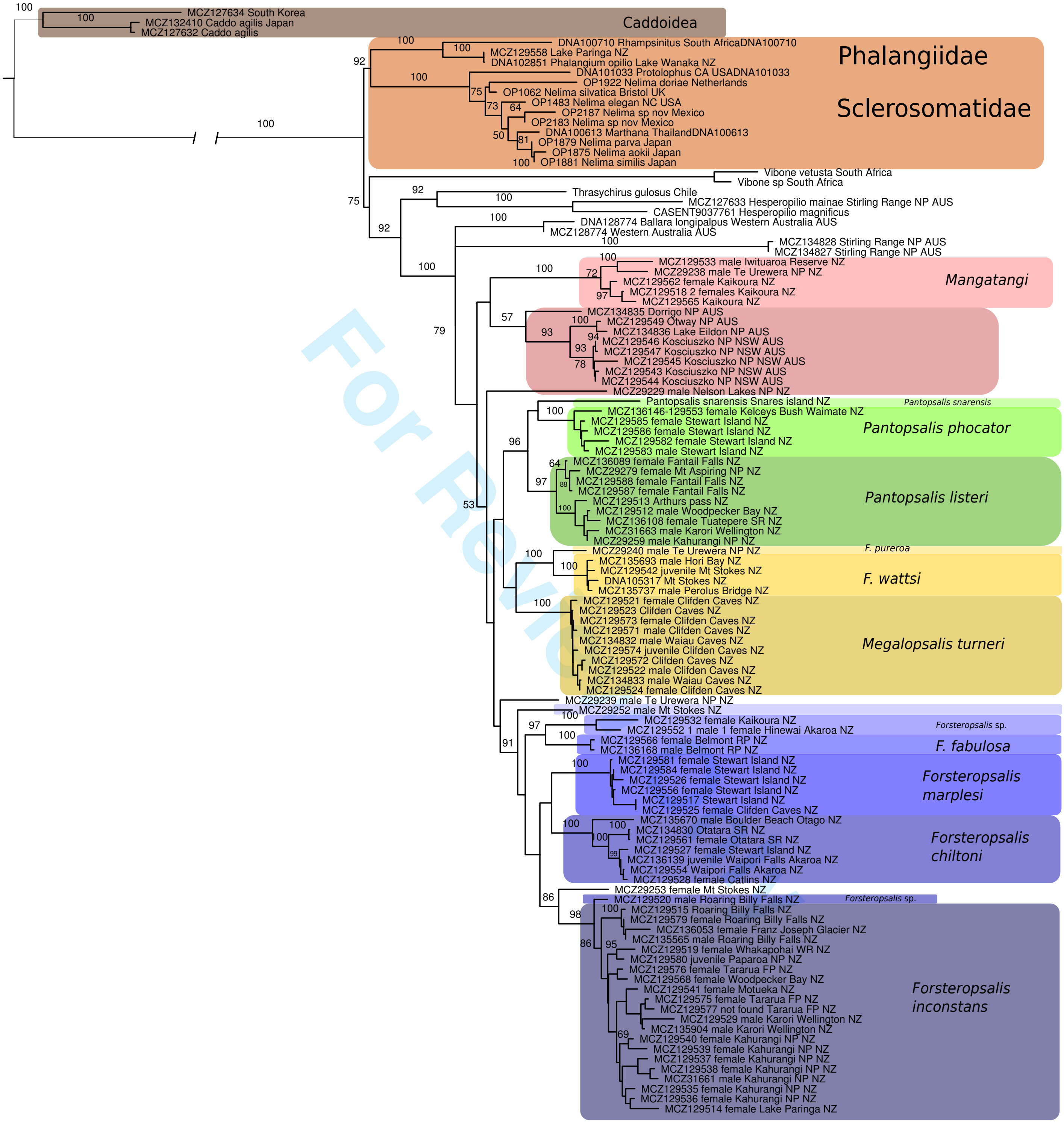
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DNA101033 Protolophus CA USADNA101033
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OP1483 Nelima elegan NC USA
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OP1879 Nelima parva Japan
OP1875 Nelima aokii Japan
OP1881 Nelima similis Japan
Phalangiidae
Sclerosomatidae
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Vibone sp South Africa
Thrasychirus gulosus Chile
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Mangatangi
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Pantopsalis snarensis Snares island NZ
Pantopsalis snarensis
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Forsteropsalis sp.
MCZ129515 Roaring Billy Falls NZ
MCZ129579 female Roaring Billy Falls NZ
MCZ136053 female Franz Joseph Glacier NZ
MCZ135565 male Roaring Billy Falls NZ
MCZ129519 female Whakapohai WR NZ
MCZ129580 juvenile Paparoa NP NZ
MCZ129576 female Tararua FP NZ
MCZ129568 female Woodpecker Bay NZ
MCZ129541 female Motueka NZ
MCZ129575 female Tararua FP NZ
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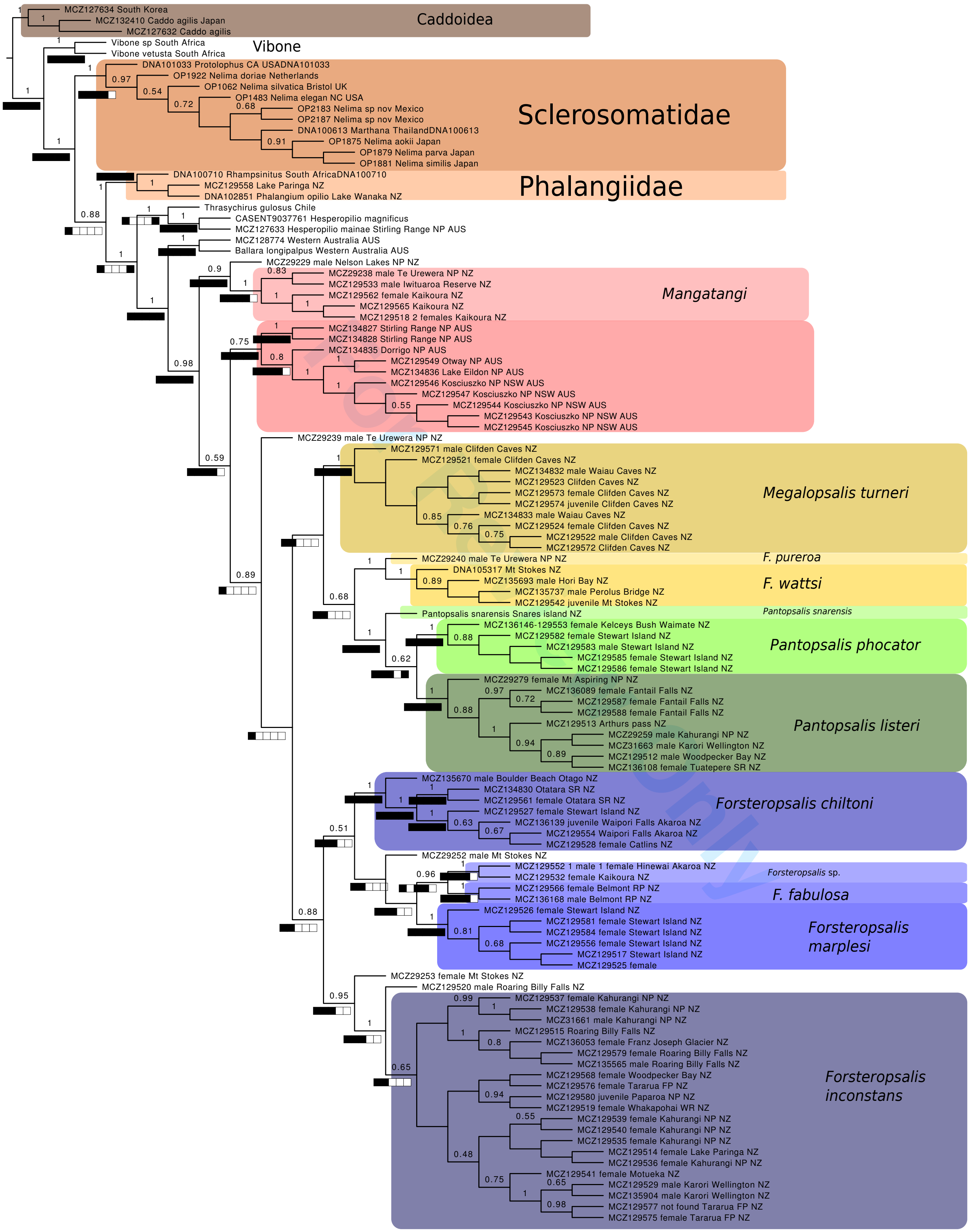
Forsteropsalis inconstans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Vibone sp South Africa
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Sclerosomatidae
DNA101033 Protolophus CA USADNA101033
OP1922 Nelima doriae Netherlands
OP1062 Nelima silvatica Bristol UK
OP1483 Nelima elegan NC USA
OP2183 Nelima sp nov Mexico
OP2187 Nelima sp nov Mexico
DNA100613 Marthana ThailandDNA100613
OP1875 Nelima aokii Japan
OP1879 Nelima parva Japan
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Phalangiidae
DNA100710 Rhampsinitus South AfricaDNA100710
MCZ129558 Lake Paringa NZ
DNA102851 Phalangium opilio Lake Wanaka NZ
Thrasychirus gulosus Chile
CASENT9037761 Hesperopilio magnificus
MCZ127633 Hesperopilio mainae Stirling Range NP AUS
MCZ128774 Western Australia AUS
Ballara longipalpus Western Australia AUS
MCZ29229 male Nelson Lakes NP NZ
Mangatangi
MCZ29238 male Te Urewera NP NZ
MCZ129533 male Iwituaroa Reserve NZ
MCZ129562 female Kaikoura NZ
MCZ129565 Kaikoura NZ
MCZ129518 2 females Kaikoura NZ
MCZ134827 Stirling Range NP AUS
MCZ134828 Stirling Range NP AUS
MCZ134835 Dorrigo NP AUS
MCZ129549 Otway NP AUS
MCZ134836 Lake Eildon NP AUS
MCZ129546 Kosciuszko NP NSW AUS
MCZ129547 Kosciuszko NP NSW AUS
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MCZ129545 Kosciuszko NP NSW AUS
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Megalopsalis turneri
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F. pureroa
MCZ29240 male Te Urewera NP NZ
F. wattsi
DNA105317 Mt Stokes NZ
MCZ135693 male Hori Bay NZ
MCZ135737 male Perolus Bridge NZ
MCZ129542 juvenile Mt Stokes NZ
Pantopsalis snarensis
Pantopsalis snarensis Snares island NZ
Pantopsalis phocator
MCZ136146-129553 female Kelceys Bush Waimate NZ
MCZ129582 female Stewart Island NZ
MCZ129583 male Stewart Island NZ
MCZ129585 female Stewart Island NZ
MCZ129586 female Stewart Island NZ
Pantopsalis listeri
MCZ29279 female Mt Aspiring NP NZ
MCZ136089 female Fantail Falls NZ
MCZ129587 female Fantail Falls NZ
MCZ129588 female Fantail Falls NZ
MCZ129513 Arthurs pass NZ
MCZ29259 male Kahurangi NP NZ
MCZ31663 male Karori Wellington NZ
MCZ129512 male Woodpecker Bay NZ
MCZ136108 female Tuatepere SR NZ
Forsteropsalis chiltoni
MCZ135670 male Boulder Beach Otago NZ
MCZ134830 Otatara SR NZ
MCZ129561 female Otatara SR NZ
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MCZ136139 juvenile Waipori Falls Akaroa NZ
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MCZ129528 female Catlins NZ
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Forsteropsalis sp.
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F. fabulosa
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Forsteropsalis inconstans
MCZ129537 female Kahurangi NP NZ
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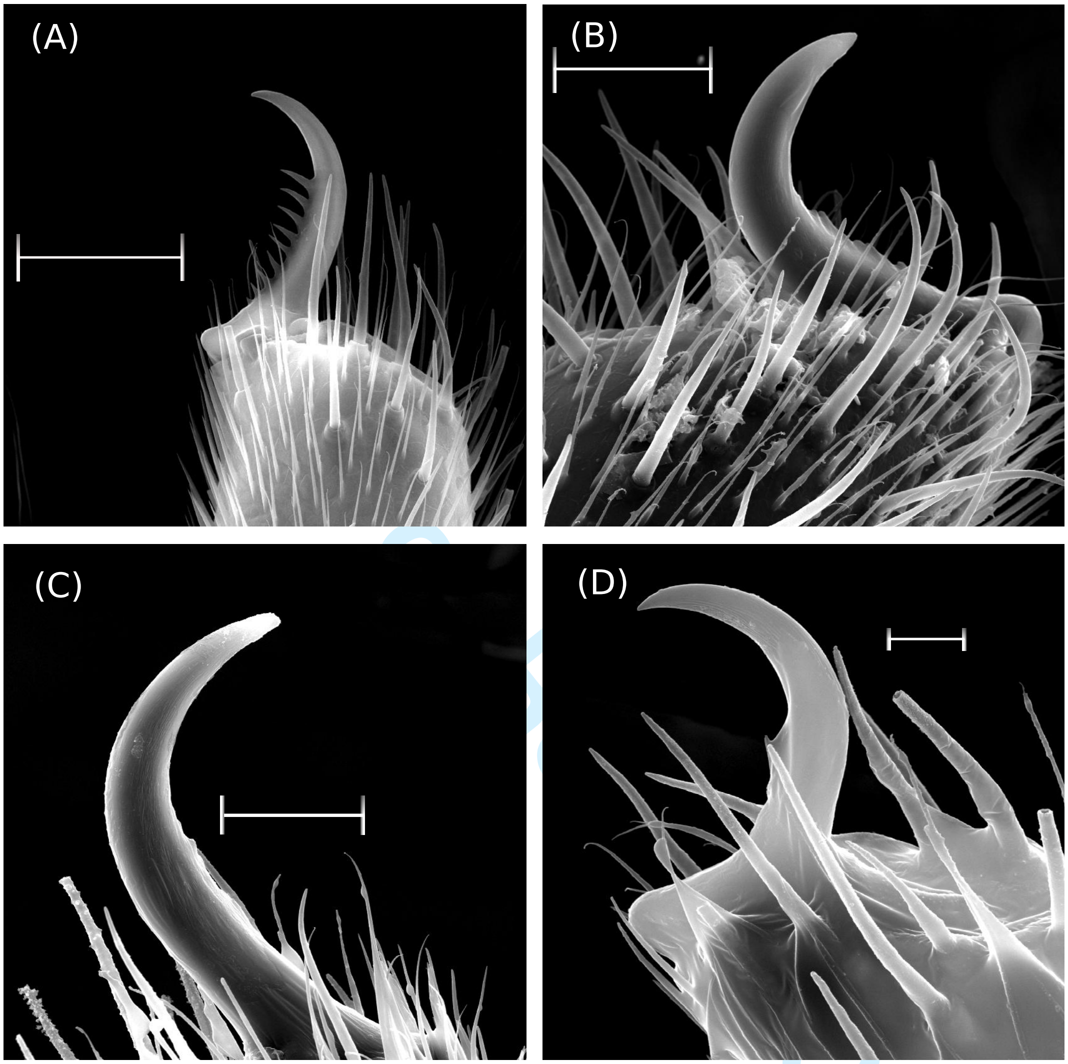
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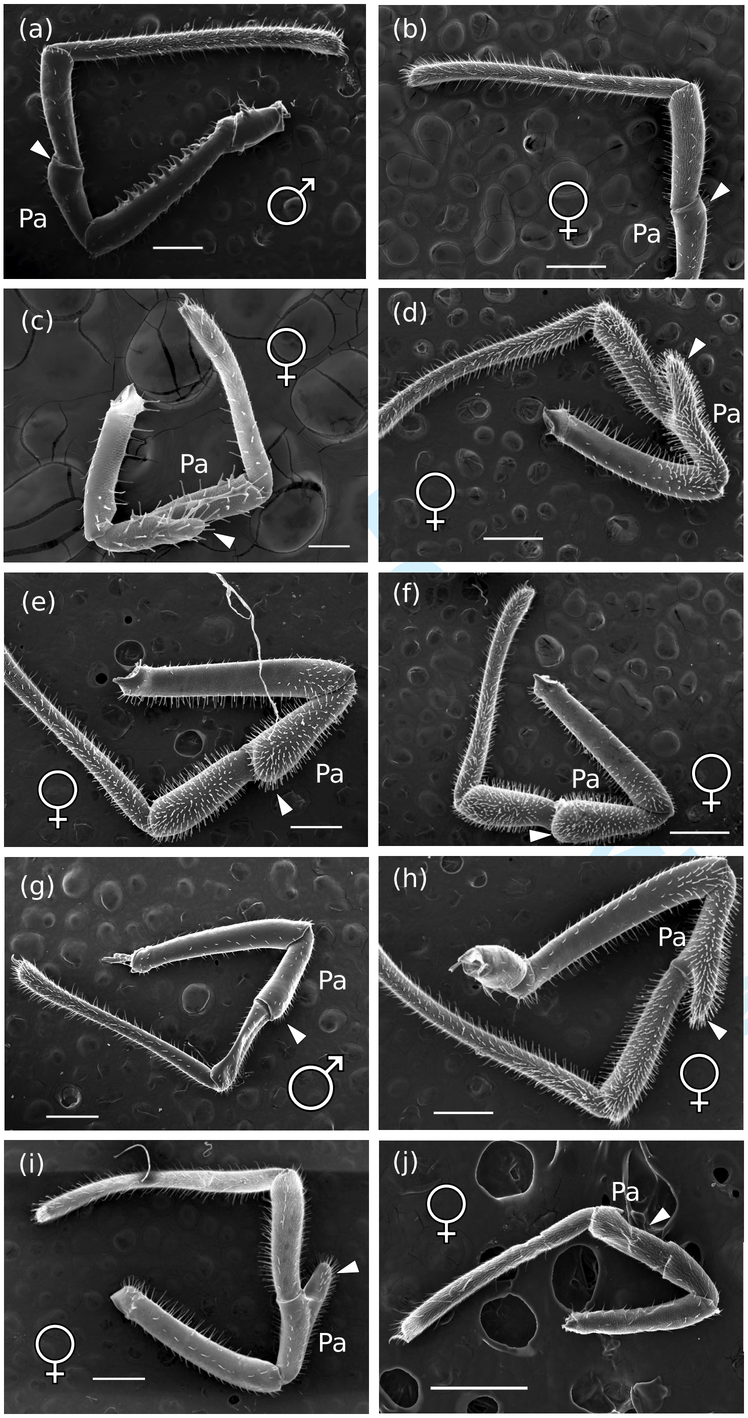
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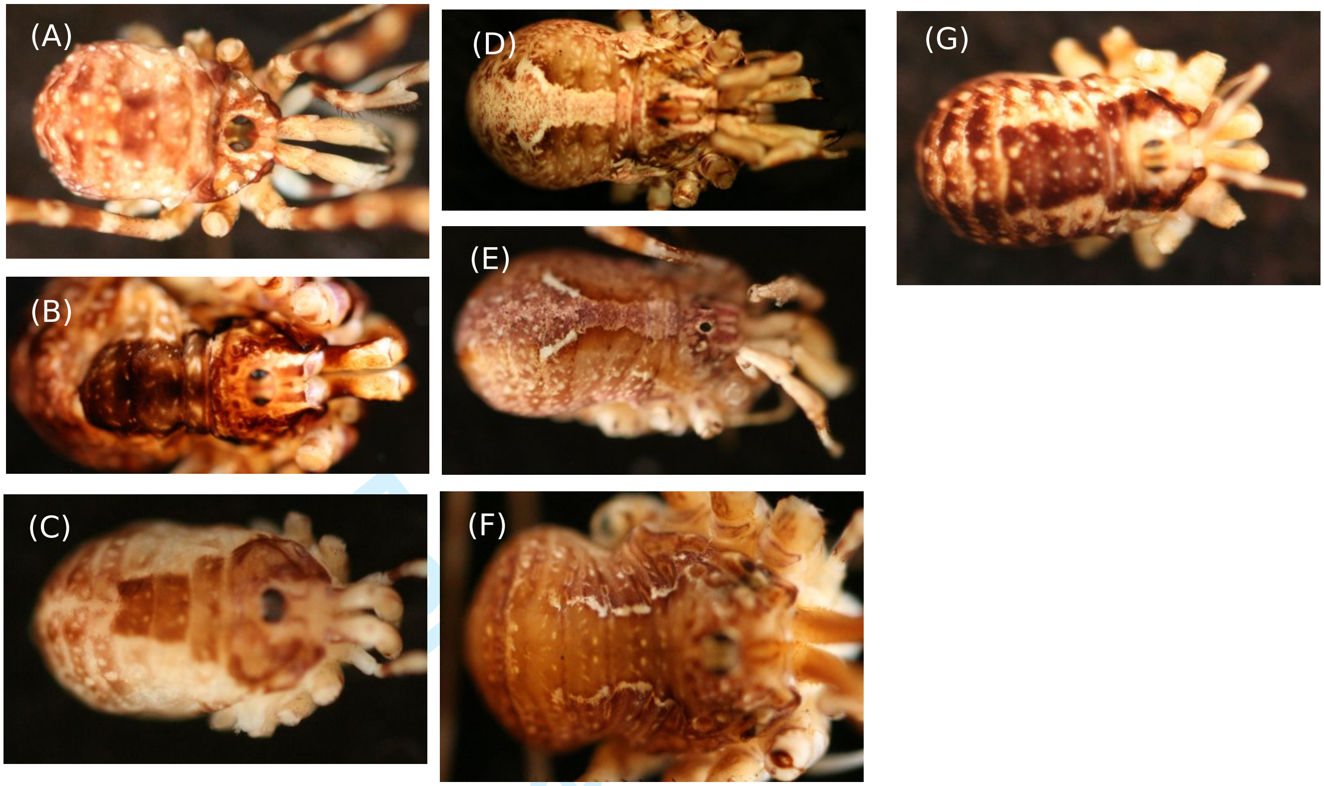
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Sheet1

Voucher	Descriptor	Locality	Other catalog number / Reference	Lat	Long
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CASENT-90	*Hesperopilio magnificus*		from Giribet and Groh (unpublished)		
MCZ127632	*Caddo agilis*	unknown	from Giribet and Groh (unpublished)	unknown	unknown
MCZ127633	*Hesperopilio ma*	Stirling Range NP	from Giribet and Groh (unpublished)	-34.3750	118.2567
MCZ127634	*Caddo pepperell*	South Korea	n/a	35.2758	127.6178
MCZ128774	*Ballara* sp	Western Australia	DNA128774	-32.6000	116.2000
MCZ129512	*Pantopsalis* sp	Woodpecker Bay N	DNA102786	-42.2172	171.3897
MCZ129513	*Pantopsalis* sp	Arthurs pass NZ	DNA102800	-43.2669	171.7097
MCZ129514	*Forsteropsalis* s	Lake Paringa NZ	DNA102823	-43.595	169.8247
MCZ129515	*Forsteropsalis* s	Roaring Billy Falls	DNA102840	-43.2989	169.2881
MCZ129517	*Forsteropsalis* s	Stewart Island NZ	DNA102882	-46.6647	168.2350
MCZ129518	*Mangatangi* sp	Kaikoura NZ	DNA102921	-42.0539	173.4006
MCZ129519	*Forsteropsalis* s	Whakapohai WR N	DNA105050	-43.56	169.0811
MCZ129520	*Forsteropsalis* s	Roaring Billy Falls	DNA105051	-43.2806	169.5097
MCZ129521	*Megalopsalis tur*	Clifden Caves NZ	DNA105144	-46.0919	167.4972
MCZ129522	*Forsteropsalis* s	Clifden Caves NZ	DNA105146	-46.0919	167.4972
MCZ129523	*Forsteropsalis* s	Clifden Caves NZ	DNA105149	-46.0919	167.4972
MCZ129524	*Forsteropsalis* s	Clifden Caves NZ	DNA105150	-46.0919	167.4972
MCZ129525	*Forsteropsalis* s	Clifden Caves NZ	DNA105152	-46.0919	167.4972
MCZ129526	*Forsteropsalis* s	Stewart Island NZ	DNA105153	-46.8347	168.5381
MCZ129527	*Forsteropsalis* s	Stewart Island NZ	DNA105162	-46.8347	168.5381
MCZ129528	*Forsteropsalis* s	Catlins NZ	DNA105197	-46.4128	169.8039
MCZ129529	*Forsteropsalis* s	Karori Wellington	DNA105355	-41.0661	174.5325
MCZ129532	*Forsteropsalis* s	Kaikoura NZ	DNA104787	-42.8953	173.3422
MCZ129533	*Mangatangi* sp	Iwituaroa Reserve	DNA105971	-41.8508	173.2486
MCZ129535	*Forsteropsalis* s	Kahurangi NP NZ	DNA105973	-41.4081	172.4922
MCZ129536	*Forsteropsalis* s	Kahurangi NP NZ	DNA105974	-41.4081	172.4922
MCZ129537	*Forsteropsalis* s	Kahurangi NP NZ	DNA105975	-41.4081	172.4922
MCZ129538	*Forsteropsalis* s	Kahurangi NP NZ	DNA105976	-41.4081	172.4922
MCZ129539	*Forsteropsalis* s	Kahurangi NP NZ	DNA105978	-41.4081	172.4922
MCZ129540	*Forsteropsalis* s	Kahurangi NP NZ	DNA105979	-41.4081	172.4922
MCZ129541	*Forsteropsalis* s	Motueka NZ	DNA105980	-41.8064	172.3867
MCZ129542	*Forsteropsalis* s	Mt Stokes NZ	DNA105981	-41.2031	174.2922
MCZ129543	*Spinicrus* sp	Kosciuszko NP NS	DNA105982	-36.0825	148.7389
MCZ129544	*Spinicrus* sp	Kosciuszko NP NS	DNA105983	-36.0825	148.7389
MCZ129545	*Spinicrus* sp	Kosciuszko NP NS	DNA105984	-36.0825	148.7389
MCZ129546	*Spinicrus* sp	Kosciuszko NP NS	DNA105985	-36.0825	148.7389
MCZ129547	*Spinicrus* sp	Kosciuszko NP NS	DNA105986	-36.0825	148.7389
MCZ129549	*Spinicrus* sp	Otway NP AUS	DNA105988	-38.1786	143.7928
MCZ129552	*Forsteropsalis* s	Hinewai Akaroa N	DNA102910	-43.6967	173.7053
MCZ129554	*Forsteropsalis* s	Waipori Falls Akar	DNA102901	-45.2983	169.2831
MCZ129556	*Forsteropsalis* s	Stewart Island NZ	DNA102897	-46.9147	168.0017
MCZ129558	*Phalangium opil*	Lake Paringa NZ	DNA102825	-43.71	169.4970
MCZ129561	*Forsteropsalis* s	Otatara SR NZ	DNA100784	-46.0072	168.0049

MCZ129562	*Mangatangi* sp	Kaikoura NZ	DNA102915		-42.6878	173.7469
MCZ129565	*Mangatangi par*	Kaikoura NZ	DNA102919		-42.8953	173.3422
MCZ129566	*Forsteropsalis* s	Belmont RP NZ	DNA102929		-41.3492	174.9275
MCZ129568	*Forsteropsalis* s	Woodpecker Bay N	DNA104785		-42.2172	171.3897
MCZ129571	*Forsteropsalis* s	Clifden Caves NZ	DNA105147		-46.0919	167.4972
MCZ129572	*Forsteropsalis* s	Clifden Caves NZ	DNA105148		-46.0919	167.4972
MCZ129573	*Forsteropsalis* s	Clifden Caves NZ	DNA105145		-46.0919	167.4972
MCZ129574	*Forsteropsalis* s	Clifden Caves NZ	DNA105151		-46.0919	167.4972
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MCZ129576	*Forsteropsalis* s	Tararua FP NZ	DNA105527		-40.2828	175.8169
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MCZ129580	*Forsteropsalis* s	Paparoa NP NZ	DNA105029		-42.555	171.5556
MCZ129581	*Forsteropsalis* s	Stewart Island NZ	DNA104789		-46.9147	168.0017
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MCZ129583	*Pantopsalis* sp	Stewart Island NZ	DNA104792		-46.9147	168.0017
MCZ129584	*Forsteropsalis* s	Stewart Island NZ	DNA104793		-46.9147	168.0017
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MCZ129586	*Pantopsalis* sp	Stewart Island NZ	DNA104795		-46.9147	168.0017
MCZ129587	*Pantopsalis* sp	Fantail Falls NZ	DNA104797		-44.6011	169.1897
MCZ129588	*Pantopsalis* sp	Fantail Falls NZ	DNA104798		-44.6011	169.1897
MCZ132410	*Caddo agilis*	Mt Takao JAPAN	DNA101716	from Giribet and Groh (unpublishe	35.6344	139.2412
MCZ132934	*Vibone vetusta*	South Africa	DNA106709		-33.9856	18.4013
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MCZ134827	*Spinicrus* sp	Stirling Range NP	DNA106783		-34.3803	118.2503
MCZ134828	*Spinicrus* sp	Stirling Range NP	DNA106784		-34.3803	118.2503
MCZ134830	*Forsteropsalis* s	Otatara SR NZ	DNA100782		-46.2069	168.1547
MCZ134832	*Forsteropsalis* s	Waiau Caves NZ	DNA100783	from Boyer 2007	-46.0003	167.0123
MCZ134833	*Forsteropsalis* s	Waiau Caves NZ	DNA100785		-46.0003	167.0123
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MCZ134836	*Spinicrus* sp	Lake Eildon NP A	DNA105990		-37.6586	146.0931
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MCZ135565	*Forsteropsalis* s	Roaring Billy Falls	DNA105073		-43.2806	169.5097
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MCZ136089	*Pantopsalis* sp	Fantail Falls NZ	DNA102848		-44.6011	169.1897
MCZ136092	*Phalangium opil*	Lake Wanaka NZ	DNA102851		-44.40	169.1873
MCZ136108	*Pantopsalis* sp	Tuatepere SR NZ	DNA102868		-46.5683	167.4114
MCZ136139	*Forsteropsalis* s	Waipori Falls Akar	DNA102900		-45.2983	169.2831
MCZ136146	*Pantopsalis* sp	Waimate NZ	DNA102907		-44.70	170.9675
MCZ136168	*Forsteropsalis* s	Belmont RP NZ	DNA105996		-41.3492	174.9275
MCZ29229	*Neopilionidae* s	Nelson Lakes NP N	n/a		-41.82	172.8079
MCZ29238	*Mangatangi* sp	Te Urewera NP NZ	n/a		-38.7254	177.1650
MCZ29239	*Neopilionidae* s	Te Urewera NP NZ	n/a		-38.7273	177.1652
MCZ29240	*Forsteropsalis* s	Te Urewera NP NZ	n/a		-38.7273	177.1652
MCZ29252	*Forsteropsalis* s	Mt Stokes NZ	n/a		-41.09	174.1382

MCZ29253	*Forsteropsalis* s	Mt Stokes NZ	n/a	-41.09	174.1382
MCZ29259	*Pantopsalis* sp	Kahurangi NP NZ	n/a	-41.18	172.7302
MCZ29279	*Pantopsalis* sp	Mt Aspiring NP NZ	n/a	-44.49	168.7874
MCZ31661	*Forsteropsalis* s	Kahurangi NP NZ	DNA105977	-41.4081	172.4922
MCZ31663	*Pantopsalis* sp	Karori Wellington	DNA100702 from Giribet et al 2010	-41.0044	174.5125
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OP1875	*Nelima aokii*	Honshu JAPAN	from Hedin et al 2012		
OP1879	*Nelima parva*	Shikoku JAPAN	from Hedin et al 2012		
OP1881	*Nelima similis*	Honshu JAPAN	from Hedin et al 2012		
OP1922	*Nelima doriae*	NETHERLANDS	from Hedin et al 2012		
OP2183	*Nelima* sp nov	Oaxaca, MEXICO	from Hedin et al 2012		
OP2187	*Nelima* sp nov	Oaxaca, MEXICO	from Hedin et al 2012		

Collectors	Voucher URL	Date	Genbank COI	18S	28S
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Michael F	http://m	24.V.2011	--	KF963313.1	KF955600.1
Mark S. F	http://m	20.06.2010	--	KF963311.1	KF955598.1
M. Lythe	http://m	30.VII.2013	KJ871355	KJ871431	KJ871516
G. Giribet	http://m	12.II.2008	KJ871372	KJ871432	KJ871579
G. Giribet	http://m	13.II.2008	KJ871362	KJ871433	KJ871580
G. Giribet	http://m	15.II.2008	KJ871366	KJ871434	KJ871517
G. Giribet	http://m	15.II.2008	KJ871364	KJ871435	KJ871518
G. Giribet	http://m	17.II.2008	KJ871373	KJ871436	KJ871519
P. Paquin.	http://m	20.II.2008	KJ871395	KJ871437	KJ871572
S. Velez	http://m	23.XII.2009	KJ871404	KJ871438	KJ871520
S. Velez	http://m	24.XII.2009	KJ871413	KJ871439	KJ871521
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S. Velez	http://m	27.XII.2009	KJ871423	KJ871442	KJ871524
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S. Velez	http://m	7.I.2010	KJ871420	KJ871447	KJ871529
P. Paquin.	http://m	20.II.2008	KJ871397	KJ871448	KJ871530
N. Scharf	http://m	10.III.2010	KJ871386	KJ871449	KJ871573
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P. Paquin.	http://m	19.II.2008	KJ871399	KJ871464	KJ871539
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Gonzalo G	http://m	15.II.2008	KJ871363	KJ871467	KJ871593
C.J. Vink	http://m	4.X.2002	KJ871356	--	KJ871542

P. Paquin	http://m	20.II.2008	KJ871394	KJ871468	KJ871574
P. Paquin	http://m	20.II.2008	KJ871400	KJ871469	KJ871575
P. Paquin	http://m	21.II.2008	KJ871396	--	KJ871543
G. Giribet	http://m	12.II.2008	KJ871369	KJ871470	KJ871544
S. Velez	http://m	27.XII.2009	KJ871416	KJ871471	KJ871545
S. Velez	http://m	27.XII.2009	KJ871422	KJ871472	KJ871546
S. Velez	http://m	27.XII.2009	KJ871407	KJ871473	KJ871547
S. Velez	http://m	27.XII.2009	KJ871403	KJ871474	KJ871548
S. Velez	http://m	9.I.2010	KJ871391	KJ871475	KJ871549
S. Velez	http://m	9.I.2010	KJ871390	KJ871476	KJ871550
S. Velez	http://m	9.I.2010	KJ871426	KJ871477	KJ871551
Sebastián	http://m	6.I.2010	KJ871425	--	KJ871552
S. Velez	http://m	24.XII.2009	KJ871405	KJ871478	KJ871553
S. Velez	http://m	21.XII.2009	KJ871424	KJ871479	KJ871554
G. Giribet	http://m	17.II.2008	KJ871378	KJ871480	KJ871555
G. Giribet	http://m	17.II.2008	KJ871379	KJ871481	KJ871581
G. Giribet	http://m	17.II.2008	KJ871383	KJ871482	KJ871582
G. Giribet	http://m	17.II.2008	KJ871380	KJ871483	KJ871556
G. Giribet	http://m	17.II.2008	KJ871381	KJ871484	KJ871583
G. Giribet	http://m	17.II.2008	KJ871382	KJ871485	KJ871584
G. Giribet	http://m	15.II.2008	KJ871370	KJ871486	KJ871585
G. Giribet	http://m	15.II.2008	KJ871371	KJ871487	KJ871586
Sarah L. I	http://m	13.IV.2005	--	KF963309.1	KF955596.1
Benjamin	http://m	5.XI.2011	--	KJ871488	KJ871605
Benjamin	http://m	7.XI.2011	--	--	--
Gonzalo (	http://m	9.IV.2011	GQ912862.1	GQ912708.1	GQ912757.1
Michael F	http://m	20.V.2011	--	KJ871489	KJ871601
Michael F	http://m	20.V.2011	--	KJ871490	KJ871602
C.J. Vink	http://m	4.X.2002	KJ871358	KJ871491	KJ871557
C.J. Vink	http://m	5.X.2002	EF108587	KJ871492	KJ871558
C.J. Vink	http://m	5.X.2002	KJ871357	--	KJ871559
N. Scharf	http://m	19.XII.2010	KJ871384	KJ871493	KJ871603
N. Scharf	http://m	25.XII.2010	KJ871353	KJ871494	KJ871604
David Lol	http://m	2002	GQ912863.1	GQ912711.1	GQ912762.1
S. Velez	http://m	24.XII.2009	KJ871414	KJ871495	KJ871560
S. Velez	http://m	31.XII.2009	KJ871417	--	KJ871561
S. Velez	http://m	4.I.2010	KJ871418	KJ871496	KJ871562
S. Velez	http://m	5.I.2010	KJ871419	KJ871497	KJ871563
S. Velez	http://m	7.I.2010	KJ871421	KJ871498	KJ871564
G. Giribet	http://m	14.II.2008	KJ871365	KJ871499	KJ871565
G. Giribet	http://m	15.II.2008	KJ871367	KJ871500	KJ871587
Gonzalo (	http://m	15.II.2008	KJ871385	KJ871501	KJ871594
G. Giribet	http://m	16.II.2008	KJ871368	KJ871502	KJ871588
G. Giribet	http://m	17.II.2008	KJ871374	KJ871503	KJ871566
Gonzalo (	http://m	18.II.2008	KJ871377	KJ871504	KJ871589
P. Paquin	http://m	21.II.2008	KJ871398	KJ871505	KJ871567
Rosa Ferr	http://m	16.I.2014	KJ870048	KJ871506	KJ871578
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Rosa Ferr	http://m	20.I.2014	KJ870080	KJ871513	KJ871591
N. Scharf	http://m	7.III.2010	KJ871354	KJ871514	KJ871571
J. Derraik	http://m	16.I.2002	GQ912861	KJ871515	KJ871592
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