



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

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

3

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11

12 Running title: Phylogenetics of the New Zealand Enantiobuninae

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

29

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

32

33 **Additional keywords:** Monoscutidae, Australia, biogeography, phylogeny

34 Introduction

35 The order Opiliones consists of 6,539 described species (Kury 2013), divided into four
36 suborders, 45 families and about 1,500 genera (Machado, Pinto-da-Rocha *et al.* 2007;
37 Sharma and Giribet 2011; Sharma, Prieto *et al.* 2011; Pinto-da-Rocha, Bragagnolo *et al.*
38 2014), with many new species being described every year. Within Opiliones, the
39 suborder Eupnoi includes the superfamilies Caddoidea and Phalangioidea (Shear 1982).
40 The first group, Phalangioidea, forms a monophyletic assemblage of those eupnoids with
41 long legs and smooth palps (Shultz 1998; Giribet, Rambla *et al.* 1999; Shultz and Regier
42 2001; Giribet, Edgecombe *et al.* 2002; e.g., Giribet, Vogt *et al.* 2010). Phalangioidea is
43 divided into the families (1) Phalangiidae Latreille, 1802, of nearly world-wide
44 distribution, and which includes the cosmopolitan “daddy-longleg” or common
45 harvestman, *Phalangium opilio* Linnaeus, 1758; (2) Sclerosomatidae Simon, 1879, a
46 speciose family with more than 1,300 species and many more to be described in dense
47 subtropical forests (Machado, Pinto-da-Rocha *et al.* 2007); (3) Protolophidae Banks,
48 1893 (Cokendolpher 2007b); (4) Monoscutidae Forster, 1948, as prior to Taylor (2011)
49 and as discussed below, from New Zealand and Australia; and (5) Neopilionidae
50 Lawrence, 1931 with a temperate Gondwanan distribution: New Zealand, Australia,
51 South Africa and South America, and diagnosed by the penis morphology (Hunt and
52 Cokendolpher 1991b). The current work is concerned with the last two, Monoscutidae
53 and Neopilionidae.

54 Prior to Taylor (2011) work on Neopilionidae included, among others, the families
55 (1) Neopilionidae, with 8 genera and 15 species from South Africa (including *Neopilio*
56 *australis*), Australia and South America, and (2) Monoscutidae Forster, 1948 with 5

57 genera and 32 species found in Australia and New Zealand (Fig. 1). The 8 genera within
58 Neopilionidae were divided into three subfamilies: (1) Neopilioninae Lawrence, 1931,
59 with a single species from South Africa; (2) Enantiobuninae Mello-Leitão, 1931 with
60 four South American species; and (3) the larger group Ballarrinae Hunt & Cokendolpher,
61 1991, which included mostly species from Australia, one from Chile, and one from South
62 America. Monoscutidae was divided into: (1) Monoscutinae Forster, 1948, from New
63 Zealand and having heavy sclerotization and small ozopores; and (2) Megalopsalidinae
64 Forster, 1949, characterized by a smooth carapace, except for small spines in some, e.g.,
65 *Forsteropsalis nigra* (Forster, 1944) and *F. inconstans* (Forster, 1944), and by the
66 presence of visible ozopores, and which contained *Megalopsalis* (Australia and New
67 Zealand), *Pantopsalis* Simon, 1879, (New Zealand endemic), and *Spinicrus* Forster, 1949
68 (Australia) (Cokendolpher 2007a; Cokendolpher and Taylor 2007b).

69 The New Zealander and Australian species of Eupnoi also show a striking sexual
70 polymorphism with conspicuously enlarged male chelicerae, and nondescript females
71 (Fig. 2). The long chelicerae in the males can reach up to 10 times the length of the body,
72 comically extending high above the individual, and which in some cases also have
73 grossly enlarged second segments that rival the girth of the main body of the animal, e.g.,
74 *Forsteropsalis fabulosa* (Phillips & Grimmett, 1932) and *Megalopsalis turneri* Marples,
75 1944 (Forster 1944b; Marples 1944; Forster 1949b; Forster and Wilton 1968; Forster and
76 Forster 1999; Taylor 2004a; Taylor 2011). This presence of sexual dimorphism, and the
77 dearth of characters in the female chelicerae in *Pantopsalis*, *Forsteropsalis*, and
78 *Megalopsalis* are largely responsible for the taxonomic instability of the species in each
79 genus (Figs. 3, 4). Females in both *Pantopsalis* and *Forsteropsalis* have a uniform brown

80 colour, with almost identical markings, so most species descriptions have been based on
81 males, and females have been assigned to species when they are collected in close
82 proximity to an identifiable male, which is not free of error, as it is common to collect
83 specimens of different species in close proximity (see also Fernández et al. submitted).
84 As an example of the confusion this has caused, in 1949 Forster corrected Pocock's
85 (1902a) purported *Megalopsalis hoggi* female as the male of *Spinicrus camelus*, although
86 a few years earlier, Forster himself had described *Megalopsalis luna* from a specimen
87 which Taylor later assigned to a *Pantopsalis* female (Forster 1944b; Taylor 2004a),
88 something that Forster must have noticed in his original description of the female of
89 *Pantopsalis mila*, which matches his own description of the *Megalopsalis luna* male
90 (Forster 1964b). Taylor (2004) also reported that Pocock described a male of *Pantopsalis*
91 *jenningsi* as a female of *Pantopsalis nigripalpis*, something that Pocock himself corrected
92 a year later (Pocock 1903a; Taylor 2011). In addition to sexual dimorphism, male
93 dimorphism has also been reported, with some species purportedly having distinct broad-
94 chelicerae and a long-chelicerae male forms, which have been dubbed the 'normal' and
95 'effeminate' forms (Forster 1964b; Taylor 2004a). In light of this, and in apparent
96 frustration, Forster (1965) spelled out the rampant taxonomic confusion brought by
97 sexual dimorphism, with what he saw as different authors describing species
98 independently from males and females, and ended the description of several new species
99 with a note that he would not attempt a key for Monoscutidae of New Zealand until the
100 issue of assigning males to females had been resolved (Forster 1962b). Lacking breeding
101 experiments or molecular studies (but see Fernández et al. submitted), it is unknown if
102 the forms belong to the same species, and if they do, how many species have either or

103 both forms, or if the forms are in discrete categories or occupy a range of sizes and
104 variants, as reported by Kauri (1954) for *Spinicrus minimus*. If true, this could mean that
105 the current designations are just an artefact from poor sampling from a highly
106 polymorphic population.

107

108 Although the phylogeny of the order Opiliones has received substantial attention
109 in the past decades (Giribet, Rambla *et al.* 1999; Giribet and Wheeler 1999; Shultz and
110 Regier 2001; Giribet, Edgecombe *et al.* 2002; Giribet and Kury 2007; Giribet, Vogt *et al.*
111 2010), only recently Giribet *et al.* (2010) published the first molecular sequences that
112 included members of the new Enantiobuninae (former Monoscutidae), although the
113 sampling and analysis was only in the context of the broader phylogenetic relationships
114 of the whole order Opiliones. Here we report the first comprehensive molecular
115 systematics study of the New Zealand species currently assigned to Enantiobuninae,
116 based on freshly collected material from New Zealand, Australia and South Africa, and in
117 context with previously published molecular data for South American Enantiobuninae,
118 Sclerosomatidae, Phalangidae, and Caddidae. We examine the congruence between our
119 molecular results against the current and historical species designations based on
120 morphology, including the assignment of females to species based on molecular data.
121 Additional population-level work is presented in an accompanying paper dealing with
122 species delimitation (Fernández *et al.*, submitted). We also analyse our data and comment
123 on the monophyly of the current genera and the validity of historical diagnostic
124 characters.

125

126 **Materials and methods**

127 *Specimen sampling*

128 Our sampling included 92 fresh specimens, 11 from Australia, 2 from South Africa and
129 79 from New Zealand, collected from 2002 to 2014 (Table 1 and Fig. 5). Specimens were
130 collected by hand and preserved in 96% ethanol and stored at -80 °C for long-term
131 preservation of DNA. Sequences from GenBank belonging to the family Caddidae were
132 used to root the trees (Table 1). A specimen of *Phalangium opilio*, also collected in New
133 Zealand, was used along GenBank sequences from other studies including Phalangiidae,
134 Sclerosomatidae, *Vibone*, *Thrasychirus*, *Hesperopilio*, *Ballara* and other Neopilionidae to
135 test the monophyly of Enantiobuninae, Neopilionidae, and Monoscutidae as presently
136 defined (Giribet, Vogt *et al.* 2010; Hedin, Tsurusaki *et al.* 2012; Groh and Giribet 2014).
137 Most specimens were collected from the vegetation, walking about, or from the underside
138 of fallen logs and rocks, and were most abundant during night time. Specimens were
139 deposited at the Museum of Comparative Zoology, Harvard University, Cambridge,
140 Massachusetts, USA (MCZ) the Zoological Museum, Natural History Museum of
141 Denmark (NHMD), and the Museum of New Zealand/Te Papa Tongarewa, Wellington,
142 New Zealand (TPT). All DNA isolates from new material were deposited at the MCZ
143 except for *Pantopsalis snarensis*, which was deposited at TPT.

144

145 *Molecular sequences*

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

149 745 bp fragment of the protein-encoding mitochondrial gene cytochrome *c* oxidase
150 subunit I (COI), all which have been recently used for the estimation of phylogenetic
151 relationships within arthropods, particularly the order Opiliones (Edgecombe, Wilson *et*
152 *al.* 2000; Giribet, Edgecombe *et al.* 2001; Prendini, Crowe *et al.* 2003; Boyer and Giribet
153 2004; Prendini, Weygoldt *et al.* 2005; Boyer, Baker *et al.* 2007; Boyer, Clouse *et al.*
154 2007; Boyer and Giribet 2007; Sharma and Giribet 2009; Murienne, Edgecombe *et al.*
155 2011)

156 COI was PCR amplified using the primer pair LCO1490 (Folmer, Black *et al.*
157 1994) and HCOoutout (Prendini, Weygoldt *et al.* 2005; Schwendinger and Giribet 2005);
158 18S rRNA using primer sets 1F-4R, 4F-18Sbi, and 18Sa2.0-9R (Giribet, Carranza *et al.*
159 1996; Whiting, Carpenter *et al.* 1997) and 28S rRNA with primer sets 28S1F-28Srd4b,
160 28Sa-28sb, and 28Srd4.8a-28Srd7b1 (Park and Ó Foighil 2000; Schwendinger and
161 Giribet 2005; Edgecombe and Giribet 2006). PCR products were visualized in 1%
162 agarose gel electrophoresis, and purified PCR products with the Millipore MultiScreen
163 PCR μ 96 filter plate system (Millipore, Waltham, MA). For the sequencing reaction we
164 used the BigDye (Applied Biosystems) and cleaned unincorporated primers and dye with
165 Performa DTR Plates (Edge Biosystems; Gaithersburg, MD). We analysed the labelled
166 fragments with an ABI Prism 3730xl Genetic Analyzer (Applied Biosystems), and edited
167 the resulting .ab1 files using SEQUENCHER 4.7 (Gene Codes Corporation 2007; Ann
168 Arbor, MI). We visually inspected all fragments, sequenced using both primers, to
169 ascertain ambiguous base calls or detect possible contamination. All sequences were
170 deposited in GenBank and accession numbers are provided (Table 1).

171

172 *Phylogenetic analysis*

173 All file format manipulations were performed with Mesquite (Maddison and Maddison
174 2010), and sequence alignments for the maximum likelihood analyses were performed
175 with MUSCLE 3.7 (Edgar 2004). For the maximum likelihood estimation of
176 phylogenetic trees we used RAxML (Stamatakis 2006). jModeltest (Posada 2009) was
177 used to select the best-fit evolutionary model under the Akaike information criterion
178 (AIC) (Akaike 1974): GTR + gamma + invariant sites (Yang 1993). Bootstrap support
179 values were calculated from 100 replicates. The direct optimization method (Wheeler
180 1996; Wheeler, Aagesen *et al.* 2006) as implemented in POY (Wheeler, Lucaroni *et al.*
181 2014) was used to evaluate trees under the parsimony criterion. The data were partitioned
182 in *a priori* segments to avoid clustering of sequences with missing ends. One of the
183 equally-parsimonious trees was selected for measuring nodal support, and jackknife
184 support was calculated by resampling the data 100 times with a 0.36 probability of
185 deletion. Consensus trees were calculated with the Consense program in the PHYLIP
186 package (Felsenstein 1989), and trees reorganized in FigTree (Rambaut 2011).

187

188

189 **Results and discussion**190 *Monophyly of Neopilionidae*

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

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

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

217 mentioning *Acihasta* Forster, 1948), recognizing variation in the palpal tarsal claw, and
218 Enantiobuninae for the South American species in the genus *Thrasychirus* Simon, 1884.
219
220 Work continued in 1970 with the addition of Megalopsalidinae (Megalopsalinae [sic]
221 which then included the genus *Monoscutum* Forster, 1948) (Martens 1976a), into an
222 sextended Neopilionidae by Šilhavý (1970) (Fig. 1). Later Martens (1976b) raised
223 Megalopsalinae to family level and corrected the name to Megalopsalididae. Two
224 decades later, Hunt and Cokendolpher (1991a) erected the taxon Ballarrinae for *Vibone*
225 Kauri, 1961 (from South Africa) with four new genera: *Ballarra* Hunt & Cokendolpher,
226 1991, *Plesioballarra* Hunt & Cokendolpher, 1991 and *Arrallaba* Hunt & Cokendolpher,
227 1991 (southern Australia), and *Americovibone* Hunt & Cokendolpher, 1991 (southern
228 South America). However, their cladistic morphological analysis did not support
229 monophyly of Neopilionidae (Fig. 1). Monoscutinae and Megalopsalidinae, however,
230 continued to be recognized by subsequent authors, e.g., Hunt (1990b), Hunt and
231 Cokendolpher (1991a), and Taylor (2004b), although the monophyly of Monoscutidae
232 was still based on a single character, the presence of paired lateral bristle groups on the
233 penis at the shaft or glans articulation (Hunt and Cokendolpher 1991a) (of importance is
234 to note that Monoscutidae has previously been incorrectly referred to as
235 Megalopsalididae, before Crawford (1992b) pointed out that the subfamily Monoscutinae
236 had priority over Megalopsalidinae).

237 Up to this point, Monoscutidae thus contained two distinctive subfamilies,
238 Monoscutinae and Megalopsalidinae, Monoscutinae containing three monotypic genera
239 (1) *Monoscutum* Forster, 1948, (2) *Acihasta* Forster, 1948, and (3) *Templar* Taylor, 2008,

240 the latter only recently added (Taylor 2008a), and an undescribed species of an uncertain
241 genus from New South Wales, Australia (Hunt 1990b; Hunt and Cokendolpher 1991a).
242 Megalopsalidinae contained three genera: (1) *Megalopsalis* (13 spp.), (2) *Pantopsalis* (11
243 spp.), and (3) *Spinicrus* (8 spp.) (see Taylor, 2004 for a checklist). In 2011 Taylor
244 synonymised Monoscutidae with Neopilionidae using results from a morphological
245 cladistic analysis that showed Monoscutidae to be nested within Neopilionidae (*Neopilio*
246 + (*Ballara* + Monoscutidae)), and which positioned the Chilean *Thrasychirus* Simon,
247 1884 (Neopilionidae: Enantiobuninae) within Monoscutidae, which, as we have
248 discussed, was up to then a group otherwise wholly constrained within New Zealand and
249 Australia (Taylor 2011). This conclusion, based on a few morphological characters, was
250 not supported in the unweighted parsimony tree, and thus awaited the inclusion of more
251 samples from Neopilionidae and the addition to the analysis of more characters,
252 molecular and morphological (see Taylor 2013 for another analysis with monophyly of
253 Neopilionidae). However, regardless of the sister vs. nested relationship between
254 Neopilionidae and Monoscutidae, the inclusion of *Thrasychirus* within Monoscutidae
255 changed the name of the family or subfamily, wherever a final taxonomic revision lands
256 the ranking, to Enantiobuninae, which has priority (Taylor 2011; Taylor 2013a).

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

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

282 Sørensen (1886) described the first Australian Eupnoi, *Macropsalis serritarsus*,
283 which was later changed to *Megalopsalis* because *Macropsalis* was pre-occupied by a
284 bird genus (Roewer 1923). The description of *Megalopsalis* included a first attempt at
285 characters for inter-generic diagnosis: (1) spines on the ocularium, (2) abdomen shorter

286 than cephalothorax, (3) tibia and patella of palpus of unequal length in *Pantopsalis*, (4)
287 tibia II with pseudoarticulations, and (5) a ramous bifurcation in the patella of the palpus
288 in *Megalopsalis*. All of these, except for the patella of the palpus, were considered
289 plesiomorphic states by later authors (Taylor 2004a; Taylor and Hunt 2009) (but see
290 below for further discussion on the cladistic value of the patella). Pocock (1902b) added
291 *Macropsalis hoggi* Pocock, 1902, *Pantopsalis albipalpis* Pocock, 1902, *P. nigripalpis*
292 Pocock, 1902, and *P. nigripalpis spiculosa* Pocock, 1902, and later (1903a) *P. coronata*
293 Pocock, 1903, *Pantopsalis trippi* Pocock, 1903 and *Pantopsalis jenningsi* Pocock, 1903,
294 followed by Hogg (1909) with *Macropsalis chiltoni* Hogg, 1909, and *Pantopsalis*
295 *tasmanica* Hogg, 1909. Roewer (1911) attempted a first taxonomic grouping with other
296 long-legged Opiliones by including *Megalopsalis* and *Pantopsalis* within the African and
297 Holarctic Phalangiinae, a classification which was quickly discarded by subsequent
298 authors. Species descriptions continued in that century with Hogg (1920) adding
299 *Pantopsalis wattsi* Hogg, 1920, *P. pococki* Hogg, 1920, *P. grayi* Hogg, 1920 and *P. halli*
300 Hogg, 1920. Roewer (1923) added *Pantopsalis continentalis* Roewer, 1923, and later
301 *Macropsalis (Megalopsalis) fabulosa* Grimmett & Phillips, 1932 was also described.
302 Forster (1944b) made the first attempt at a complete revision of the New Zealand and
303 Australian Eupnoi genera, adding several species to *Megalopsalis* without apparently
304 looking into the many species already described in *Pantopsalis*. Despite expressing
305 doubts about the cladistic value of the only remaining diagnostic character separating the
306 *Megalopsalis* from *Pantopsalis*, the ramous patella of the palp, Forster added
307 *Megalopsalis chiltoni* Forster, 1944, *M. chiltoni nigra* Forster, 1944, *M. inconstans*
308 Forster, 1944, *M. tumida* Forster, 1944, *M. triascuta* Forster, 1944, *M. luna* Forster, 1944,

309 *M. marplei* Forster, 1944, and *M. grimmetti* Forster, 1944. Forster also later made the
310 first conjectures about phylogeographic relationships among the described species, and
311 noted the probable close relationship between the New Zealand and Australia opilionid
312 fauna (Forster 1947). A year later, Forster (1948c) also established Monoscutinae
313 (although joined by plesiomorphies), and added two monotypic genera with *Acihasta*
314 *salebrosa* Forster, 1948 and *Monoscutum titirangiensis* Forster, 1948. In the first
315 comprehensive treatment of the Australian monoscutids, Forster (1949b) established
316 Megalopsalinae (as per our historical overview above, later corrected for spelling and
317 upgraded to the family level Megalopsalididae (Martens 1976a).) However, from a
318 family status, Megalopsalididae was later downgraded again under Monoscutidae (Hunt
319 1990a; Hunt and Cokendolpher 1991b; Crawford 1992a). Forster subsequently raised the
320 genus *Spinicrus* Forster, 1949 to distinguish the Australian and New Zealand species,
321 adding *S. camellus* Forster, 1949, *S. stewarti* Forster, 1949, and transferring from
322 *Pantopsalis* both *S. tasmanica* (Hogg 1909) and just based on the published description,
323 *S. continentalis* (Rower 1923). Kauri (1954) and later Hickman (1957) added *S. minus*
324 Kauri, 1954, *S. porongorupensis* Kauri, 1954, *S. thrypticum* Hickman, 1957, and *S.*
325 *nigricans* Hickman, 1957. Back in New Zealand, and again despite doubting the
326 diagnostic value of the palpal patellar character on which the whole classification rested,
327 Forster added *Pantopsalis johnsi* Forster, 1964, *P. mila* Forster, 1964, *P. distincta*
328 Forster, 1964, *P. snaresensis* Forster, 1964 and *P. rennelli* Forster, 1964. In one of the
329 last chapters or the taxonomic history of the group, Taylor revised *Pantopsalis*, adding *P.*
330 *phocator* Taylor, 2004, synonymizing *P. nigripalpis* and *P. jenningsi* (with *P. albipalpis*),
331 *P. trippi* (with *P. coronata*), *P. mila* (with *P. johnsi*), and making the following generic

332 transfers: *Pantopsalis wattsi*, *P. grayi*, *P. distincta* to *Megalopsalis*, and *Megalopsalis*
333 *luna* to *Pantopsalis*. In 2008 Taylor (2008b) added *Megalopsalis linaei* Taylor, 2008,
334 which he later (Taylor 2011) transferred to a new genus, *Tercentenarium* Taylor, 2011.
335 Taylor (2009) then went on to erect the new genus *Neopantopsalis* Taylor, 2009, in an
336 attempt to reorganize *Spinicrus* from geography-based to cladistics, using the following
337 characters for *Neopantopsalis*: raised bumps in the dorsal prosomal plate (only in ‘major’
338 males), the presence of hyperthorped spines on leg I (‘major’ males again), and oblong
339 dorsoventrally flattened glans of the penis; kept *Megalopsalis* defined with the character
340 of the patellar ramification, and added for *Spinicrus* the characters of dorsal margin of the
341 prosoma horizontal rather than sloping, and flattened glans of the penis. Taylor (2009)
342 also added *Neopantopsalis quasimodo* Taylor, 2009, *N. pentheter* Taylor, 2009, *N. psile*
343 Taylor, 2009 and *N. thaumatopios* Taylor, 2009, while noting that probably none of the
344 Australian genera of Monoscutidae, as listed then, formed monophyletic groups. The
345 same reorganization was done for the New Zealand *Megalopsalis*, and all species in the
346 country were either declared *nomina dubia*, synonymized, or transferred to a new genus,
347 *Forsteropsalis* Taylor, 2011, to which one species was subsequently added,
348 *Forsteropsalis pureroa* Taylor, 2013 (Taylor 2011; Taylor 2013a). Left standing were
349 thus: *Forsteropsalis chiltoni* (Hogg, 1910), *F. distincta* (Forster 1964), *F. fabulosa*
350 (Phillipps & Grimmett, 1932), *F. grayi* (Hogg, 1920), *F. grimmetti* (Forster, 1944), *F.*
351 *inconstans* (Forster, 1944), *F. marplei* (Forster, 1944), *F. nigra* (Forster, 1944), *F. wattsi*
352 (Hogg, 1920) and *F. pureroa* Taylor, 2013; with a new Australian species added to
353 *Megalopsalis* based on the patellar character: *M. epizephyros* Taylor, 2011, *M. eremiotis*
354 Taylor, 2011, *M. leptekes* Taylor, 2011, and *M. pilliga* Taylor, 2011.

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

369 Taylor's (2011) morphological cladistic analysis found that none of the then-
370 "neopilionid" genera formed monophyletic groups (although, it must be noted, they did
371 form a clade under the weighted analysis) and based on these results, he synonymised
372 Monoscutidae with Neopilionidae. Our sampling does not allow for a complete resolution
373 of this long-standing controversy (e.g., Šilhavý 1970; Hunt and Cokendolpher 1991a;
374 Taylor 2011), as many key genera were not sampled: e.g. *Neopilio*, some members of
375 Monoscutinae, e.g. *Acihata*, *Monoscutum*, or *Australiscutum*, nor some key genera from
376 Megalopsalidinae: e.g. *Tercentenarium*. However, our results do show that our clade of
377 Australian/New Zealand species does not include the South African *Vibone*, originally

378 described in Neopilionidae (Kauri 1961). Although Hunt and Cokendolpher (1991a)
379 transferred *Vibone* from Neopilioninae to their new subfamily Ballarrinae, our analyses
380 reject this relationship, as *Ballarra* groups with the Australasian clade that includes
381 *Pantopsalis*, *Forsteropsalis*, *Spinicrus*, *Mangatangi*, etc., and does not group with its
382 Neopilionidae clade (Hunt and Cokendolpher 1991a; their figure 4A) or with Ballarrinae
383 (their figure 4B). Our results therefore agree with Taylor's (2011) unweighted
384 morphological cladistic analysis, in that it separates *Ballarra* from the other
385 Neopilionidae (although *Vibone* was not sampled in that study).

386

387 *Broader relationships among the New Zealand + Australia native eupnoids*

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

398

399 *The Megalopsalidinae of New Zealand: a taxonomic overview of *Pantopsalis* and*

400 *Forsteropsalis*

401 The distinction among the genera within the former Monoscutidae has been problematic
402 since the description of each genus (Cokendolpher and Taylor 2007a). For example,
403 when Sørensen (1886) described *Macropsalis* (now *Megalopsalis*), he used as diagnostic
404 characters the spines on the ocularium of *Megalopsalis* vs. smooth in *Pantopsalis*, but
405 since then, many species that now belong in *Megalopsalis* have been described with a
406 smooth ocularium, while some *Pantopsalis* continue to be described with spines (Taylor
407 2004a), and in any case, the character might be variable within species. Another
408 character, that of the opisthosoma being longer than prosoma, has the problem that the
409 opisthosoma is soft and prone to deformation during preservation (Taylor 2004a) and in
410 our observation of freshly collected material from type localities, can vary between molts.
411 The difference in size between the patella and the tibia in *Pantopsalis*, Sørensen's (1886)
412 "*palporum partibus patellari et tibiali sibi longitudine sub aequalibus*", is also of
413 doubtful validity since both characters can vary within species (Hickman 1957, see
414 Taylor, 2004). The last remaining characters are the presence of a spiny process in the
415 patella of the palp (between *Pantopsalis* vs. *Forsteropsalis* and between *Spinicrus* +
416 *Neopantopsalis* and *Megalopsalis*), the number of brushes in the penis between
417 *Forsteropsalis* and *Pantopsalis*, the bowing of the cheliceral claw between *Pantopsalis*
418 vs. *Forsteropsalis*, and a 'triangular dorsolateral keel on the glans, with the apex of the
419 triangle at the distal end of the glans' (Taylor 2011), also between *Forsteropsalis* and
420 *Pantopsalis*. All of these characters are of suspect validity: for example, from Taylor's
421 (2004) illustrations the scoring of abundance of penis bristles seems to be subjective. The
422 palpal patellar structure, also described as a branch (Sørensen's (1886) "*parte patellari*
423 *non ramosa*"), splitting, spur, process (Forster 1944b), or apophysis (Taylor 2004a;

424 Taylor and Hunt 2009), has been especially problematic, since it has been used as the
425 sole basis in the erection of new genera and in the transfer species between genera. For
426 example, using the patellar process as a character, Taylor (2004) transferred Forster's
427 (1964b) *Pantopsalis distincta* to *Megalopsalis distincta* even though the purported female
428 of the species does not have a patellar process, and the purported male only has a small,
429 pointed one. In his key, Forster (1944b) used the apophysis to distinguish among the two
430 genera, but then used this character to assign a female specimen of what otherwise
431 seemed like a typical *Pantopsalis* female to *Megalosalis luna* (Taylor 2011). Two
432 decades later, Forster again described a new species, *Pantopsalis distincta*, and included
433 in the description a female with a "well developed process on the prodistal surface of the
434 patella of the palp" (Forster 1964b), the exact then-synapomorphy for the sympatric
435 *Megalopsalis* (now *Forsteropsalis* for the New Zealand species). Taylor (2004)
436 continued to use this character throughout his revision of *Pantopsalis*, making
437 adjustments as to its shape to assign specimens with a patellar process to *Pantopsalis*.
438 Surprisingly, in Taylor's (2011) own morphology-based cladistic analysis, the patellar
439 process comes as a plesiomorphy. Forster himself had also noted that it might vary within
440 molts of the same individual (Forster 1964b). The distinctive shape of the keel of the
441 glans, the last character state supporting *Pantopsalis* together, was reported as absent in
442 the resurrection of *Pantopsalis cheliferoideis* (Taylor 2013a).

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

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

455

456 *Mangatangi*

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

469 claw in the higher systematics of the group.

470

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

472 This clade includes species originally described as *Pantopsalis* (*P. wattsi* Hogg, 1920),

473 *Forsteropsalis* (*F. pureora* Taylor, 2013) and *Megalopsalis* (*M. turneri* Marples, 1944),

474 but its relationship to the other *Pantopsalis* or *Forsteropsalis* remains unsupported.

475 *Forsteropsalis pureora* Taylor, 2013 (Note: The species is referred to as *F. pureroa* in the

476 abstract and figure captions of the original description) was described by Taylor (2013a)

477 based on a single male specimen from Waipapa Reserve, Pureora, which matches our

478 specimens from Te Urewera National Park (MCZ 29240), but this species also closely

479 matches the description of another North Island species, *Forsteropsalis inconstans*

480 (Forster 1944b), a species with a problematic history that starts with an original

481 description that included specimens from three different species (Forster 1944b; Taylor

482 2011), and a striking similarity to *Forsteropsalis nigra* (Forster 1944) except for a few

483 small red markings on the propeltidium (Taylor 2011). *Forsteropsalis inconstans* also has

484 the same coloration pattern (the “white” markings in the preserved animals of Forster and

485 Taylor are orange in living specimens), from which Taylor distinguished in “not having

486 the posterior part of the propeltidium and the mesopeltidium heavily denticulate”, while

487 also mentioning how *F. pureora* can be confused with *F. distincta*, *F. chiltoni*, *F.*

488 *marplei* and *F. wattsi*.

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

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

508 *Pantopsalis*: *The listeri* group

509 The remaining samples of *Pantopsalis* constitute a clade including specimens from
510 Southland to Te Urewera N.P. This clade includes dark species (black carapace) with a

511 brown to reddish pigmented pedipalpal femur (from half to most of its length), not pink,
512 the rest of the pediplap being white. It also includes specimens with black opisthosomas
513 or with different degrees of a white-silver strip in the intercalary membrane of the
514 opisthosomal tergites.

515 Our analyses identify two main clades of specimens similar to *P. listeri* (White,
516 1849). Taylor (2013b) provides a redescription and a discussion of this species, based on
517 examination of a neotype from the MNHN, Paris, and uses Simon (1879b) concept of the
518 species, adding the following to the description “Dorsum of opisthosoma with pale
519 silvery, narrow, transverse stripes on posterior margins of segments”, illustrated in a live
520 specimen photographed by Simon Pollard (of unspecified precedence). We have
521 observed such transverse stripes with a large degree of variation, from very broad in
522 specimens from Kahurangi N.P. and Arthur’s Pass N.P. to less conspicuous in Westland
523 Tai Puitini N.P. and Te Urewera N.P., or totally absent in Mount Aspiring N.P. (see
524 Fernández et al., submitted). Taylor (2013b) also illustrated *P. cheliferooides* (Colenso
525 1882a), the only *Pantopsalis* reported from the North Island, an animal similar in
526 morphology to some of the “*listeri*” morphotypes with swollen chelicera, similar to some
527 of our specimens from Kahurangi N.P. and Mount Aspiring N.P.. Many of these localities
528 find astonishing disparity in cheliceral size and shape, or in the banding pattern of the
529 opisthosoma, despite belonging to the same clade. Our two clades of “*listeri*” include (1)
530 specimens from the North and South Islands: Te Urewera N.P., Wellington, Kahurangi
531 N.P., Arthur’s Pass N.P., and a female from Waimate, spanning almost the whole
532 country, which we assign to *P. cheliferooides* following Taylor (2013b); and (2) specimens
533 from Mt. Aspiring N.P., and Westland Tai Puitini N.P., of much more restricted

534 geographical distribution, with smoother ocularium, which we assign to *P. listeri*. The
535 original description of *P. listeri* is inaccurate, and no types or type locality exist, although
536 the species was probably based on specimens from the North Island. However, Simon
537 (1879b) designated a neotype from Westland-Tai Poutini, and we follow Taylor (2013b)
538 with respect to the stability of the type of the genus.

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

551 *Pantopsalis albipalpis* Pocock, 1903b is another dark species with the clear palps
552 from the South Island, described based on specimens from near Dunedin (Pocock 1903b),
553 including multiple synonymies, such as *Pantopsalis nigripalpis* Pocock, 1903b, *P.*
554 *nigripalpis spiculosa* Pocock, 1903b and *P. jenningsi* Pocock, 1903a; all synonymised by
555 Taylor (2004b). It is unlikely that *P. albipalpis* would remain as a valid species. name for
556 the South Island. Taylor (2013b) appealed to the criterion of stability to assign *P. listeri*

557 to the MNHN specimens examined by Simon from Westland, and thus we use the name
558 *P. listeri* for our restricted clade, including specimens from Westland-Tai Poutini and Mt.
559 Aspiring N.P.

560 *Pantopsalis albipalpis* Pocock, 1903b is another dark species with the clear palps
561 from the South Island, described based on specimens from near Dunedin (Pocock 1903b),
562 including multiple synonymies, such as *Pantopsalis nigripalpis* Pocock, 1903b, *P.*
563 *nigripalpis spiculosa* Pocock, 1903b and *P. jenningsi* Pocock, 1903a; all synonymised by
564 Taylor (2004b). It is unlikely that *P. albipalpis* would remain as a valid species. While
565 the genetic diversity of *P. phocator* was relatively high, both *P. cheliferooides* and *P.*
566 *listeri* showed a low percentage of pairwise differences (0.5%) and medium to low levels
567 of haplotypic and nucleotidic diversity.

568

569 *A discussion of the distinctions between Forsteropsalis and Pantopsalis*

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

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

581

582 *Forsteropsalis*

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

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

594

595 *Forsteropsalis fabulosa*

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

604

605 *Forsteropsalis chiltoni*

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

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

619

620 *Forsteropsalis inconstans*

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

629 Originally *F. nigra* was described as a subspecies of *F. chiltoni*, which had the red
630 markings on the carapace. Forster (1944a) described *Megalopsalis inconstans* Forster,
631 1944 based on a female specimen. In the same paper he described *Megalopsalis chiltoni*
632 *nigra* Forster, 1944, based on two male specimens, a subspecies that was elevated to
633 species by Taylor (2011). Our analyses clearly show that the red markings vary with
634 specimens and thus we consider both names to be co-specific. Since *Megalopsalis*
635 *inconstans* was published as a species and *M. chiltoni nigra* as a subspecies, the former
636 name takes priority. We thus consider *Forsteropsalis nigra* a junior synonym of
637 *Forsteropsalis inconstans* (**new synonymy**).

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

642

643 **Conclusions**

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

652

653 **Figure and table captions**

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

660

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

666

667

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

675

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

680

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

684

685 **Figure 6.** Phylogenetic relationships based on a tree selected under the maximum
686 likelihood criterion, with tree search strategy as implemented in RAxML. Numbers above
687 branches indicate bootstrap support values after 100 replicates. Only bootstrap values
688 >50% are presented.

689

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

698

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

703

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

711

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

717

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

720

721

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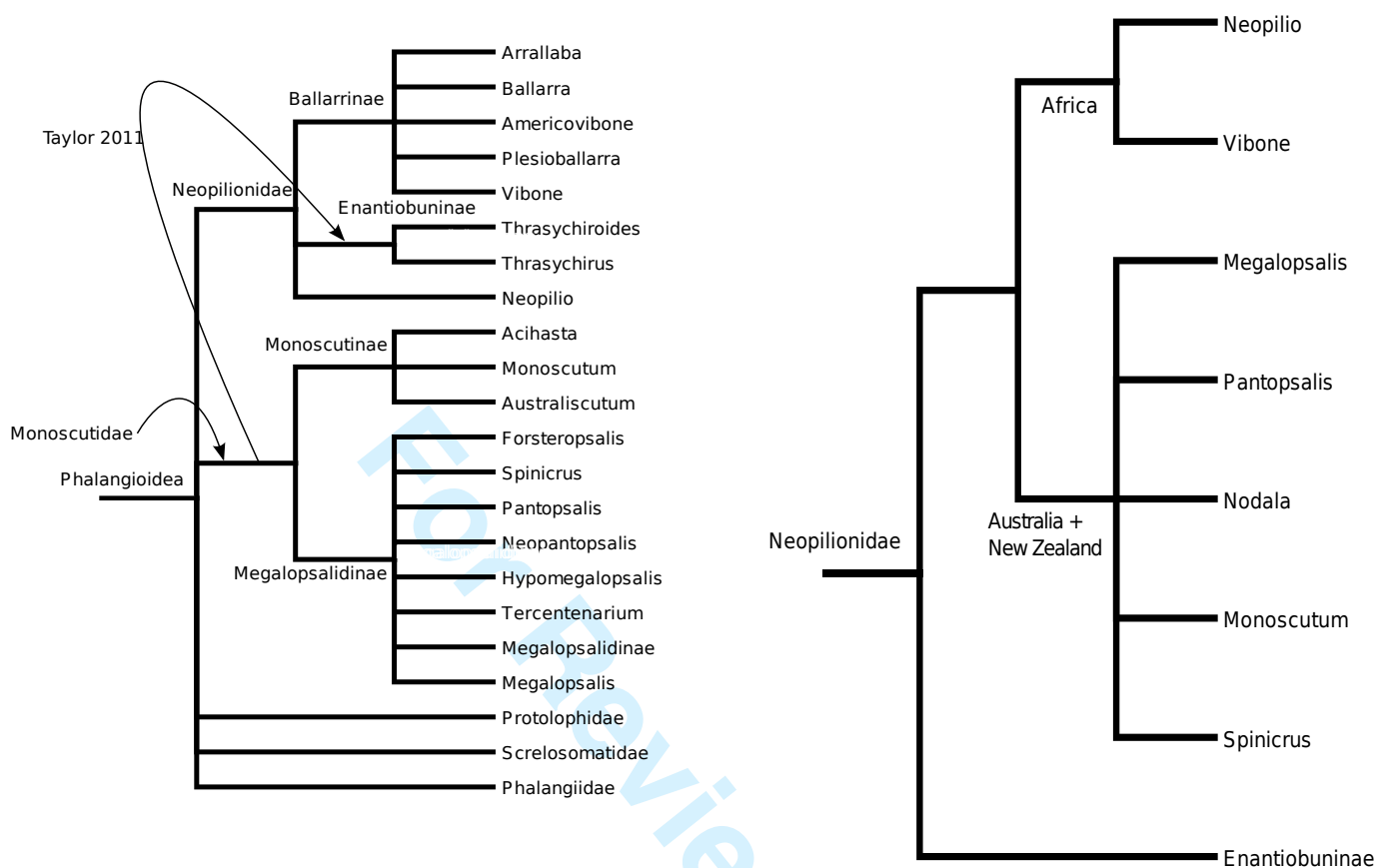
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1100
- 1101 White, A. (1849b) Descriptions of apparently new species of Aptera from New Zealand.
1102 *Proceedings of the Zoological Society of London* **17**, 3-6.
1103

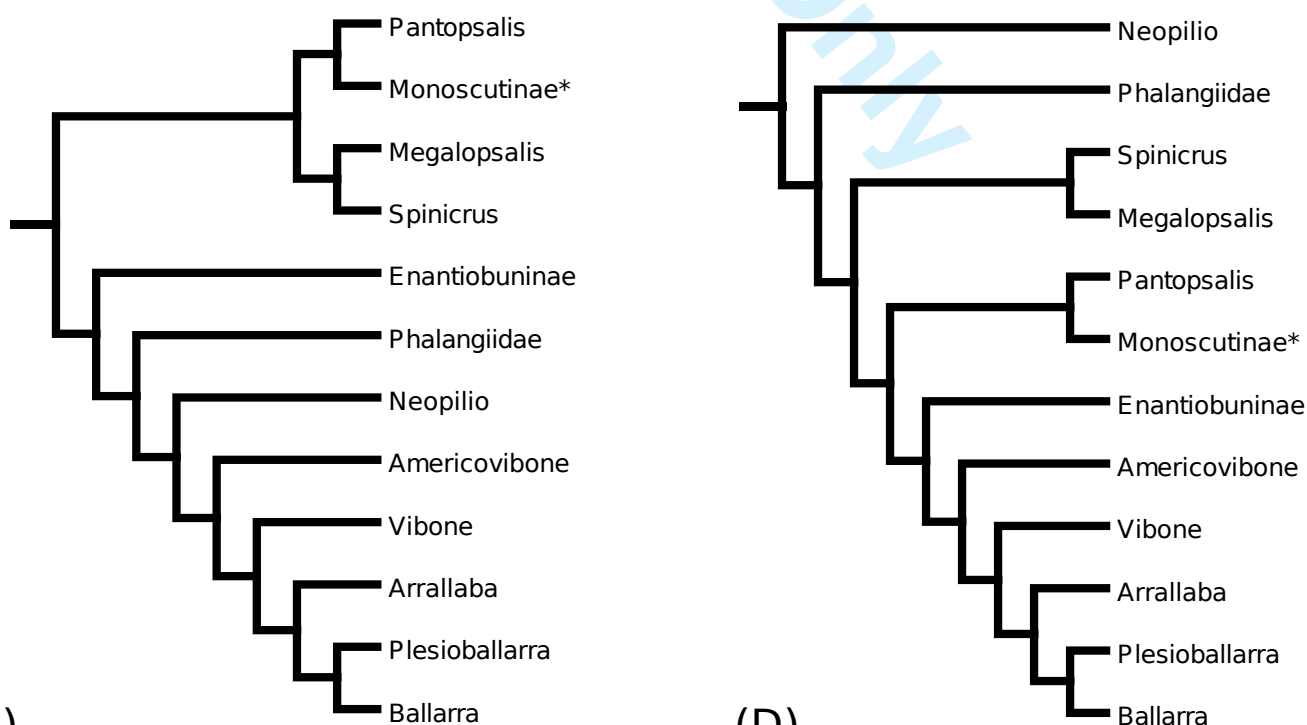
- 1104 Whiting, M.F., Carpenter, J.M., Wheeler, Q.D., and Wheeler, W.C. (1997) The
1105 Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S
1106 and 28S ribosomal DNA sequences and morphology. *Systematic Biology* **46**, 1-68.
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1109 when substitution rates differ over sites. *Molecular Biology and Evolution* **10**, 1396-1401.
1110
1111
1112

For Review Only



(A)

(B)



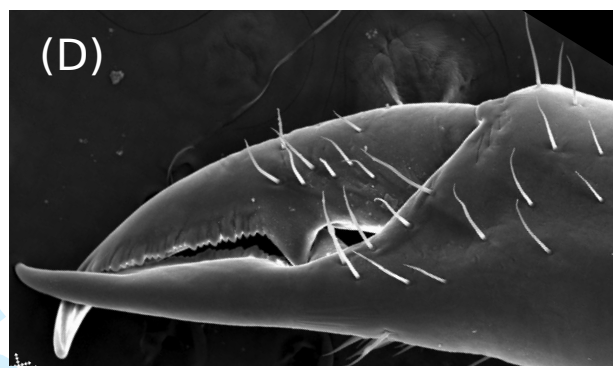
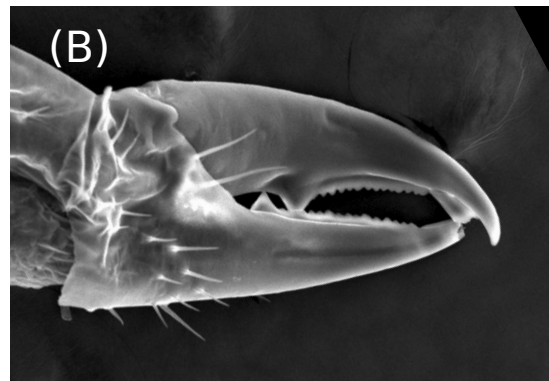
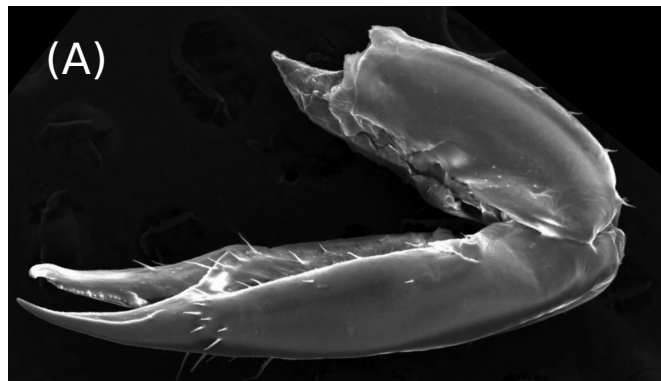
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(D)

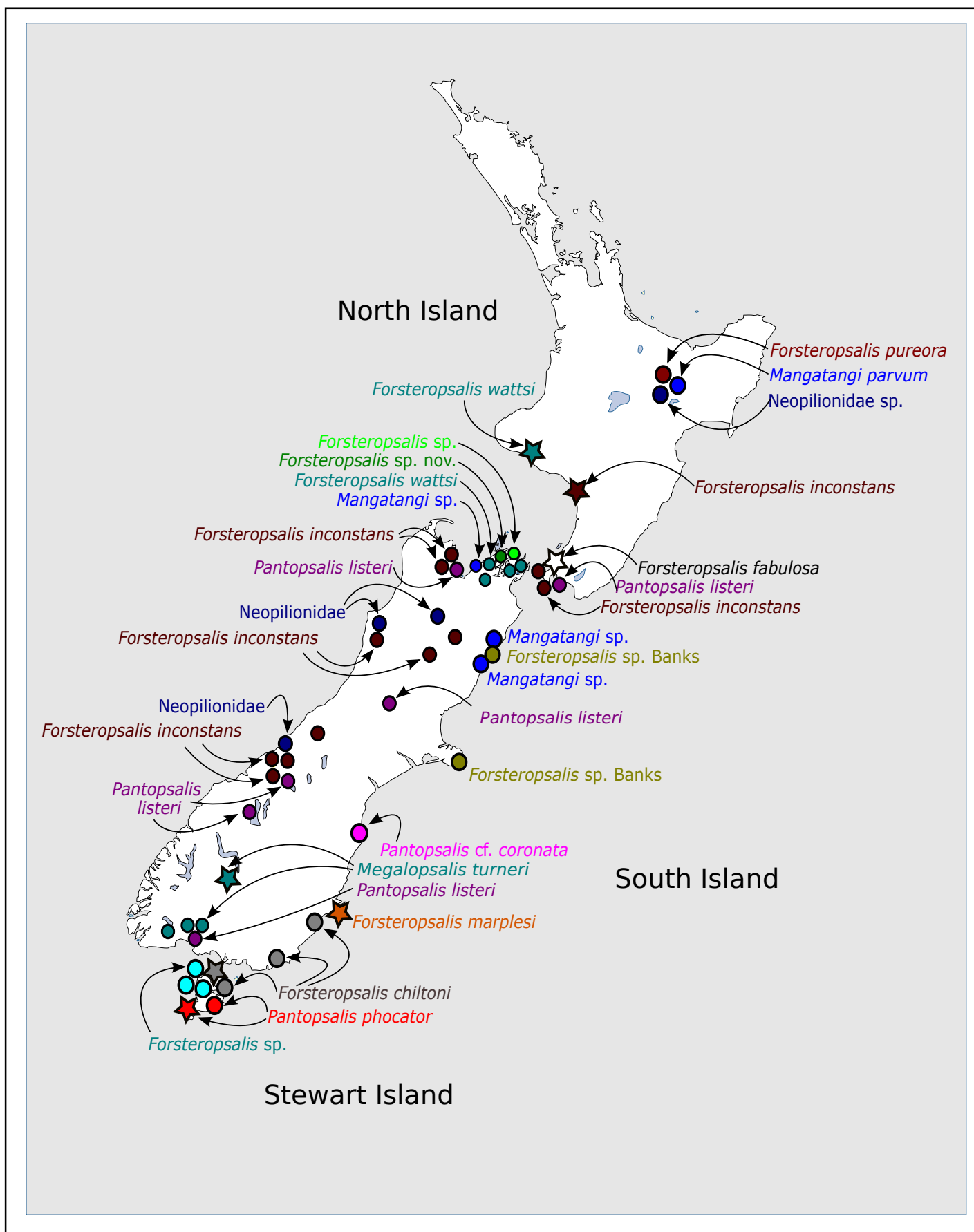


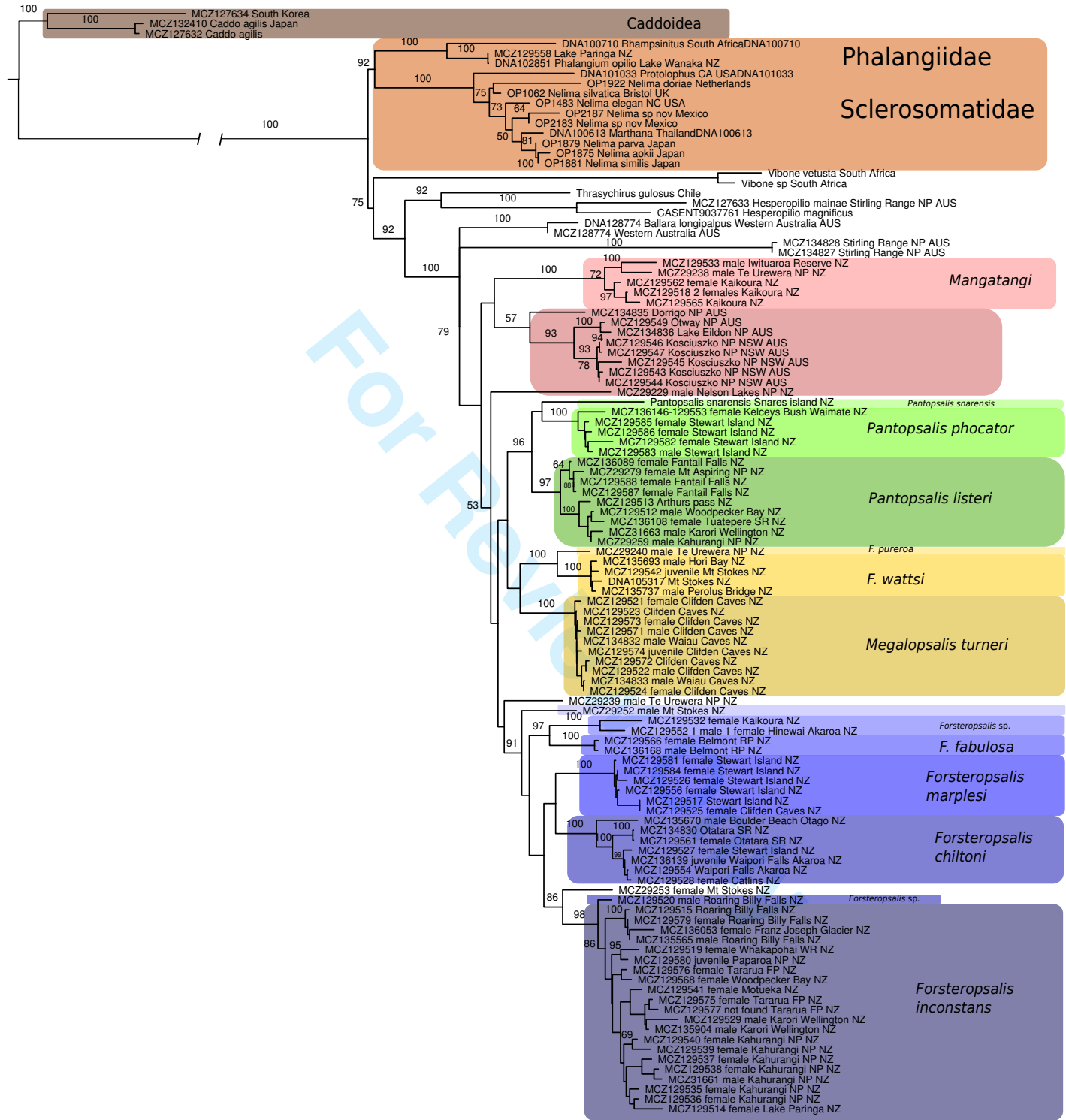
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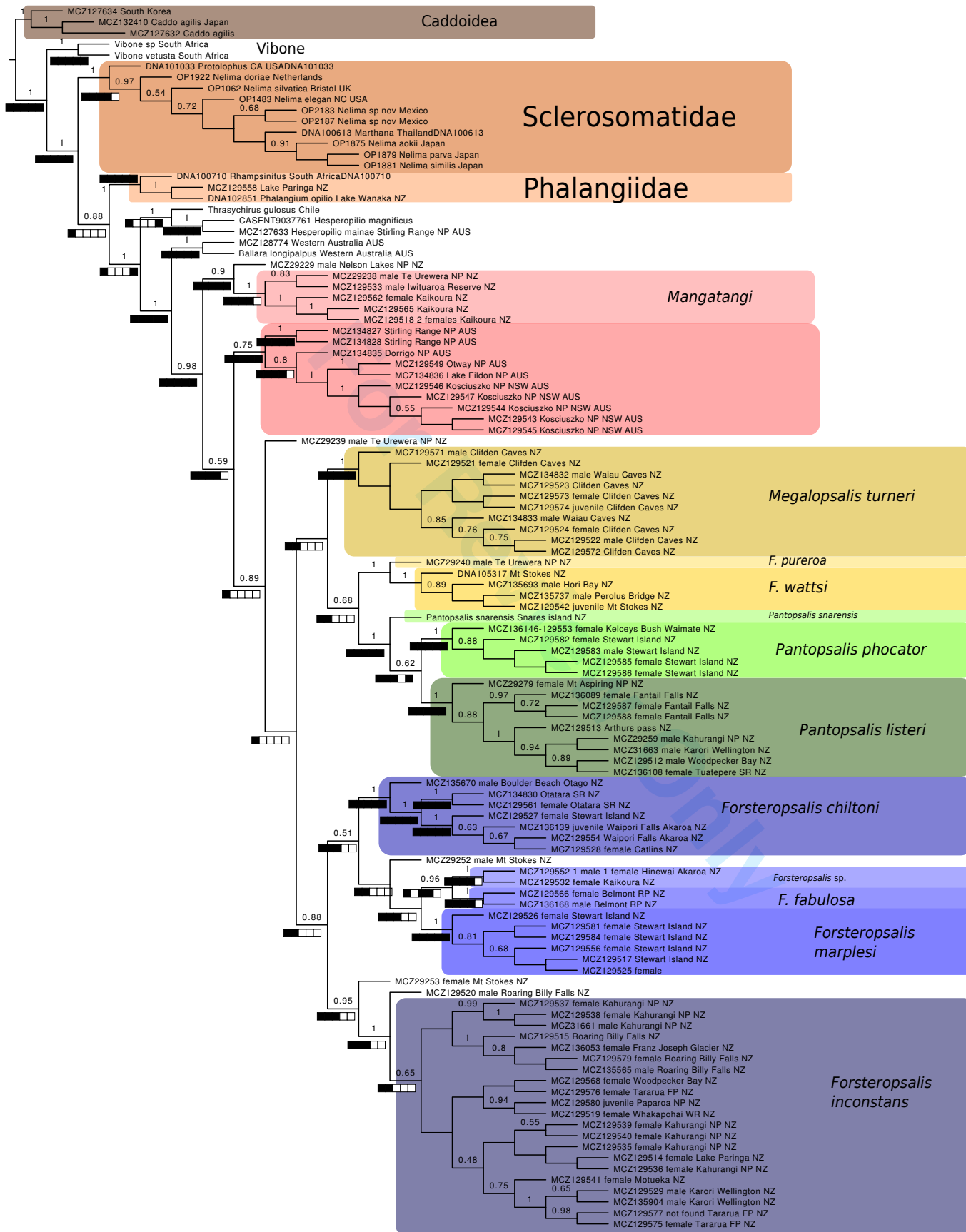


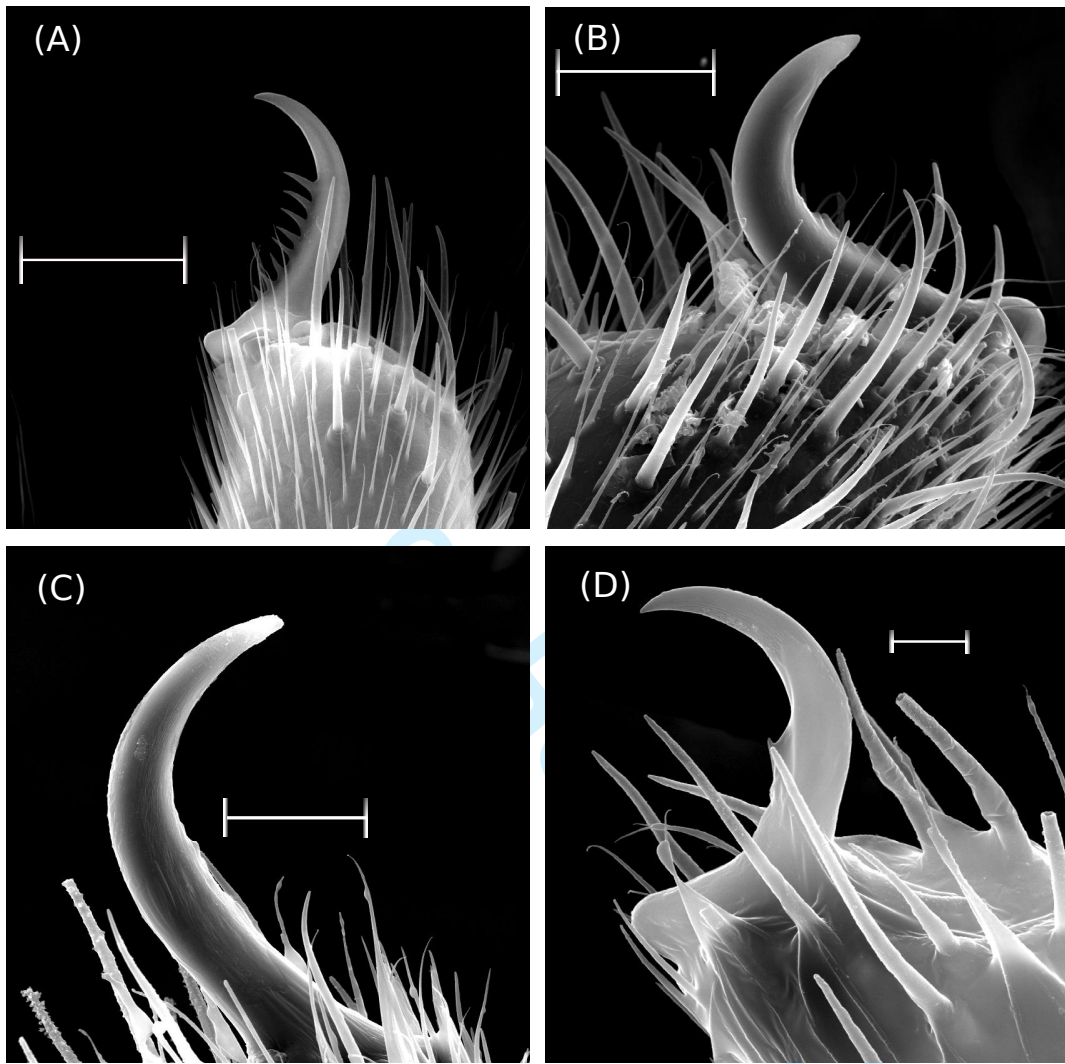


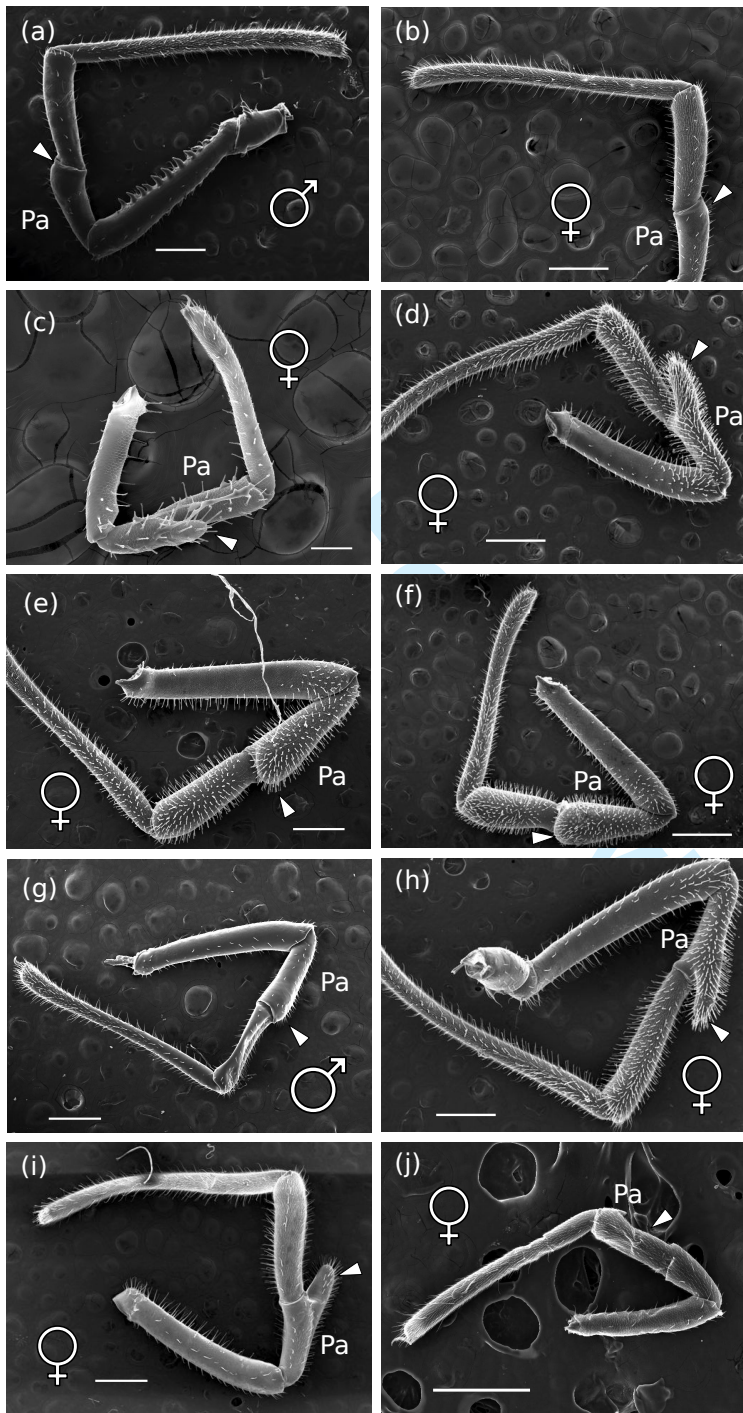
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Voucher	Descriptor	Locality	Other catalog number / Reference	Lat	Long
AH.001078	<i>Pantopsalis snar</i>	Snares Island, NZ	n/a	-8.0205	166.6113
CASENT-90:	<i>Hesperopilio magnificus</i>		from Giribet and Groh (unpublished)		
MCZ127632	<i>Caddo agilis</i>	unknown	from Giribet and Groh (unpublished)	unknown	unknown
MCZ127633	<i>Hesperopilio ma</i>	Stirling Range NP	from Giribet and Groh (unpublished)	-34.3750	118.2567
MCZ127634	<i>Caddo pepperell</i>	South Korea	n/a	35.2758	127.6178
MCZ128774	<i>Ballara</i> sp	Western Australia	DNA128774	-32.6000	116.2000
MCZ129512	<i>Pantopsalis</i> sp	Woodpecker Bay	NDNA102786	-42.2172	171.3897
MCZ129513	<i>Pantopsalis</i> sp	Arthurs pass NZ	DNA102800	-43.2669	171.7097
MCZ129514	<i>Forsteropsalis</i> s	Lake Paringa NZ	DNA102823	-43.595	169.8247
MCZ129515	<i>Forsteropsalis</i> s	Roaring Billy Falls	DNA102840	-43.2989	169.2881
MCZ129517	<i>Forsteropsalis</i> s	Stewart Island NZ	DNA102882	-46.6647	168.2350
MCZ129518	<i>Mangatangi</i> sp	Kaikoura NZ	DNA102921	-42.0539	173.4006
MCZ129519	<i>Forsteropsalis</i> s	Whakapohai WR	NDNA105050	-43.56	169.0811
MCZ129520	<i>Forsteropsalis</i> s	Roaring Billy Falls	DNA105051	-43.2806	169.5097
MCZ129521	<i>Megalopsalis tur</i>	Clifden Caves NZ	DNA105144	-46.0919	167.4972
MCZ129522	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105146	-46.0919	167.4972
MCZ129523	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105149	-46.0919	167.4972
MCZ129524	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105150	-46.0919	167.4972
MCZ129525	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105152	-46.0919	167.4972
MCZ129526	<i>Forsteropsalis</i> s	Stewart Island NZ	DNA105153	-46.8347	168.5381
MCZ129527	<i>Forsteropsalis</i> s	Stewart Island NZ	DNA105162	-46.8347	168.5381
MCZ129528	<i>Forsteropsalis</i> s	Catlins NZ	DNA105197	-46.4128	169.8039
MCZ129529	<i>Forsteropsalis</i> s	Karori Wellington	DNA105355	-41.0661	174.5325
MCZ129532	<i>Forsteropsalis</i> s	Kaikoura NZ	DNA104787	-42.8953	173.3422
MCZ129533	<i>Mangatangi</i> sp	Iwituaroa Reserve	DNA105971	-41.8508	173.2486
MCZ129535	<i>Forsteropsalis</i> s	Kahurangi NP NZ	DNA105973	-41.4081	172.4922
MCZ129536	<i>Forsteropsalis</i> s	Kahurangi NP NZ	DNA105974	-41.4081	172.4922
MCZ129537	<i>Forsteropsalis</i> s	Kahurangi NP NZ	DNA105975	-41.4081	172.4922
MCZ129538	<i>Forsteropsalis</i> s	Kahurangi NP NZ	DNA105976	-41.4081	172.4922
MCZ129539	<i>Forsteropsalis</i> s	Kahurangi NP NZ	DNA105978	-41.4081	172.4922
MCZ129540	<i>Forsteropsalis</i> s	Kahurangi NP NZ	DNA105979	-41.4081	172.4922
MCZ129541	<i>Forsteropsalis</i> s	Motueka NZ	DNA105980	-41.8064	172.3867
MCZ129542	<i>Forsteropsalis</i> s	Mt Stokes NZ	DNA105981	-41.2031	174.2922
MCZ129543	<i>Spinicrus</i> sp	Kosciuszko NP NS	DNA105982	-36.0825	148.7389
MCZ129544	<i>Spinicrus</i> sp	Kosciuszko NP NS	DNA105983	-36.0825	148.7389
MCZ129545	<i>Spinicrus</i> sp	Kosciuszko NP NS	DNA105984	-36.0825	148.7389
MCZ129546	<i>Spinicrus</i> sp	Kosciuszko NP NS	DNA105985	-36.0825	148.7389
MCZ129547	<i>Spinicrus</i> sp	Kosciuszko NP NS	DNA105986	-36.0825	148.7389
MCZ129549	<i>Spinicrus</i> sp	Otway NP AUS	DNA105988	-38.1786	143.7928
MCZ129552	<i>Forsteropsalis</i> s	Hinewai Akaroa NZ	DNA102910	-43.6967	173.7053
MCZ129554	<i>Forsteropsalis</i> s	Waipori Falls Akar	DNA102901	-45.2983	169.2831
MCZ129556	<i>Forsteropsalis</i> s	Stewart Island NZ	DNA102897	-46.9147	168.0017
MCZ129558	<i>Phalangium opil</i>	Lake Paringa NZ	DNA102825	-43.71	169.4970
MCZ129561	<i>Forsteropsalis</i> s	Otatara SR NZ	DNA100784	-46.0072	168.0049

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MCZ129562	<i>Mangatangi</i> sp	Kaikoura NZ	DNA102915	-42.6878	173.7469
MCZ129565	<i>Mangatangi</i> par	Kaikoura NZ	DNA102919	-42.8953	173.3422
MCZ129566	<i>Forsteropsalis</i> s	Belmont RP NZ	DNA102929	-41.3492	174.9275
MCZ129568	<i>Forsteropsalis</i> s	Woodpecker Bay NZ	DNA104785	-42.2172	171.3897
MCZ129571	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105147	-46.0919	167.4972
MCZ129572	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105148	-46.0919	167.4972
MCZ129573	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105145	-46.0919	167.4972
MCZ129574	<i>Forsteropsalis</i> s	Clifden Caves NZ	DNA105151	-46.0919	167.4972
MCZ129575	<i>Forsteropsalis</i> s	Tararua FP NZ	DNA105528	-40.2828	175.8169
MCZ129576	<i>Forsteropsalis</i> s	Tararua FP NZ	DNA105527	-40.2828	175.8169
MCZ129577	<i>Forsteropsalis</i> s	Tararua FP NZ	DNA105526	-40.2828	175.8169
MCZ129578	<i>Forsteropsalis</i> s	Mt Stokes NZ	DNA105317	-41.09	174.1381
MCZ129579	<i>Forsteropsalis</i> s	Roaring Billy Falls	DNA105056	-43.2806	169.5097
MCZ129580	<i>Forsteropsalis</i> s	Paparoa NP NZ	DNA105029	-42.555	171.5556
MCZ129581	<i>Forsteropsalis</i> s	Stewart Island NZ	DNA104789	-46.9147	168.0017
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MCZ129583	<i>Pantopsalis</i> sp	Stewart Island NZ	DNA104792	-46.9147	168.0017
MCZ129584	<i>Forsteropsalis</i> s	Stewart Island NZ	DNA104793	-46.9147	168.0017
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MCZ134833	<i>Forsteropsalis</i> s	Waiiau Caves NZ	DNA100785	-46.0003	167.0123
MCZ134835	<i>Spinicrus</i> sp	Dorrigo NP AUS	DNA105989	-30.0644	152.7186
MCZ134836	<i>Spinicrus</i> sp	Lake Eildon NP AU	DNA105990	-37.6586	146.0931
MCZ134862	<i>Marthana</i> sp.	Thailand	DNA100613 from Giribet et al 2010	unknown	unknown
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MCZ135737	<i>Forsteropsalis</i> s	Perolus Bridge NZ	DNA105280	-41.9264	173.3761
MCZ135904	<i>Forsteropsalis</i> s	Karori Wellington I	DNA105459	-41.4364	174.1625
MCZ136053	<i>Forsteropsalis</i> s	Franz Joseph Glaci	DNA102811	-43.5403	170.0694
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MCZ136092	<i>Phalangium opil</i>	Lake Wanaka NZ	DNA102851	-44.40	169.1873
MCZ136108	<i>Pantopsalis</i> sp	Tuatepere SR NZ	DNA102868	-46.5683	167.4114
MCZ136139	<i>Forsteropsalis</i> s	Waipori Falls Akaroa	DNA102900	-45.2983	169.2831
MCZ136146	<i>Pantopsalis</i> sp	Waimate NZ	DNA102907	-44.70	170.9675
MCZ136168	<i>Forsteropsalis</i> s	Belmont RP NZ	DNA105996	-41.3492	174.9275
MCZ29229	<i>Neopilionidae</i> s	Nelson Lakes NP NZ	n/a	-41.82	172.8079
MCZ29238	<i>Mangatangi</i> sp	Te Urewera NP NZ	n/a	-38.7254	177.1650
MCZ29239	<i>Neopilionidae</i> s	Te Urewera NP NZ	n/a	-38.7273	177.1652
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MCZ29252	<i>Forsteropsalis</i> s	Mt Stokes NZ	n/a	-41.09	174.1382

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OP1152	<i>Thrasychirus gui</i>	Chiloe, CHILE	from Hedin et al 2012		
OP1483	<i>Nelima elegans</i>	North Carlina USA	from Hedin et al 2012		
OP1875	<i>Nelima aokii</i>	Honshu JAPAN	from Hedin et al 2012		
OP1879	<i>Nelima parva</i>	Shikoku JAPAN	from Hedin et al 2012		
OP1881	<i>Nelima similis</i>	Honshu JAPAN	from Hedin et al 2012		
OP1922	<i>Nelima doriae</i>	NETHERLANDS	from Hedin et al 2012		
OP2183	<i>Nelima</i> sp nov	Oaxaca, MEXICO	from Hedin et al 2012		
OP2187	<i>Nelima</i> sp nov	Oaxaca, MEXICO	from Hedin et al 2012		

Sheet 1

Genbank

Collector	Voucher	Date	COI	18S	28S
A. Kusabs		3.XII.2013	KJ920342	--	--
Prashant	http://tr	2000	--	KF963312.1	KF955599.1
Michael F	http://tr	24.V.2011	--	KF963310.1	KF955597.1
Mark S. F	http://tr	20.06.2010	--	KF963313.1	KF955600.1
M. Lythe	http://tr	30.VII.2013	KJ871355	KJ871431	KJ871516
G. Giribet	http://tr	12.II.2008	KJ871372	KJ871432	KJ871579
G. Giribet	http://tr	13.II.2008	KJ871362	KJ871433	KJ871580
G. Giribet	http://tr	15.II.2008	KJ871366	KJ871434	KJ871517
G. Giribet	http://tr	15.II.2008	KJ871364	KJ871435	KJ871518
G. Giribet	http://tr	17.II.2008	KJ871373	KJ871436	KJ871519
P. Paquin	http://tr	20.II.2008	KJ871395	KJ871437	KJ871572
S. Velez	http://tr	23.XII.2009	KJ871404	KJ871438	KJ871520
S. Velez	http://tr	24.XII.2009	KJ871413	KJ871439	KJ871521
S. Velez	http://tr	27.XII.2009	KJ871406	KJ871440	KJ871522
S. Velez	http://tr	27.XII.2009	KJ871415	KJ871441	KJ871523
S. Velez	http://tr	27.XII.2009	KJ871423	KJ871442	KJ871524
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S. Velez	http://tr	27.XII.2009	KJ871409	--	--
S. Velez	http://tr	28.XII.2009	KJ871410	KJ871444	KJ871526
S. Velez	http://tr	28.XII.2009	KJ871411	KJ871445	KJ871527
S. Velez	http://tr	29.XII.2009	KJ871412	KJ871446	KJ871528
S. Velez	http://tr	7.I.2010	KJ871420	KJ871447	KJ871529
P. Paquin	http://tr	20.II.2008	KJ871397	KJ871448	KJ871530
N. Scharf	http://tr	10.III.2010	KJ871386	KJ871449	KJ871573
N. Scharf	http://tr	7.III.2010	KJ871402	KJ871450	KJ871531
N. Scharf	http://tr	7.III.2010	KJ871392	KJ871451	KJ871532
N. Scharf	http://tr	7.III.2010	KJ871428	KJ871452	KJ871533
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P. Paquin	http://tr	19.II.2008	KJ871399	KJ871464	KJ871539
G. Giribet	http://tr	17.II.2008	KJ871375	KJ871465	KJ871540
G. Giribet	http://tr	17.II.2008	KJ871376	KJ871466	KJ871541
Gonzalo C	http://tr	15.II.2008	KJ871363	KJ871467	KJ871593
C.J. Vink	http://tr	4.X.2002	KJ871356	--	KJ871542

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G. Giribet	http://tr 12.II.2008	KJ871369	KJ871470	KJ871544
S. Velez	http://tr 27.XII.2009	KJ871416	KJ871471	KJ871545
S. Velez	http://tr 27.XII.2009	KJ871422	KJ871472	KJ871546
S. Velez	http://tr 27.XII.2009	KJ871407	KJ871473	KJ871547
S. Velez	http://tr 27.XII.2009	KJ871403	KJ871474	KJ871548
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S. Velez	http://tr 9.I.2010	KJ871390	KJ871476	KJ871550
S. Velez	http://tr 9.I.2010	KJ871426	KJ871477	KJ871551
Sebastián	http://tr 6.I.2010	KJ871425	--	KJ871552
S. Velez	http://tr 24.XII.2009	KJ871405	KJ871478	KJ871553
S. Velez	http://tr 21.XII.2009	KJ871424	KJ871479	KJ871554
G. Giribet	http://tr 17.II.2008	KJ871378	KJ871480	KJ871555
G. Giribet	http://tr 17.II.2008	KJ871379	KJ871481	KJ871581
G. Giribet	http://tr 17.II.2008	KJ871383	KJ871482	KJ871582
G. Giribet	http://tr 17.II.2008	KJ871380	KJ871483	KJ871556
G. Giribet	http://tr 17.II.2008	KJ871381	KJ871484	KJ871583
G. Giribet	http://tr 17.II.2008	KJ871382	KJ871485	KJ871584
G. Giribet	http://tr 15.II.2008	KJ871370	KJ871486	KJ871585
G. Giribet	http://tr 15.II.2008	KJ871371	KJ871487	KJ871586
Sarah L. F	http://tr 13.IV.2005	--	KF963309.1	KF955596.1
Benjamin	http://tr 5.XI.2011	--	KJ871488	KJ871605
Benjamin	http://tr 7.XI.2011	--	--	--
Gonzalo C	http://tr 9.IV.2011	GQ912862.1	GQ912708.1	GQ912757.1
Michael F	http://tr 20.V.2011	--	KJ871489	KJ871601
Michael F	http://tr 20.V.2011	--	KJ871490	KJ871602
C.J. Vink	http://tr 4.X.2002	KJ871358	KJ871491	KJ871557
C.J. Vink	http://tr 5.X.2002	EF108587	KJ871492	KJ871558
C.J. Vink	http://tr 5.X.2002	KJ871357	--	KJ871559
N. Scharf	http://tr 19.XII.2010	KJ871384	KJ871493	KJ871603
N. Scharf	http://tr 25.XII.2010	KJ871353	KJ871494	KJ871604
David Lol	http://tr 2002	GQ912863.1	GQ912711.1	GQ912762.1
S. Velez	http://tr 24.XII.2009	KJ871414	KJ871495	KJ871560
S. Velez	http://tr 31.XII.2009	KJ871417	--	KJ871561
S. Velez	http://tr 4.I.2010	KJ871418	KJ871496	KJ871562
S. Velez	http://tr 5.I.2010	KJ871419	KJ871497	KJ871563
S. Velez	http://tr 7.I.2010	KJ871421	KJ871498	KJ871564
G. Giribet	http://tr 14.II.2008	KJ871365	KJ871499	KJ871565
G. Giribet	http://tr 15.II.2008	KJ871367	KJ871500	KJ871587
Gonzalo C	http://tr 15.II.2008	KJ871385	KJ871501	KJ871594
G. Giribet	http://tr 16.II.2008	KJ871368	KJ871502	KJ871588
G. Giribet	http://tr 17.II.2008	KJ871374	KJ871503	KJ871566
Gonzalo C	http://tr 18.II.2008	KJ871377	KJ871504	KJ871589
P. Paquin	http://tr 21.II.2008	KJ871398	KJ871505	KJ871567
Rosa Fern	http://tr 16.I.2014	KJ870048	KJ871506	KJ871578
Rosa Fern	http://tr 12.I.2014	KJ870092	KJ871507	KJ871576
Rosa Fern	http://tr 12.I.2014	KJ870062	KJ871508	KJ871577
Rosa Fern	http://tr 12.I.2014	KJ870056	KJ871509	KJ871568
Rosa Fern	http://tr 14.I.2014	KJ870093	KJ871510	KJ871569

Sheet 1

Rosa Fern http://tr	14.I.2014	KJ870083	KJ871511	KJ871570
Rosa Fern http://tr	15.I.2014	KJ870071	KJ871512	KJ871590
Rosa Fern http://tr	20.I.2014	KJ870080	KJ871513	KJ871591
N. Scharf http://tr	7.III.2010	KJ871354	KJ871514	KJ871571
J. Derraik http://tr	16.I.2002	GQ912861	KJ871515	KJ871592
		--	--	JQ437120
		--	JQ437009	JQ437101
		--	JQ437025	JQ437135
		JQ437212	JQ437026	JQ437141
		JQ437213	JQ437027	JQ437143
		JQ437214	JQ437028	JQ437144
		JQ437210	JQ437016	JQ437117
		--	JQ437049	JQ437177
		--	JQ437046	--
