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A molecular phylogeny of the circum-Antarctic Opiliones family Neopilionidae

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Abstract. The Opiliones family Neopilionidae is restricted to the terranes of the former temperate Gondwana: South America, Africa, Australia, New Caledonia and New Zealand. Despite decades of morphological study of this unique fauna, it has been difficult reconciling the classic species of the group (some described over a century ago) with recent cladistic morphological work and previous molecular work. Here we attempted to investigate the pattern and timing of diversification of Neopilionidae by sampling across the distribution range of the family and sequencing three markers commonly used in Sanger-based approaches (*18S* rRNA, *28S* rRNA and cytochrome-*c* oxidase subunit I). We recovered a well-supported and stable clade including *Ballarra* (an Australian ballarrine) and the Enantiobuninae from South America, Australia, New Caledonia and New Zealand, but excluding *Vibone* (a ballarrine from South Africa). We further found a division between West and East Gondwana, with the South American *Thrasychirus*/*Thrasychiroides* always being sister group to an Australian–Zealandian (i.e. Australia + New Zealand + New Caledonia) clade. Resolution of the Australian–Zealandian taxa was analysis-dependent, but some analyses found *Martensopsalis*, from New Caledonia, as the sister group to an Australian–New Zealand clade. Likewise, the species from New Zealand formed a clade in some analyses, but *Mangatangi* often came out as a separate lineage from the remaining species. However, the Australian taxa never constituted a monophyletic group, with *Ballarra* always segregating from the remaining Australian species, which in turn constituted 1–3 clades, depending on the analysis. Our results identify several generic inconsistencies, including the possibility of *Thrasychiroides* nested within *Thrasychirus*, *Forsteropsalis* being paraphyletic with respect to *Pantopsalis*, and multiple lineages of *Megalopsalis* in Australia. In addition, the New Zealand *Megalopsalis* need generic reassignment: *Megalopsalis triascuta* will require its own genus and *M. turneri* is here transferred to *Forsteropsalis*, as *Forsteropsalis turneri* (Marples, 1944), **comb. nov.**

Keywords: Australia, biogeography, Enantiobuninae, Eupnoi, Gondwana, New Caledonia, New Zealand, Oligocene drowning, South America, vicariance, Zealandia.

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Introduction

The harvestman family Neopilionidae Lawrence, 1931 (Fig. 1) includes a diverse array of Eupnoi. Many neopilionids are characterised by extreme sexual dimorphism with pronounced colour differences and enlarged male chelicerae commonplace. Male polymorphism is also well known, with two or more forms known for some species (Painting *et al*. 2015; Powell *et al*. 2020). Historically, the palp played a large role in establishing the taxonomy of the family, but as palp morphology can vary enormously throughout ontogeny, it is troublesome to define the group based on this trait. Likewise, the genera are rather poorly characterised morphologically, and many species have

Fig. 1. Live habitus of selected specimens. *A*, *Thrasychirus* sp. nov., MCZ IZ-138060 from Monumento Natural Contulmo, Chile. *B*, *Thrasychirus* sp. nov., MCZ IZ-138064 from Monumento Natural Contulmo, Chile. *C*, *Thrasychirus modestus* MCZ IZ-49762 from Reserva Nacional Magallanes, Chile. *D*, *Thrasychirus* sp. nov., MCZ IZ-138102 from Parque Nacional Alerce Andino, Chile [not used in this study]. *E*, *Martensopsalis* sp., from Mé Maoya, New Caledonia. *F*, Example of a *Megalopsalis* sp. MCZ IZ-152651 from Yarra State Forest, Victoria, Australia (photo courtesy of S. Derkarabetian) [not used in this study]. *G*, Example of a *Megalopsalis* sp. MCZ IZ-152667 from Great Otway National Park, Victoria, Australia (photo courtesy of S. Derkarabetian) [not used in this study]. *H*, *Mangatangi parvum* MCZ IZ-133381 from Hunua Ranges Regional Park, North Island, New Zealand. *I*,

been transferred between genera in more recent cladistic morphological analyses. Neopilionidae is perhaps best defined geographically, as it is distributed in the southern temperate regions of the world (Šilhavý 1970), including South America, South Africa, Australia, New Zealand, New Caledonia and some of New Zealand's sub-Antarctic islands – terranes most of which once constituted temperate Gondwana (Fig. 2). In previous molecular phylogenetic studies based on transcriptomic data, the few sampled members of the family constituted the sister group to the remaining Phalangioidea (the non-caddid Palpatores) (Fernández *et al*. 2017) and, as such, may represent a possible example of an ancient Pangaean divergence in Phalangioidea. However, other studies based on Sanger sequencing data of a handful of genes failed to support the monophyly of the family (Vélez *et al*. 2014; Groh and Giribet 2015), did not provide a rooting that could resolve the specific pattern within Phalangioidea (Hedin *et al*. 2012), or found Neopilionidae (as 'Monoscutidae') as an ingroup member of Phalangioidea (Giribet *et al*. 2010).

Its current 21 genera and 66 described species (Kury *et al*. 2021) are divided into 3 subfamilies: Neopilioninae Lawrence, 1931, Enantiobuninae Mello-Leitão, 1931 and Ballarrinae Hunt & Cokendolpher, 1991 (see Kury 2013) (Table 1). In addition, the genus *Hesperopilio* Shear, 1996, formerly in Caddidae, is probably related to, or an ingroup member of, Neopilionidae (Groh and Giribet 2015). Neopilionidae's geographic distribution in today's landmasses has prompted discussion as a potential case of Gondwanan vicariance (Šilhavý 1970; Giribet and Boyer 2010; Vélez *et al*. 2014; Giribet and Baker 2019). However, little phylogenetic work has examined questions related to the global pattern and timing of internal neopilionid divergences.

Taxonomically, Neopilioninae is restricted to two South African species, the type species of the family, *Neopilio australis* Lawrence, 1931, and the more recently described *N. inferi* Lotz, 2011. Ballarrinae, with 10 species, is distributed more broadly and includes 2 species of *Americovibone* Hunt & Cokendolpher, 1991 from Chile and New Zealand; the monotypic Australian genus *Arrallaba* Hunt & Cokendolpher, 1991; *Ballarra* Hunt & Cokendolpher, 1991, with 6 species from Australia; the monotypic *Plesioballarra* Hunt & Cokendolpher, 1991 from Australia; and the monotypic *Vibone* Kauri, 1961 from South Africa. Enantiobuninae includes 14 genera and 52 species from Australia, New Zealand (and its sub-Antarctic islands: Auckland, Snares, Campbell Islands), and southern South America, the type being *Enantiobunus spinulosus* Mello-Leitão, 1931, from Isla de los Estados (Argentina), in Tierra del Fuego, based on a single female, which is now considered a junior synonym of *Thrasychirus gulosus* Simon, 1884 (see Ringuelet 1959). More recently, the first species were reported from New Caledonia (see Giribet and Baker 2019; Giribet *et al*. 2021*a*), but the recently described genus *Martensopsalis* Giribet & Baker, 2021 was not assigned to any subfamily given the lack of molecular support for the subfamilies. A multitude of undescribed neopilionid species have also been collected from across the family's known range. In addition, *Hesperopilio* includes two species, one from Australia and one from South America (Shear 1996; Shultz and Cekalovic 2006).

The phylogenetic understanding of the family has benefited from morphological phylogenetic work (Hunt and Cokendolpher 1991; Taylor 2011, 2013*a*) and a few molecular studies (Fernández *et al*. 2014; Vélez *et al*. 2014), but most of the work is specific to the faunas of Australia or New Zealand, so global phylogenetic knowledge of the family is quite poor. In addition, some neopilionids have been classified historically in different families, including Phalangiidae, Monoscutidae and Megalopsalididae, especially the New Zealand species. For example, Pinto-da-Rocha and Giribet (2007) listed Monoscutidae Forster, 1948 and Neopilionidae as separate families (see respective chapter sections by Cokendolpher 2007; Cokendolpher and Taylor 2007), as had been done since Crawford (1992) elevated Monoscutinae to family. Monoscutinae was proposed as a subfamily of

Table 1. Accepted classification of Neopilionidae before this study

Ballarrinae Hunt & Cokendolpher, 1991
Americovibone Hunt & Cokendolpher, 1991 [2 spp., Chile and New Zealand]
Arrallaba Hunt & Cokendolpher, 1991 [1 sp.; Australia]
Ballarra Hunt & Cokendolpher, 1991 [6 spp.; Australia]
Plesioballarra Hunt & Cokendolpher, 1991 [1 sp.; Australia]
Vibone Kauri, 1961 [1 sp.; South Africa]
Enantiobuninae Mello-Leitão, 1931
Acihasta Forster, 1948 [1 sp.; New Zealand]
Australiscutum Taylor, 2009 [3 spp.; Australia]
Forsteropsalis Taylor, 2011 [12 spp.; New Zealand]
Mangatangi Taylor, 2013 [1 sp.; New Zealand]
Megalopsalis Roewer, 1923 [22 spp.; Australia and New Zealand]
Monoscutum Forster, 1948 [1 sp.; New Zealand]
Neopantopsalis Taylor & Hunt, 2009 [6 spp.; Australia]
Pantopsalis Simon, 1879 [10 spp.; New Zealand]
Templar Taylor, 2008 [1 sp.; New Zealand]
Tercentenarium Taylor, 2011 [1 sp.; Australia]
Thrasychiroides Soares & Soares, 1947 [4 spp.; Brazil]
Thrasychirus Simon, 1884 [3 spp.; Argentina and Chile]
Neopilioninae Lawrence, 1931
Neopilio Lawrence, 1931 [2 spp.; South Africa]
Neopilionidae *incertae sedis*
Martensopsalis Giribet & Baker, 2021 [1 sp.; New Caledonia]
Incertae sedis
Hesperopilio Shear, 1996 [2 spp.; Chile and Australia]

Monoscutum sp. MCZ IZ-133348, from Awahuri Forest | Kitchener Park, Feilding, North Island, New Zealand. *J*, *Mangatangi* sp. nov. from Awahuri Forest | Kitchener Park, Feilding, North Island, New Zealand. *K*, *Forsteropsalis pureora*, from Te Urewera National Park, North Island, New Zealand. *L*, *Forsteropsalis* sp. nov. MCZ IZ-29252 from Mount Stokes, Nelson–Marlborough, South Island, New Zealand. *M*, *Forsteropsalis* sp. nov. MCZ IZ-132834, from Kelceys Bush, Waimate, South Island, New Zealand. *N*, *Pantopsalis coronata* MCZ IZ-132830 from Kelceys Bush, Waimate, South Island, New Zealand [not used in this study]. *O*, *Pantopsalis cheliferoides* MCZ IZ-29259, from Flora Hut, Kahurangi National Park, Nelson–Marlborough, South Island, New Zealand.

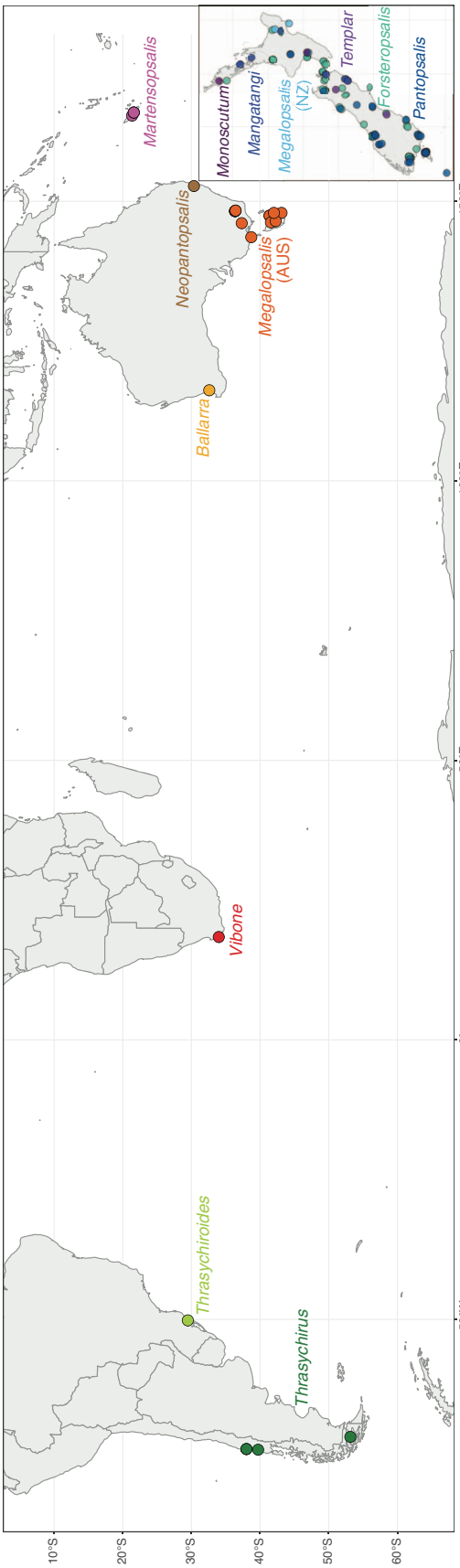


Fig. 2. Distribution of sampled specimens. Different genera appear in different colours, including the New Zealand '*Megalopsalis*'.

Phalangiidae by Forster (1948) for the species *Monoscutum titirangiense* Forster, 1948 and *Acihasta salebrosa* Forster, 1948, both from New Zealand. Crawford (1992) also placed Megalopsalididae [as Megalopsalinae] Forster, 1949 as a junior synonym of Monoscutidae, which therefore contained two subfamilies, Monoscutinae and Megalopsalidinae.

The relationship of all these Southern Hemisphere species without an entapophysis in the spiracle (a condition that distinguishes them from Phalangiidae and Sclerosomatidae) had been recognised for a while, and in fact Šilhavý (1970) used the term Neopilionidae in the sense understood today. However, Hunt and Cokendolpher (1991) thought that the synapomorphy of the spiracle proposed by Šilhavý (1970) was a symplesiomorphy and considered Neopilionidae to be paraphyletic with respect to Phalangiidae and Gagrellidae (now Sclerosomatidae), and proposed Ballarrinae as a new subfamily of Neopilionidae, thus implying monophyly of Ballarrinae.

In his morphological revision of the genus *Megalopsalis* Roewer, 1923, Taylor (2011) conducted a phylogenetic analysis where, again, Neopilionidae was not monophyletic, as *Ballarra* branched out earlier than the divergence between Phalangiidae, Sclerosomatidae, Caddidae and the remaining neopilionids. A second morphological phylogenetic analysis by Taylor (2013*a*) recognised monophyly of Enantiobuninae and of the Australasian species (but only one *Thrasychirus* Simon, 1884 exemplar was included), as well as of Ballarrinae, although only two ballarrine species were included. Monophyly of Neopilionidae was also supported in a study on palpal evolution across Opiliones (Wolff *et al.* 2016) that mapped characters onto a tree compiled from prior analyses.

To complicate things further, the few molecular analyses considering neopilionid species have found results that contrast with these morphological hypotheses. Groh and Giribet (2015) included *Vibone vetusta* Kauri, 1961 from South Africa, *Ballarra longipalpa* Hunt & Cokendolpher, 1991 from Australia, and two enantiobunine species from New Zealand, but found *Vibone* branching outside a clade composed of Sclerosomatidae and Protolophidae plus the remaining Neopilionidae, thus rendering the family as well as Ballarrinae non-monophyletic. Perhaps more interesting was the placement of *Hesperopilio*, until then classified as a member of Caddidae, which appeared as sister group to the Australasian neopilionids – but with the caveat that no South American neopilionid samples were included in that study. Another study by Hedin *et al.* (2012) used two representatives, one from New Zealand (labelled *Megalopsalis* sp.) and the South American *Thrasychirus gulosus*, which in this case formed a clade, as was also the case in the phylotranscriptomic analysis of Fernández *et al.* (2017).

Neopilionid relationships, focusing on the New Zealand species, were more explicitly addressed by Vélez *et al.* (2014), who again found *Hesperopilio* nesting within Neopilionidae, as sister group to *Thrasychirus*, and thus rejected the monophyly of Enantiobuninae. The position of *Vibone* differed between a maximum likelihood analysis with static homology, where it was sister group to the remaining Neopilionidae (including *Hesperopilio*), and a parsimony

direct optimisation analysis in which *Vibone* was sister group to all the remaining Phalangioidea. However, that study lacked proper sampling within Australia, South America and some key New Zealand lineages. Another molecular study focusing exclusively on species delimitation and internal relationships of selected New Zealand species (Fernández *et al*. 2014) did not address the global patterns within the family. Therefore, no phylogenetic analysis using molecular data has properly tested relationships among a broader diversity of neopilionids.

The aim of this study is thus to provide a first comprehensive molecular approach to the phylogeny of Neopilionidae by maximising taxon sampling across its distribution range and to provide the temporal framework for future biogeographic analyses in this fascinating family of Opiliones that has emerged as a model to study behavioural and reproductive biology (Painting *et al*. 2015; Powell *et al*. 2020).

Materials and methods

Specimen sampling

Specimens for this study were gathered during nearly 20 years of sampling across all the landmasses where Neopilionidae are known, and includes some previously unsampled areas, such as New Caledonia, which now is known to include multiple species in the recently described genus *Martensopsalis*. Specimens were collected mostly through direct sampling, either by sifting leaf litter or else by looking under logs and boulders during the day, or intercepting active animals, often at night.

Our sampling included 65 newly sequenced specimens plus our own sequences from previous studies (Fernández *et al*. 2014; Vélez *et al*. 2014), as well as outgroups including Dyspnoi (Table 2). Specimens are deposited in the Invertebrate Zoology collection at the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ), and at the University of Auckland, New Zealand. Specimens were preserved in 96% EtOH and kept at –20°C for long-term preservation. All DNA extracts from the new material were deposited at the MCZ cryogenic collection.

Molecular sequences

Total genomic DNA was isolated from one or two legs from each specimen. In cases where legs could not be positively correlated with or directly removed from a specimen, a palp was used. Each specimen in a multispecimen vial was given a separate subnumber and stored within a smaller vial for future studies. DNA was isolated with either the AutoGenPrep 965 (AutoGen Inc. Holliston, MA, USA) or DNeasy Tissue Kit (Qiagen Inc., Valencia, CA, USA). Both extraction systems followed the manufacturer-provided Mouse Tail protocol; Autogen extractions were resuspended manually instead of the suggested automated method.

We sequenced the mitochondrial gene cytochrome *c* oxidase subunit I (*COI*), which has been used as a 'barcoding gene' and as a common marker in previous studies on New Zealand neopilionids (Fernández *et al*. 2014). The primer pairs LCO1490 and HCO2198 (Folmer *et al*. 1994) were used to PCR-amplify *COI* with illustra PuReTaq Ready-To-Go PCR Beads (GE Healthcare Life Sciences, Marlborough, MA, USA) or GoTaq DNA Polymerase (Promega Corporation, Madison, WI, USA). Samples that failed to amplify for *COI* using the above-described process were amplified using a nested PCR. The first round of amplification used the primer pairs LCO1490–HCOoutout (Prendini *et al*. 2005; Schwendinger and Giribet 2005) and the second round used primer pairs LCO1490–HCO2198. Amplification products were visualised with 1% agarose gel electrophoresis and purified with Exosap-IT (Applied Biosystems, Foster City, CA, USA). Part of the dataset was sequenced at the Harvard University Bauer Core (Cambridge, MA, USA), and for these we used ABI BigDye Terminator (ver. 3.0, Applied Biosystems, Foster City, CA, USA) for the sequencing reaction, cleaned the labelled products with AGTC gel filtration plates (Edge BioSystems, Gaithersburg, MD, USA), and analysed the products with an ABI Prism 3730xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). The rest of the dataset was sequenced at GENEWIZ (South Plainfield, NJ, USA) using their Purified PCR product premixed service. Resultant chromatograms were read, edited, assembled and visually inspected using Sequencher (ver. 4.7, Gene Codes Corporation, Ann Arbor, MI, USA) and Geneious Prime (ver. 2019.0.3, Biomatters, see https://www.geneious.com).

After amplification of *COI* for a large number of specimens (>600), we selected all putative species represented in the dataset for a multilocus approach. For these (see Table 2), we amplified the nuclear ribosomal genes *18S* rRNA and *28S* rRNA using the overlapping primer sets 18S 1F–18S 4R, 18S 3F–18Sbi, 18Sa2.0–18S 9R for *18S* rRNA (Giribet *et al*. 1996; Whiting *et al*. 1997) and 28Srd1a–28Sb, 28Srd3a–28Sb, 28Sa–28Srd5b, 28S4.8a–28Srd7i, 28SF2012–28SR2762 for *28S* rRNA (Whiting *et al*. 1997; Schwendinger and Giribet 2005; Edgecombe and Giribet 2006; see Giribet and Shear 2010; Giribet *et al*. 2010). All primer sequences are listed in Table 3. All new sequences were deposited in GenBank under accession codes MW837082–MW837141, MW843168–MW843285 and MW849326–MW849476 (Table 2).

Phylogenetic analyses

Individual FASTA files for the three markers were aligned with the MAFFT plug-in for Geneious (Katoh and Standley 2013). The resulting individual alignments were further edited against the original chromatograms and visualised in MacGDE (E. W. Linton, see www.msu.edu/~lintone/macgde/), realigned with MAFFT (ver. 7, see https://mafft.cbrc.jp/alignment/server/large.html; Katoh and Standley 2014; Katoh *et al*. 2019). The *28S* rRNA gene was subsequently partitioned into four fragments (*a*, *b*, *c*, *d*) according to four regions amplified with the four sets of overlapping primer pairs to facilitate downstream analyses, as amplification of some of these fragments was not consistent across taxa or with legacy data. Two final alignments were generated in MAFFT with a gap opening cost of 3.0, and a gap extension cost of 0.123, one containing all taxa and another excluding the Dyspnoi representatives, as they have branches that are considerably longer than those of Eupnoi. Each individual alignment was

Table 2. Taxon sampling with repository accession numbers
New sequences generated for this study are shown in bold

Taxon	Accession number	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
DYSPNOI						
Acropsopilio chilensis		KF963303	KF955592	GQ912899		
Acropsopilio neozealandiae	MCZ IZ-64837	KF963304	KF955591	–		
Caddella sp.	MCZ IZ-127629	KF963308	KF955595	–		
Caddella sp.	MCZ IZ-127631	KF963307	KF955594	–		
Ischyropsalis pyrenaea	MNHN-JAA33	JN018255	JN018352	JN018138		
Dendrolasma parvulum		EF108574	EF108578	EF108589		
Trogulus nepaeformis	MNHN-JAC77	JN018259	JN018356	JN018142		
EUPNOI						
Caddo agilis		KF963310	KF955597	MF817159		
Phalangium opilio		AF124937	KJ871587	KJ871385		
Rhampsinitus sp.	MCZ IZ-133900	GQ912708	GQ912757	GQ912862		
Metopilio cf. *diazi*	MH2012 OP2186	JQ437012	JQ437104	–		
Marthana sp.	MCZ IZ-134862	GQ912711	–	GQ912863		
Nelima sylvatica		U91486	–	KY270309		
Protolophus singularis		EF028095	EF028096	EF108586		
Hesperopilio magnificus	CASENT9027761	KF963312	KF955599	–		
Hesperopilio mainae	MCZ IZ-127633	KF963313	KF955600	–		
Neopilionidae						
Ballarra longipalpa	MCZ IZ-128774	KJ857510	KJ857513	KJ871355	–32.600000	116.200000
Forsteropsalis bona	CP0237	**MW849326**	**MW843168**	**MW837082**	–38.267325	175.071460
Forsteropsalis bona	CP0238	**MW849327**	**MW843169**	**MW837083**	–38.267325	175.071460
Forsteropsalis chiltoni	MCZ IZ-129526	**MW849328**	KJ871526	KJ871410	–46.897000	168.092278
Forsteropsalis chiltoni	MCZ IZ-129581	**MW849329**	KJ871555	KJ871378	–46.898490	168.100164
Forsteropsalis chiltoni	MCZ IZ-129584	**MW849330**	KJ871556	KJ871380	–46.898490	168.100164
Forsteropsalis fabulosa	MCZ IZ-129566	**MW849331**	**MW843170–71**	KJ871396	–41.155778	174.965194
Forsteropsalis fabulosa	MCZ IZ-136168	**MW849332–33**	**MW843172–73**	KJ871398	–41.155778	174.965194
Forsteropsalis grimmetti	CP0190	**MW849334**	**–**	**MW837084**	–43.937331	169.289047
Forsteropsalis inconstans	MCZ IZ-129515	KJ871435	KJ871518	KJ871364	–43.938092	169.288235
Forsteropsalis inconstans	MCZ IZ-129519	**MW849335**	**MW843175**	KJ871404	–42.377503	172.403320
Forsteropsalis inconstans	MCZ IZ-129520	**MW849336**	KJ871521	KJ871413	–42.377503	172.403320
Forsteropsalis inconstans	MCZ IZ-129529	**MW849337–38**	KJ871529	KJ871420	–41.267694	174.758667
Forsteropsalis inconstans	MCZ IZ-129535	**MW849339–40**	**MW843176–77**	KJ871402	–41.190083	172.741333
Forsteropsalis inconstans	MCZ IZ-129536	**MW849341–42**	KJ871532	KJ871392	–41.190083	172.741333
Forsteropsalis inconstans	MCZ IZ-129537	**MW849343–44**	**MW843178–79**	KJ871428	–41.190083	172.741333
Forsteropsalis inconstans	MCZ IZ-129538	**MW849345–46**	KJ871534	KJ871429	–41.190083	172.741333
Forsteropsalis inconstans	MCZ IZ-129539	**MW849347–48**	KJ871535	KJ871361	–41.190083	172.741333
Forsteropsalis inconstans	MCZ IZ-129540	**MW849349–50**	KJ871536	KJ871393	–41.190083	172.741333
Forsteropsalis inconstans	MCZ IZ-129541	**MW849351–52**	**MW843180–81**	KJ871430	–41.096750	172.906194
Forsteropsalis inconstans	MCZ IZ-129568	**MW849353**	KJ871544	KJ871369	–42.036950	171.389884
Forsteropsalis inconstans	MCZ IZ-129575	**MW849354**	KJ871549	KJ871391	–40.230222	175.230222
Forsteropsalis inconstans	MCZ IZ-129576	**MW849355**	KJ871550	KJ871390	–40.230222	175.230222
Forsteropsalis inconstans	MCZ IZ-129577	**MW849356**	**MW843268–69**	KJ871426	–40.230222	175.230222
Forsteropsalis inconstans	MCZ IZ-129579	**MW849357**	KJ871553	KJ871405	–42.152357	172.931598
Forsteropsalis inconstans	MCZ IZ-129580	**MW849358**	KJ871554	KJ871424	–42.109222	171.342500
Forsteropsalis inconstans	MCZ IZ-135565	**MW849359**	**MW843182–83**	KJ871414	–43.937750	169.291750
Forsteropsalis inconstans	MCZ IZ-135904	**MW849360**	KJ871564	KJ871421	–41.290528	174.752500
Forsteropsalis inconstans	MCZ IZ-136053	**MW849361**	KJ871565	KJ871365	–43.423500	170.168000
Forsteropsalis marplesi	CP0339	**MW849362**	**MW843184**	**MW837085**	–46.456829	169.492913
Forsteropsalis marplesi	CP0376	**MW849363**	**MW843185**	**MW837086**	–45.804916	170.520384
Forsteropsalis marplesi	MCZ IZ-129517	KJ871436	KJ871519	KJ871373	–46.894249	168.104017
Forsteropsalis marplesi	MCZ IZ-129554	KJ871465	**MW843186–88**	KJ871375	–45.904814	169.987974
Forsteropsalis photophaga	CP0268	**MW849364**	**MW843189**	**MW837087**	–38.261250	175.013056
Forsteropsalis pureora	CP0223	**MW849365–66**	**MW843190**	**MW837088**	–38.226854	177.213924
Forsteropsalis pureora	CP0287	**MW849367**	**MW843191**	**MW837089**	–38.261250	175.013056
Forsteropsalis pureora	MCZ IZ-29240	**MW849368**	KJ871568	**MW837090**	–38.727334	177.165198
Forsteropsalis turneri	CP0475	**MW849369**	**MW843192**	**MW837091**	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129521	**MW849370**	KJ871522	KJ871406	–46.018194	167.741417

(*continued next page*)

Table 2. (*continued*)

Taxon	Accession number	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Forsteropsalis turneri	MCZ IZ-129522	**MW849371**	KJ871523	KJ871415	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129523	**MW849372**	KJ871524	KJ871423	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129524	**MW849373**	KJ871525	KJ871408	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129571	**MW849374**	KJ871545	KJ871416	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129572	**MW849375**	KJ871546	KJ871422	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129573	**MW849376**	KJ871547	KJ871407	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-129574	**MW849377**	KJ871548	KJ871403	–46.018194	167.741417
Forsteropsalis turneri	MCZ IZ-134832	**MW849378**	KJ871558	EF108587	–46.019750	167.740950
Forsteropsalis wattsi	MCZ IZ-135693	**MW849379**	KJ871562	KJ871418	–41.137694	173.516750
Forsteropsalis wattsi	MCZ IZ-135737	**MW849380–81**	**MW843193–94**	KJ871419	–41.298694	173.572778
Forsteropsalis cf. *wattsi*	MCZ IZ-129542	**MW849382–83**	KJ871538	KJ871401	–46.018194	167.741417
Forsteropsalis sp.	MCZ IZ-129527	**MW849384**	KJ871527	KJ871411	–46.897000	168.092278
Forsteropsalis sp.	MCZ IZ-129528	**MW849385**	**MW843195–96**	KJ871412	–46.573389	169.346639
Forsteropsalis sp.	MCZ IZ-134830	**MW849386**	KJ871557	KJ871358	–46.429505	168.295733
Forsteropsalis sp.	MCZ IZ-129525	**MW849387**	**MW843197–98**	KJ871409	–46.018194	167.741417
Forsteropsalis sp.	CP0581	**MW849388**	**MW843199**	**MW837092**	–46.573389	169.346639
Forsteropsalis sp.	MCZ IZ-129511	**MW849389**	**MW843200–02**	**MW837093**	–41.086747	174.138106
Forsteropsalis sp.	MCZ IZ-129552	**MW849390**	**MW843203–04**	KJ871399	–43.811389	173.028417
Forsteropsalis sp.	MCZ IZ-132834	**MW849391**	**–**	**MW837094**	–44.700550	170.967150
Forsteropsalis sp.	MCZ IZ-135579	**MW849392**	**MW843207**	**MW837095**	–43.937750	169.291750
Forsteropsalis sp.	MCZ IZ-136136	**MW849393**	**MW843208–10**	–	–46.898490	168.100164
Forsteropsalis sp.	MCZ IZ-136139	**MW849394**	**MW843211–13**	KJ871374	–45.904722	169.987778
Forsteropsalis sp.	MCZ IZ-29239	**MW849395**	KJ871577	KJ870062	–38.727334	177.165198
Forsteropsalis sp.	MCZ IZ-29252	**MW849396**	KJ871569	**MW837096**	–41.086656	174.138189
Forsteropsalis sp.	MCZ IZ-29253	**MW849397**	KJ871570	KJ870083	–41.086656	174.138189
Forsteropsalis sp.	CP0775	**MW849398**	**MW843214–15**	**MW837097**	–35.682869	173.575810
Mangatangi parvum	MCZ IZ-133096 1	**MW849399**	**MW843216–17**	**MW837100**	–36.452580	174.651540
Mangatangi parvum	MCZ IZ-133381	**MW849400**	**MW843218–19**	**MW837099**	–37.118460	175.208080
Mangatangi sp.	MCZ IZ-29238	**MW849401**	KJ871576	KJ870092	–38.725356	177.164972
Mangatangi sp.	MCZ IZ-129518	**MW849402**	KJ871572	KJ871395	–42.331505	173.638874
Mangatangi sp.	MCZ IZ-129533	**MW849403–04**	KJ871573	KJ871386	–41.264111	173.920556
Mangatangi sp.	MCZ IZ-129534	**MW849405–06**	**MW843220–22**	–	–41.264111	173.920556
Mangatangi sp.	MCZ IZ-129562	KJ871468	KJ871574	KJ871394	–42.478000	173.528972
Mangatangi sp.	MCZ IZ-129565	**MW849407**	**MW843223**	KJ871400	–42.331505	173.638874
Mangatangi sp.	MCZ IZ-133096 3	**MW849408**	**MW843224–25**	**MW837098**	–36.452580	174.651540
Mangatangi sp.	MCZ IZ-136154	**MW849409**	**MW843226–27**	**–**	–42.478000	173.528972
Martensopsalis sp. NCA	MCZ IZ-151588	**MW849410**	**MW843228**	**MW837101**	–21.361070	165.326690
Martensopsalis dogny	MCZ IZ-151592	**MW849411**	**MW843229**	**MW837102**	–21.609730	165.879170
Martensopsalis dogny	MCZ IZ-152401	**MW849412**	**MW843230**	**MW837103**	–21.609730	165.879170
Martensopsalis dogny	MCZ IZ-152402	**MW849413**	**MW843231**	**MW837104**	–21.609730	165.879170
'*Megalopsalis*' *triascuta*	MCZ IZ-133415	**MW849414**	**MW843232**	**MW837105**	–40.245360	175.541160
'*Megalopsalis*' *triascuta*	MCZ IZ-133421_7	**MW849415**	**MW843233–34**	**MW837106**	–40.246040	175.541390
'*Megalopsalis*' sp. nov.	CP0208C	**MW849416**	**MW843235**	**MW837107**	–38.290753	177.383219
'*Megalopsalis*' sp. nov.	CP0215C	**MW849417**	**MW843236**	**MW837108**	–39.164879	177.771329
Megalopsalis nigricans	TAS008	**MW849418**	**MW843237**	**MW837109**	–43.119900	147.926800
Megalopsalis stewarti	MCZ IZ-129549	**MW849419–20**	KJ871600	KJ871389	–38.719444	143.579722
Megalopsalis stewarti	MCZ IZ-134836	**MW849421–22**	**MW843238**	**MW837110**	–37.327556	146.084861
Megalopsalis tasmanica	MCZ IZ-148948	**MW849423**	**MW843239**	**MW837111**	–42.015200	147.927600
Megalopsalis sp. nov. NSW	MCZ IZ-129543	**MW849424–25**	KJ871595	KJ871387	–36.351278	148.245583
Megalopsalis sp. nov. NSW	MCZ IZ-129544	**MW849426–27**	**MW843240–41**	KJ871388	–36.351278	148.245583
Megalopsalis sp. nov. NSW	MCZ IZ-129545	**MW849428–29**	KJ871597	KJ871359	–36.351278	148.245583
Megalopsalis sp. nov. NSW	MCZ IZ-129546	**MW849430–31**	KJ871598	KJ871360	–36.430222	148.331472
Megalopsalis sp. nov. NSW	MCZ IZ-129547	**MW849432–33**	KJ871599	KJ871427	–36.430222	148.331472
Megalopsalis sp. TAS	TAS147	**MW849434**	**MW843242**	**MW837112**	–42.276800	146.459700
Megalopsalis sp. TAS	TAS280 1	**MW849435**	**MW843243**	**MW837113**	–41.578600	146.223800
Megalopsalis sp. TAS	TAS333 1	**MW849436**	**MW843244**	**MW837115**	–41.373800	147.427700
Megalopsalis sp. TAS	TAS333 2	**MW849437**	**MW843245**	**MW837114**	–41.373800	147.427700
Monoscutum sp.	MCZ IZ-132846	–	–	**MW837116**	–35.190260	173.483290
Monoscutum sp.	MCZ IZ-133348	–	–	**MW837117**	–40.244520	175.542050

(*continued next page*)

Table 2. (*continued*)

Taxon	Accession number	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Monoscutum sp.	ZMUC Mono2 2	–	**MW843246–47**	–	–	–
Neopantopsalis thaumatopoios	MCZ IZ-134835	**MW849438–39**	KJ871603	KJ871384	–30.367639	152.728444
Pantopsalis albipalpis	CP0337	**MW849440**	**MW843248**	**MW837118**	–46.456829	169.492913
Pantopsalis albipalpis	CP0372	**MW849441**	**MW843249**	**MW837119**	–45.806998	170.520488
Pantopsalis cheliferoides	MCZ IZ-29259	**MW849442**	KJ871590	**MW837120**	–41.182496	172.730188
Pantopsalis cheliferoides	MCZ IZ-129512	**MW849443**	**MW843250**	KJ871372	–42.036950	171.389884
Pantopsalis coronata	CP0656	**MW849444**	**MW843251**	**MW837121**	–43.980383	171.464431
Pantopsalis cf. *coronata*	MCZ IZ-133453	**MW849445**	**MW843252**	**MW837122**	–45.957320	167.672410
Pantopsalis listeri	CP0001	**MW849446**	**MW843253**	**MW837123**	–44.318975	168.660326
Pantopsalis listeri	CP0002	**MW849447**	**MW843254**	**MW837124**	–44.318975	168.660326
Pantopsalis listeri	CP0093	**MW849448**	**MW843255**	**MW837125**	–43.939444	169.290833
Pantopsalis listeri	MCZ IZ-29279	**MW849449**	KJ871591	KJ870080	–44.487558	168.787364
Pantopsalis listeri	MCZ IZ-129513	**MW849450**	**MW843256–57**	KJ871362	–43.021323	171.595022
Pantopsalis listeri	MCZ IZ-129587	**MW849451**	KJ871585	KJ871370	–44.076874	169.386562
Pantopsalis listeri	MCZ IZ-129588	**MW849452–53**	**MW843258–59**	KJ871371	–44.076874	169.386562
Pantopsalis listeri	MCZ IZ-136089	–	**MW843260–61**	KJ871367	–44.076874	169.386562
Pantopsalis phocator	CP0483	**MW849454**	**MW843262**	**MW837126**	–45.990000	167.381944
Pantopsalis phocator	CP0566	**MW849455**	**MW843263**	**MW837127**	–46.573389	169.346639
Pantopsalis phocator	CP0572	**MW849456**	**MW843264**	**MW837128**	–46.573389	169.346639
Pantopsalis phocator	MCZ IZ-129583	**MW849457–58**	KJ871582	KJ871383	–46.898490	168.100164
Pantopsalis sp.	MCZ IZ-129582	**MW849459–60**	KJ871581	KJ871379	–46.898490	168.100164
Pantopsalis sp.	MCZ IZ-129585	**MW849461–62**	KJ871583	KJ871381	–46.898490	168.100164
Pantopsalis sp.	MCZ IZ-129586	**MW849463**	KJ871584	KJ871382	–46.898490	168.100164
Pantopsalis cf. *phocator*	MCZ IZ-133437	**MW849464**	**MW843265**	**MW837129**	–46.891000	168.096810
Pantopsalis pococki	CP0669	**MW849465**	**MW843266**	**MW837130**	–43.980383	171.464431
Pantopsalis snaresensis		–	–	KJ920342	–48.024438	166.602295
Pantopsalis sp.	CP0491	**MW849466**	**MW843267**	**MW837131**	–45.990000	167.381944
Pantopsalis sp.	MCZ IZ-133326	**MW849467**	**MW843270–71**	**MW837132**	–39.356090	175.476430
Pantopsalis sp.	MCZ IZ-133330	**MW849468**	**MW843272–73**	**MW837133**	–39.356090	175.476430
Templar sp.	MCZ IZ-29229	**MW849469**	KJ871578	**MW837134**	–41.821107	172.807901
Templar sp.	MCZ IZ-149444	**MW849470**	**MW843274–75**	**MW837135**	–44.700550	170.967150
Templar sp.	ZMUC Temp1	**MW849471**	**MW843276**	**MW837136**	–	–
Thrasychiroides toryba	MZUSP-70937_1	**MW849472**	**MW843277**	**MW837137**	–29.479472	-50.173694
Thrasychirus gulosus	OP1152	JQ437009	JQ437101	–	–	–
Thrasychirus modestus	MCZ IZ-49762_1	**MW849473**	**MW843278–79**	**MW837138**	–53.147430	–71.008500
Thrasychirus sp. nov.	MCZ IZ-138060	**MW849474**	**MW843280–81**	**MW837139**	–38.012560	–73.185170
Thrasychirus sp. nov.	MCZ IZ-138064_1	**MW849475**	**MW843282–83**	**MW837140**	–38.012560	–73.185170
Thrasychirus sp. nov.	CAS9063504 2	**MW849476**	**MW843284–85**	**MW837141**	–39.712500	–73.308333
Vibone vetusta	MCZ IZ-132934	KJ857511	KJ857514	–	–33.985637	18.401276

then submitted to Gblocks (ver. 0.91b, see http://molevol.cmima.csic.es/castresana/Gblocks_server.html; Castresana 2000; Talavera and Castresana 2007) with the following options activated: (1) allow smaller final blocks; (2) allow gap positions with the final blocks; and (3) allow less strict flanking positions. The individual gene fragments (untrimmed and trimmed) were then concatenated with SequenceMatrix (ver. 1.8, see http://www.ggvaidya.com/taxondna/; Vaidya *et al*. 2011) and exported for subsequent analyses of a 'trimmed' and an 'untrimmed' dataset.

For each of the trimmed and untrimmed matrices we then proceeded with two datasets: one consisting of all the terminals (see Table 2), and a reduced dataset excluding all taxa with only 1 or 2 markers. All FASTA files (trimmed and untrimmed), for individual partitions as well as all alignments and partition files are available in the Harvard Dataverse portal (see https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/4VHTBG).

Thus, our analyses consisted of the following eight datasets:

1. All data, untrimmed (159 taxa, 5081 bp) (Fig. 3)
2. All data, trimmed (159 taxa, 4741 bp)
3. Reduced dataset, untrimmed (135 taxa, 5081 bp)
4. Reduced dataset, trimmed (135 taxa, 4741 bp)
5. No Dyspnoi, all data, untrimmed (146 taxa, 4937 bp)
6. No Dyspnoi, all data, trimmed (146 taxa, 4734 bp)
7. No Dyspnoi, reduced dataset, untrimmed (131 taxa, 4937 bp) (Fig. 4)
8. No Dyspnoi, reduced dataset, trimmed (131 taxa, 4734 bp)

Maximum likelihood analyses were constructed with IQ-TREE (ver. 1.6, see http://iqtree.cibiv.univie.ac.at; Nguyen *et al*. 2015) through the IQ-TREE web server (Trifinopoulos *et al*. 2016) using an edge-unlinked partition model (Lopez *et al*. 2002; Chernomor *et al*. 2016), with the best-fit model estimated with ModelFinder, as incorporated in IQ-TREE (Kalyaanamoorthy *et al*. 2017). Nodal support was

Table 3. List of primer sequences used for amplification and sequencing with original references of the primer sequences

Ribosomal genes were amplified at annealing temperatures ranging between 46 and 52°C. Protein-coding genes were amplified at annealing temperatures between 42 and 48°C

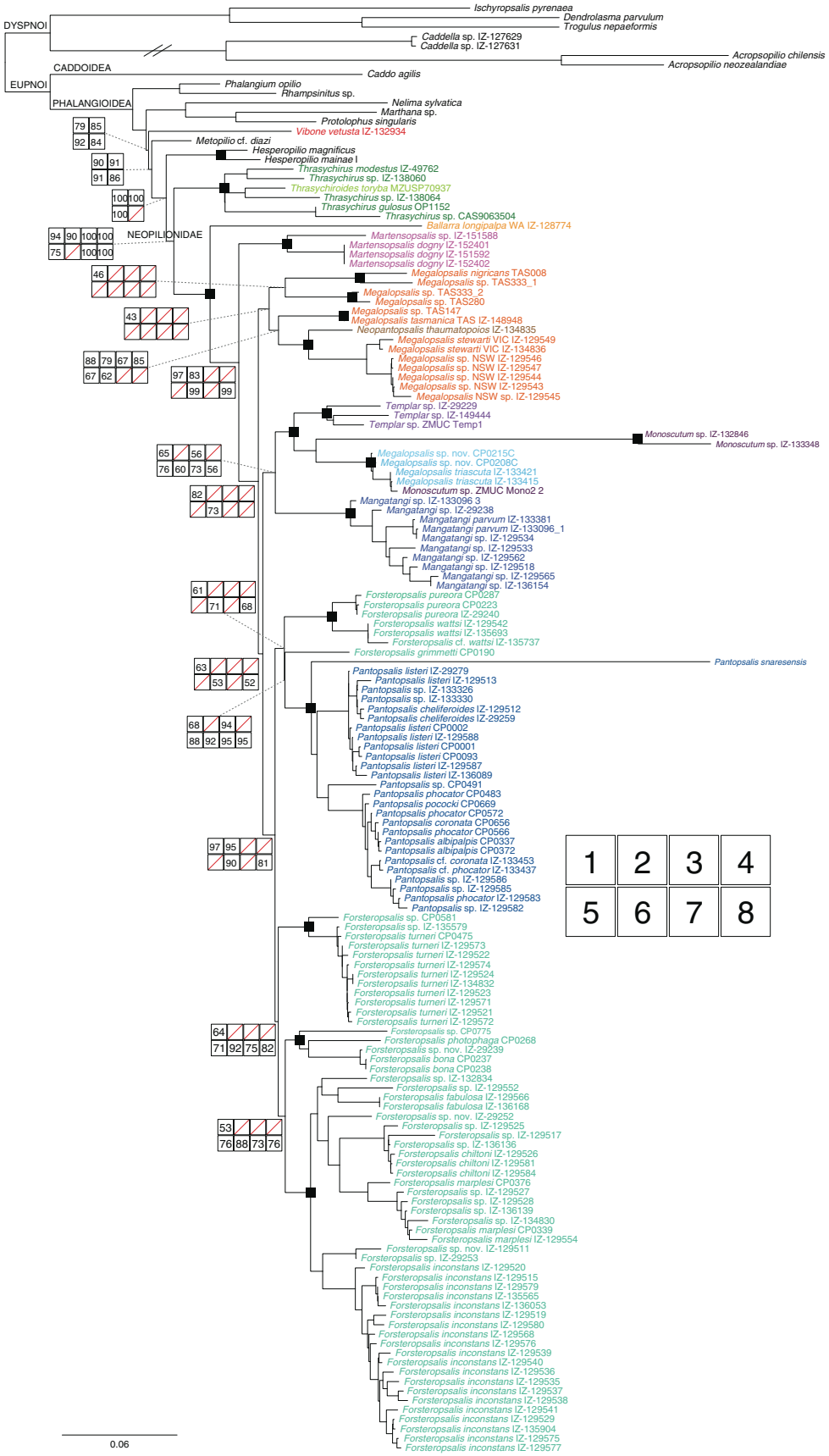
Primer sequence	Original reference
18S rRNA	
18S 1F 5′-TAC CTG GTT GAT CCT GCC AGT AG-3′	Giribet *et al*. (1996)
18S 3F 5′-GTT CGA TTC CGG AGA GGG A-3′	Giribet *et al*. (1996)
18S 4R 5′-GAA TTA CCG CGG CTG CTG G-3′	Giribet *et al*. (1996)
18S 9R 5′-GAT CCT TCC GCA GGT TCA CCT AC-3′	Giribet *et al*. (1996)
18S a2.0 5′-ATG GTT GCA AAG CTG AAA C-3′	Whiting *et al*. (1997)
18S bi 5′-GAG TCT CGT TCG TTA TCG GA-3′	Whiting *et al*. (1997)
28S rRNA	
28Sa 5′-GAC CCG TCT TGA AAC ACG GA-3′	Whiting *et al*. (1997)
28Sb 5′-TCG GAA GGA ACC AGC TAC-3′	Whiting *et al*. (1997)
28S rd1a 5′-CCC SCG TAA YTT AGG CAT AT-3′	Edgecombe and Giribet (2006)
28S rd3a 5′-AGT ACG TGA AAC CGT TCA GG-3′	Schwendinger and Giribet (2005)
28S rd4b 5′-CCT TGG TCC GTG TTT CAA GAC-3′	Edgecombe and Giribet (2006)
28S rd4.8a 5′-ACC TAT TCT CAA ACT TTA AAT GG-3′	Schwendinger and Giribet (2005)
28S rd5b 5′-CCA CAG CGC CAG TTC TGC TTA C-3′	Schwendinger and Giribet (2005)
28S rd7b1 5′-GAC TTC CCT TAC CTA CAT-3′	Schwendinger and Giribet (2005)
28S F2012 5′-CCA AGG TKA RYA GCC TCT RG-3′	Giribet *et al*. (2010)
28S R2762 5′-CCG CCC CAG CCA AAC TCC CC-3′	Giribet *et al*. (2010)
COI	
LCO1490 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′	Folmer *et al*. (1994)
HCO2148 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′	Folmer *et al*. (1994)
HCOoutout 5′-GTA AAT ATA TGR TGD GCT C-3′	Prendini *et al*. (2005)

calculated in IQ-TREE using the ultrafast bootstrap algorithm (Minh *et al*. 2013; Hoang *et al*. 2018). The resulting trees were then adjusted and manipulated in FigTree (ver. 1.4.3, A. Rambaut, Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK, see http://tree.bio.ed.ac.uk/software/figtree/). All binary trees are available in the Harvard Dataverse portal link provided above.

Node dating analysis

For the dating analysis we selected the dataset including Dyspnoi, but reduced to exclude taxa with fewer than three genes and trimmed, to minimise missing data (*Dataset 4*). This dataset was analysed in BEAST (ver. 2.6.3, see https://www.beast2.org; Bouckaert *et al*. 2019) using unlinked nucleotide substitution model averaging, as implemented in bModelTest, part of the BEAST package (Bouckaert and Drummond 2017), an unlinked Relaxed Clock Exponential model, and a Yule model of speciation, following prior testing on a similar family-level Opiliones dataset (Baker *et al*. 2020*b*). It is generally understood that the use of a Yule tree prior on our dataset, which includes both inter- and intraspecific divergences, is a theoretical violation of that speciation model and, as such, could bias divergence time estimates. However, simulation-based analysis of mixed inter- and intraspecific datasets in a Bayesian dating framework has shown that in sampling schemes such as the one presented here, where many nodes correspond to interspecies divergences, estimates of node times were robust to tree prior choice, and that model selection procedures were effective in rejecting models likely to cause highly inaccurate node time estimates (Ritchie *et al*. 2017).

The following nodes were calibrated under a uniform distribution using known Opiliones fossils to constrain crown-group ages of specified nodes, with a minimum age specified for each constraint: (1) Dyspnoi was constrained to 305 Ma, reflecting the age of the fossil *Ameticos scolos* Garwood, Dunlop, Giribet & Sutton, 2011, from the Montceau-les-Mines Lagerstätte, the upper limit of which is biostratigraphically dated to *c*. 305 Ma (Garwood *et al*. 2011), and the maximum age of 405 Ma was set based on the oldest known Opiliones fossil *Eophalangium sheari* Dunlop, Anderson, Kerp & Hass, 2004 (Dunlop *et al*. 2004; Garwood *et al*. 2014); *Ameticos scolos* is considered a member of crown-group Dyspnoi (Garwood *et al*. 2014). (2) The age of Phalangioidea was constrained to 340 Ma, reflecting the age of *Brigantibunum listoni* Dunlop & Andersen, 2005 from the Carboniferous of East Kirkton Quarry, West Lothian, Scotland (Dunlop and Anderson 2005), with a maximum age of 405 Ma; given its unique leg morphology, typical of long-legged Eupnoi, *Brigantibunum listoni* is here considered a member of crown-group Phalangioidea. (3) Phalangiidae was constrained to 41.2 Ma, the upper limit of the Lutetian, based on the several phalangiid fossils from the Eocene Baltic amber (Mitov *et al*. 2014; Elsaka *et al*. 2019), with a


Ischyropsalis pyrenaea
Dendrolasma parvulum
Trogulus nepaeformis
DYSPNOI
Caddella sp. IZ-127629
Caddella sp. IZ-127631
Acropsopilio chilensis
Acropsopilio neozealandiae
CADDOIDEA
Caddo agilis
EUPNOI
Phalangium opilio
Rhampsinitus sp.
PHALANGIOIDEA
Nelima sylvatica
Marthana sp.
Protolophus singularis
Vibone vetusta IZ-132934
Metopilio cf. diazi
Hesperopilio magnificus
Hesperopilio mainae I
Thrasychirus modestus IZ-49762
Thrasychirus sp. IZ-138060
Thrasychiroides toryba MZUSP70937
Thrasychirus sp. IZ-138064
Thrasychirus gulosus OP1152
Thrasychirus sp. CAS9063504
Ballarra longipalpa WA IZ-128774
NEOPILIONIDAE
Martensopsalis sp. IZ-151588
Martensopsalis dogny IZ-152401
Martensopsalis dogny IZ-151592
Martensopsalis dogny IZ-152402
Megalopsalis nigricans TAS008
Megalopsalis sp. TAS333_1
Megalopsalis sp. TAS333_2
Megalopsalis sp. TAS280
Megalopsalis sp. TAS147
Megalopsalis tasmanica TAS IZ-148948
Neopantopsalis thaumatopoios IZ-134835
Megalopsalis stewarti VIC IZ-129549
Megalopsalis stewarti VIC IZ-134836
Megalopsalis sp. NSW IZ-129546
Megalopsalis sp. NSW IZ-129547
Megalopsalis sp. NSW IZ-129544
Megalopsalis sp. NSW IZ-129543
Megalopsalis NSW sp. IZ-129545
Templar sp. IZ-29229
Templar sp. IZ-149444
Templar sp. ZMUC Temp1
Monoscutum sp. IZ-132846
Monoscutum sp. IZ-133348
Megalopsalis sp. nov. CP0215C
Megalopsalis sp. nov. CP0208C
Megalopsalis triascuta IZ-133421
Megalopsalis triascuta IZ-133415
Monoscutum sp. ZMUC Mono2 2
Mangatangi sp. IZ-133096 3
Mangatangi sp. IZ-29238
Mangatangi parvum IZ-133381
Mangatangi parvum IZ-133096_1
Mangatangi sp. IZ-129534
Mangatangi sp. IZ-129533
Mangatangi sp. IZ-129562
Mangatangi sp. IZ-129518
Mangatangi sp. IZ-129565
Mangatangi sp. IZ-136154
Forsteropsalis pureora CP0287
Forsteropsalis pureora CP0223
Forsteropsalis pureora IZ-29240
Forsteropsalis wattsi IZ-129542
Forsteropsalis wattsi IZ-135693
Forsteropsalis cf. wattsi IZ-135737
Forsteropsalis grimmetti CP0190
Pantopsalis snaresensis
Pantopsalis listeri IZ-29279
Pantopsalis listeri IZ-129513
Pantopsalis sp. IZ-133326
Pantopsalis sp. IZ-133330
Pantopsalis cheliferoides IZ-129512
Pantopsalis cheliferoides IZ-29259
Pantopsalis listeri CP0002
Pantopsalis listeri IZ-129588
Pantopsalis listeri CP0001
Pantopsalis listeri CP0093
Pantopsalis listeri IZ-129587
Pantopsalis listeri IZ-136089
Pantopsalis sp. CP0491
Pantopsalis phocator CP0483
Pantopsalis pococki CP0669
Pantopsalis phocator CP0572
Pantopsalis coronata CP0656
Pantopsalis phocator CP0566
Pantopsalis albipalpis CP0337
Pantopsalis albipalpis CP0372
Pantopsalis cf. coronata IZ-133453
Pantopsalis cf. phocator IZ-133437
Pantopsalis sp. IZ-129586
Pantopsalis sp. IZ-129585
Pantopsalis phocator IZ-129583
Pantopsalis sp. IZ-129582
Forsteropsalis sp. CP0581
Forsteropsalis sp. IZ-135579
Forsteropsalis turneri CP0475
Forsteropsalis turneri IZ-129573
Forsteropsalis turneri IZ-129522
Forsteropsalis turneri IZ-129574
Forsteropsalis turneri IZ-129524
Forsteropsalis turneri IZ-134832
Forsteropsalis turneri IZ-129523
Forsteropsalis turneri IZ-129571
Forsteropsalis turneri IZ-129521
Forsteropsalis turneri IZ-129572
Forsteropsalis sp. CP0775
Forsteropsalis photophaga CP0268
Forsteropsalis sp. nov. IZ-29239
Forsteropsalis bona CP0237
Forsteropsalis bona CP0238
Forsteropsalis sp. IZ-132834
Forsteropsalis sp. IZ-129552
Forsteropsalis fabulosa IZ-129566
Forsteropsalis fabulosa IZ-136168
Forsteropsalis sp. nov. IZ-29252
Forsteropsalis sp. IZ-129525
Forsteropsalis sp. IZ-129517
Forsteropsalis sp. IZ-136136
Forsteropsalis chiltoni IZ-129526
Forsteropsalis chiltoni IZ-129581
Forsteropsalis chiltoni IZ-129584
Forsteropsalis marplesi CP0376
Forsteropsalis sp. IZ-129527
Forsteropsalis sp. IZ-129528
Forsteropsalis sp. IZ-136139
Forsteropsalis sp. IZ-134830
Forsteropsalis marplesi CP0339
Forsteropsalis marplesi IZ-129554
Forsteropsalis sp. nov. IZ-129511
Forsteropsalis sp. IZ-29253
Forsteropsalis inconstans IZ-129520
Forsteropsalis inconstans IZ-129515
Forsteropsalis inconstans IZ-129579
Forsteropsalis inconstans IZ-135565
Forsteropsalis inconstans IZ-136053
Forsteropsalis inconstans IZ-129519
Forsteropsalis inconstans IZ-129580
Forsteropsalis inconstans IZ-129568
Forsteropsalis inconstans IZ-129576
Forsteropsalis inconstans IZ-129539
Forsteropsalis inconstans IZ-129540
Forsteropsalis inconstans IZ-129536
Forsteropsalis inconstans IZ-129535
Forsteropsalis inconstans IZ-129537
Forsteropsalis inconstans IZ-129538
Forsteropsalis inconstans IZ-129541
Forsteropsalis inconstans IZ-129529
Forsteropsalis inconstans IZ-135904
Forsteropsalis inconstans IZ-129575
Forsteropsalis inconstans IZ-129577
0.06
1 2 3 4
5 6 7 8

maximum age based on the first known Phalangioidea, at 340 Ma. The root (corresponding to Palpatores) was constrained to a maximum age of 405 and a minimum age of 340 Ma, following the fossils discussed above.

We ran 223 547 000 generations, sampling one tree every 10 000 and discarding the first 10% of the trees as burn-in. Stationarity of the run and parameter ESS values were visualised in Tracer (ver. 1.6.0, A. Rambaut, A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard, see http://tree.bio.ed.ac.uk/software/tracer/), and used to determine burn-in, the analyses running until all ESS values exceeded 200. A summary tree was generated with TreeAnnotator (ver. 2.6.3, see https://www.beast2.org/treeannotator/), from the BEAST package, using median heights and a maximum clade credibility tree. However, the alternate phylogenetic hypotheses obtained for the different phylogenetic analyses make these conclusions tentative.

All individual gene alignments (in FASTA format), concatenated alignments (in RAXML-ready format), partition txt files, trees inferred from each analysis (in Newick format and pdf format) and the BEAST xml file are available as supplementary information via the Harvard Dataverse (https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/4VHTBG).

Results and discussion

Neopilionid monophyly and basal relationships

Phylogenetic analysis of the combined data, irrespective of outgroup composition or trimming treatment, found a clade including all specimens currently considered members of Neopilionidae, plus *Hesperopilio* (family unassigned) and *Metopilio* Roewer, 1911 (now a member of the new family Globipedidae; see Kury and Cokendolpher 2020), but ultrafast bootstrap support (UFBS) for this clade was low, ranging from 79 to 92% (e.g. Fig. 3). All analyses that include *Vibone* (*Datasets 1, 2, 5* and *6*) placed it as the sister group to a clade that includes all other neopilionid taxa in this clade, but also including *Hesperopilio* (and *Metopilio*), and thus Neopilionidae, as currently circumscribed, was not monophyletic. However, until *Neopilio* can be included in an analysis, no formal rearrangement at the family level can be proposed. *Metopilio* appeared as the next branch in this clade, although with moderate support (86–91% UFBS) (e.g. Fig. 3). The sister group relationship of *Hesperopilio* to all remaining Neopilionidae, however, was supported with 100% UFBS in all but one analysis (*Dataset 6*, where *Hesperopilio* was the sister group to *Thrasychirus*/*Thrasychiroides* with 68% UFBS, this in turn forming the sister group to the remaining Neopilionidae with 100% UFBS). *Hesperopilio* was represented here by its two species, from Australia (*H. mainae* Shear, 1996) and Chile (*H. magnificus* Schultz & Cekalovic, 2006), a trans-Antarctic distribution found only in a few clades of arachnids (e.g. Sharma *et al*. 2018), probably reflecting a Gondwanan origin of the group (as these landmasses were connected via Antarctica until *c.* 35 Ma) (McLoughlin 2001). Because *Hesperopilio*, *Metopilio* and *Vibone* lacked the critical *COI* fragment (as did some other outgroup taxa), they were excluded from some of the analyses, including the BEAST analysis. In all the trees without these taxa, *Protolophus singularis* Banks, 1893 was the sister group of the included Neopilionidae.

Within the latter clade of Neopilionidae, the South American *Thrasychirus*/*Thrasychiroides* was sister group to a clade including all the remaining samples from the Australian–Zealandian (i.e. Australia, New Zealand and New Caledonia) region, finding another parallel to *Hesperopilio*, with a trans-Antarctic distribution, but with a much larger diversity. *Thrasychiroides* currently includes four species from Brazil (Soares and Soares 1947; Pinto-da-Rocha *et al*. 2014) and has always been hypothesised to be related to the Chilean–Argentinean genus *Thrasychirus*, which currently has three accepted species (Cokendolpher and Lanfranco 1985), though with several undescribed ones, some included in this study. *Thrasychiroides* was originally distinguished from *Thrasychirus* based on the lack of a median apical apophysis on the palp patella (Soares and Soares 1947) and later rediagnosed based on genitalic characters (Pinto-da-Rocha *et al*. 2014), but the only phylogenetic analysis including these two genera did not allow for testing monophyly of *Thrasychirus*, as it was represented by a single species (Pinto-da-Rocha *et al*. 2014). The latter analysis and that of Taylor (2011) placed *Thrasychirus* (and *Thrasychiroides*) in a clade of Australian and New Zealand species (with *Australiscutum* Taylor, 2009; *Forsteropsalis* Taylor, 2011; and *Pantopsalis* Simon, 1879), but excluding others (e.g. *Monoscutum* Forster, 1948; *Templar* Taylor, 2008; *Spinicrus* Forster, 1949; *Megalopsalis*), a result that contrasts strikingly with our molecular results. All our analyses found a clade including all the Australian–New Zealand–New Caledonian species – our 'Australian–Zealandian clade' – to the exclusion of the South American ones. This divergence between the South American and the Australian–Zealandian clade was dated to the Middle Jurassic, 169 Ma, but the 95% HPD (119–228 Ma) spans from the Early Cretaceous to the Late Triassic (Fig. 5). Considering an initial rifting of Gondwana (dividing it into West [South America–Africa] and East [Antarctica–Australia–Zealandia] Gondwana) in the Middle Jurassic, *c*. 170 Ma (Ali and Aitchison 2008), this result closely aligns with a Gondwanan vicariance scenario, although we recognise that the lack of ingroup fossils poses a caveat to our dating analyses. However, the role of Africa in this early split cannot be addressed in the present study.

Fig. 3. IQ-TREE result of *Dataset 1*, all taxa (159 taxa) for the untrimmed data (5081 bp). Neopilionidae are coloured as in Fig. 2. Numbers on nodes indicate ultrafast bootstrap support values >50% (values are omitted for the internal nodes of some genera and species; unedited Newick files are available in the Harvard Dataverse). Abbreviations: CP, Christina Painting coll.; IZ, Museum of Comparative Zoology, Invertebrate Zoology collection; NCA, New Caledonia; NSW, New South Wales; TAS, Tasmania; VIC, Victoria; WA, Western Australia; ZMUC, Zoological Museum, University of Copenhagen. Solid square indicates full support for all the analyses conducted for the relevant node.

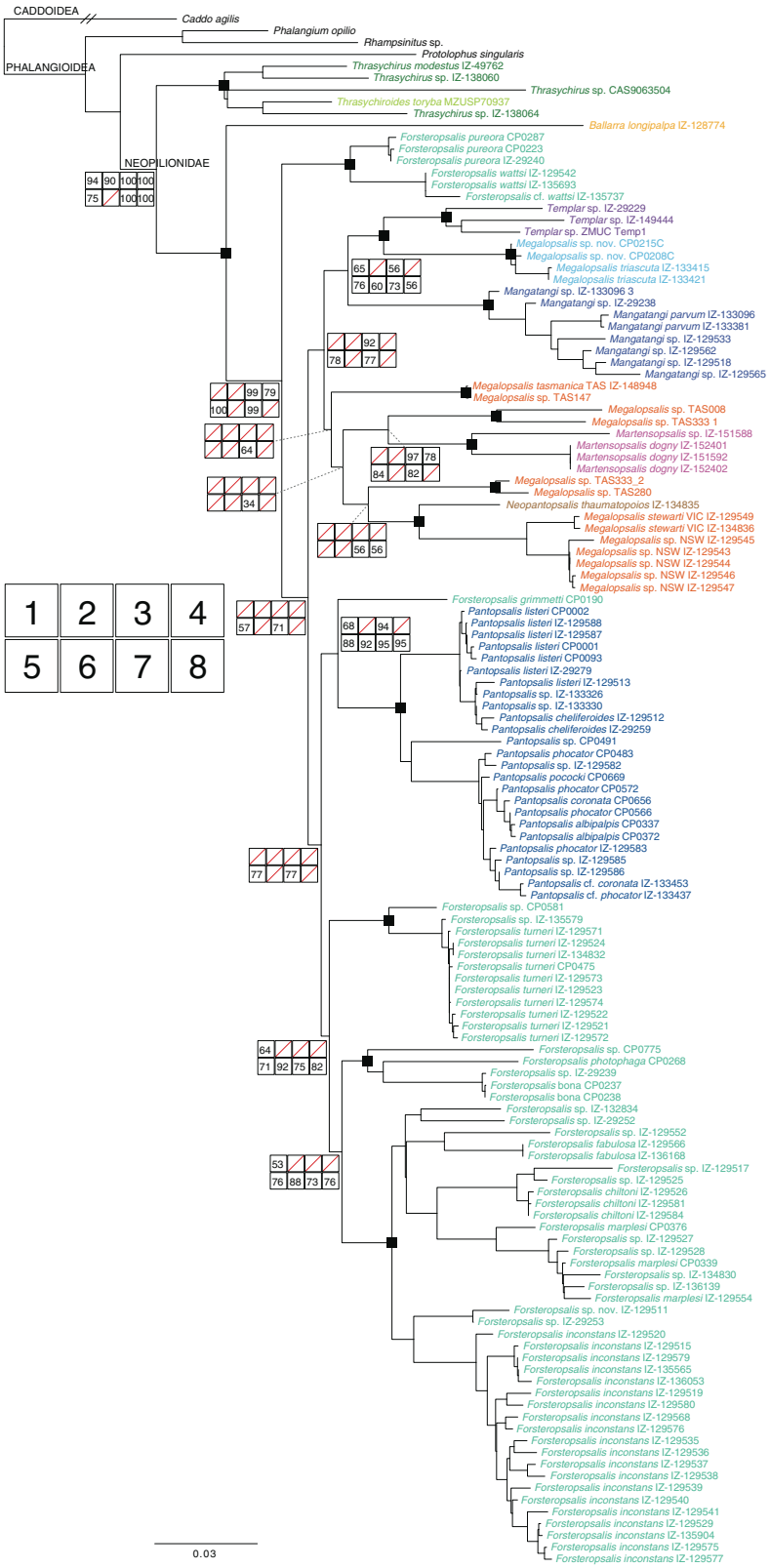


Fig. 4. IQ-TREE result of Eupnoi *Dataset 7*, reduced dataset without Dyspnoi (131 taxa), untrimmed (4937 bp). Legend, symbols and colours as in Fig. 3.

Although outside of the scope of this paper, the members of this well supported South American clade display enormous disparity in palp morphology. For example, *Thrasychirus* sp. IZ-138060 (Fig. 1*A*) has wide, hypertrophied palps, whereas *Thrasychirus modestus* Simon, 1902 MCZ IZ-49762 (Fig. 1*C*), recovered as its sister species in our phylogeny, has short, slender palps; and *Americovibone* (which may or may not belong to this clade) has extremely elongated and thin palps (see Hunt and Cokendolpher 1991, fig. 23). Future work will address the taxonomy of the South American neopilionids, which will require detailed information about the ontogeny of the palps.

The initial diversification of the South American species was estimated to have occurred between 33 and 92 Ma, in the Oligocene to Upper Cretaceous (Fig. 5), a range too wide to postulate any meaningful biogeographic hypothesis. However, the divergence between the sampled terminals corroborates the idea of multiple undescribed species, as well as the paraphyly of *Thrasychirus* with respect to *Thrasychiroides* (Fig. 3–5). Given the broad disparity in palp morphology, the large number of undescribed species, and the lack of a proper phylogenetic framework for this clade, taxonomic changes at the genus level will certainly be required once the group is properly revised, including its genital morphology, which was used by Pinto-da-Rocha *et al*. (2014) to rediagnose the genera.

An Australian–Zealandian clade

All the samples from Australia and Zealandia (see Mortimer *et al*. 2017) formed a clade supported by 100% UFBS, irrespective of the analysis. In the BEAST analysis, the original diversification of the Australian–Zealandian clade dated back to the Cretaceous (110 Ma; 95% HPD: 85–141 Ma). Even the most recent estimate predates the rafting of Zealandia from Australia, *c.* 80 Ma, thus indicating a history in this part of East Gondwana before the opening of the Tasman Sea. This ancient cladogenesis probably explains why the neopilionid faunas from Australia and New Zealand may not be monophyletic. However, we recognise that the poor resolution of the backbone of this part of the tree could allow for alternative biogeographic hypotheses.

In order to facilitate discussion of the multiple lineages within this clade, the following taxa can be recognised: (1) *Martensopsalis* from New Caledonia; (2) *Ballarra* (our only representative of this Australian lineage that probably includes several other Ballarrinae); (3) one to three additional clades of eastern Australian species; (4) the New Zealand genus *Mangatangi*; (5) a second New Zealand clade including the genera *Monoscutum*, *Templar* and some New Zealand species currently placed in the otherwise Australian genus *Megalopsalis*; and (6) a third large clade of New Zealand species (including all *Forsteropsalis*, *Pantopsalis* and *Megalopsalis turneri* Marples, 1944). These 6–8 clades were well supported at least in some analyses, but their interrelationships were not, thus providing weak resolution for the backbone of the Australian–Zealandian Neopilionidae, which is dataset-dependent:

- *Dataset 1* found two Australian clades, with *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae and monophyly of New Zealand (63% UFBS).
- *Dataset 2* found four Australian clades, with *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae and non-monophyly of New Zealand, which divides between *Mangatangi* and the remaining New Zealand species, a clade that receives 84% UFBS (Fig. 3).
- *Dataset 3* found *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae, and a clade of Australian–New Caledonian species (68% UFBS) deeply nested within the New Zealand taxa.
- *Dataset 4* found *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae, and *Mangatangi* nesting within an Australian–New Caledonian clade (which receives 74% UFBS). This clade in turn was deeply nested within the remaining New Zealand taxa. The BEAST analysis of this dataset, however, found *Ballarra* more deeply nested in the Australian–Zealandian clade, as the sister group to all the New Zealand species except for *Mangatangi*. It also recovered three additional Australian clades, and placed the New Caledonian species as the first divergence in the Australian–New Zealandia clade (Fig. 5).
- *Dataset 5* found *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae, and a clade of Australian–New Caledonian species (66% UFBS) nesting within the New Zealand taxa.
- *Dataset 6* found three Australian clades, with *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae and monophyly of New Zealand's taxa (with 53% UFBS).
- *Dataset 7* found *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae, and a clade of Australian–New Caledonian species (64% UFBS) nesting within taxa from New Zealand (Fig. 4).
- *Dataset 8* found four Australian clades, with *Ballarra* as sister group to all other Australian–Zealandian Neopilionidae and monophyly of New Zealand's taxa with 52% UFBS.

Excepting *Ballarra*, reciprocal monophyly of Australia and New Zealand's groups was found in one analysis (*Dataset 1*). Two additional analyses showed monophyly of the New Zealand taxa (*Datasets 6* and *8*), but Australian taxa were paraphyletic. These two scenarios are compatible with those of other animals that diverged before the opening of the Tasman Sea (Giribet *et al*. 2018; Baker *et al*. 2020*a*), but while our sampling of New Zealand is exhaustive, our representation of Australian species relies on just a few specimens from Western Australia, Tasmania, Victoria and New South Wales, and should be improved in future studies.

Our only representative of the Australian Ballarrinae, from Western Australia, appeared as sister group to the remaining Australian–Zealandian species in all the IQ-TREE analyses (Fig. 3, 4), or as sister group to the New Zealand clade excepting *Mangatangi* in the BEAST analysis (Fig. 5). *Ballarra longipalpa* was, together with *Vibone vetusta*, the only member of Ballarrinae included in our analyses, but they never formed a clade. Until the other nine species in the subfamily, including *Americobivone* – now also with a species from New Zealand (Taylor 2016) – are sampled, little can be said about the validity of the subfamily, as already stated in earlier molecular studies (Vélez *et al*.

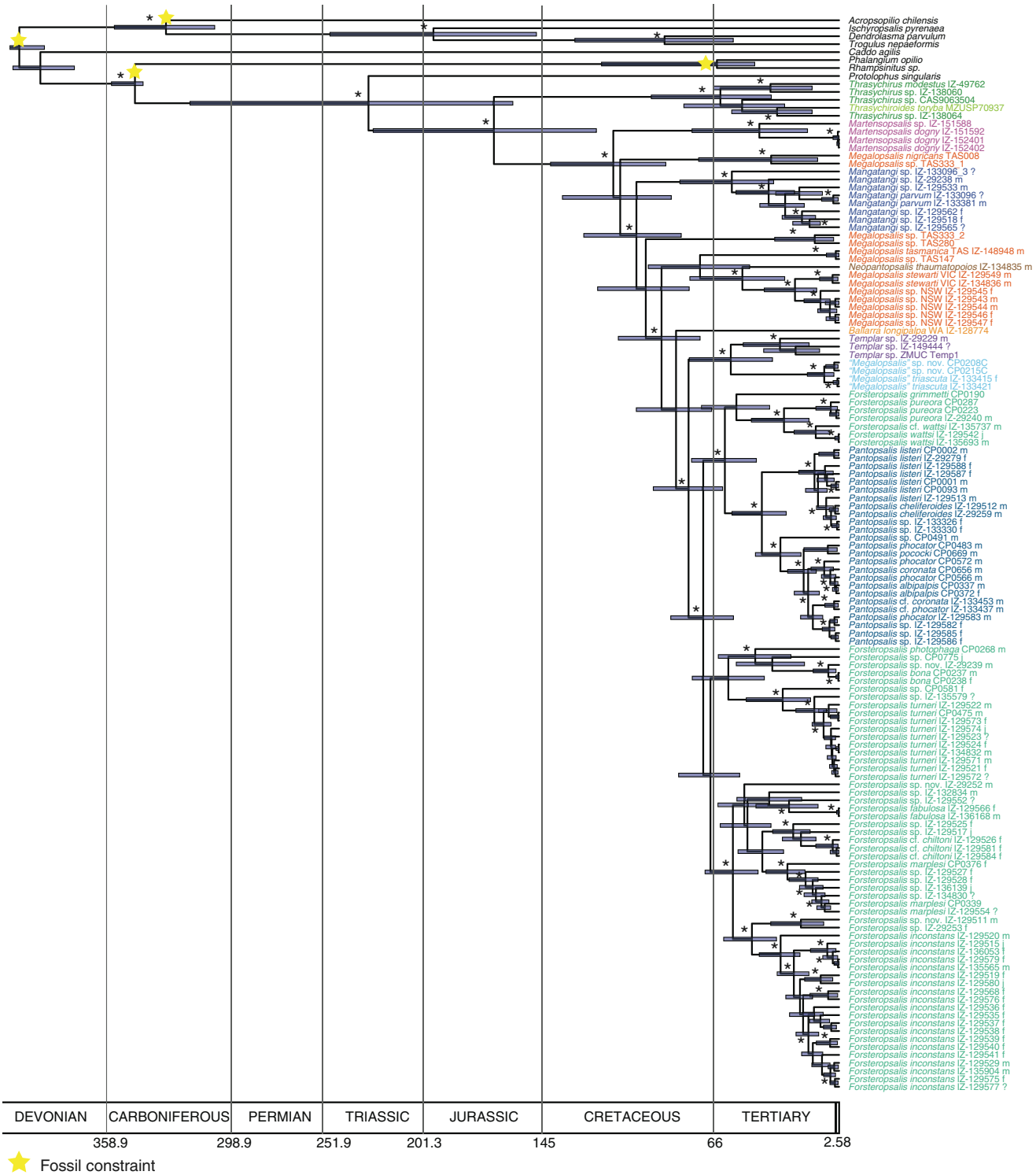


Fig. 5. BEAST chronogram of *Dataset 4*, reduced dataset including Dyspnoi (135 taxa) for the trimmed data (4741 bp). Error bars at nodes show 95% highest probability densities of estimated divergence times. Yellow stars indicate fossil calibrations (see text for details). Legend as in Fig. 3. Males (m), females (f) and juveniles (j) are indicated in key specimens. Asterisks on nodes indicate a posterior probability >0.95. Colours as in Fig. 3.

2014). We hope to focus on these species in future studies using ultraconserved elements so as to be able to utilise museum specimens, given that specimens in the wild can be extremely elusive.

The New Caledonian specimens included two species (one undescribed) in the genus *Martensopsalis*, and probably constitute an early divergence in the Australian–Zealandian clade (Fig. 3–5). Alternative resolutions placed the New Caledonian species nested within a larger Australian or Australian–New Zealand clade (*Datasets 3, 4, 5, 7*). The BEAST analysis (Fig. 5) placed *Martensopsalis* as the sister group to all other Australia–Zealandia specimens, diverging from these in the Cretaceous and starting to diversify on Grande Terre around the time of its re-emergence under oceanic crust in the Eocene *c.* 37 Ma (Grandcolas *et al*. 2008) (95% HPD: 15–72 Ma). This is an extraordinary result when compared against the biogeographic patterns of the other three New Caledonian families of Opiliones. In Triaenonychidae, the New Caledonian samples are deeply nested within a clade of New Zealand species, constituting one or two recent invasions in the Palaeogene–Neogene (Baker *et al*. 2020*b*; Derkarabetian *et al*. 2021*b*). In the case of the other major family of Opiliones, the Laniatores family Zalmoxidae, the New Caledonian species are also of a Cretaceous origin, but in this case they arrived from other South Pacific islands, and not from the landmasses of the former temperate Gondwana, and started diversifying in New Caledonia in the Palaeogene (48.9 Ma; 95% HPD: 37.1–65.8 Ma) (Sharma and Giribet 2012). Finally, for Cyphophthalmi, New Caledonia hosts an ancestral lineage with its endemic family Troglosironidae (Sharma and Giribet 2009; Nattier *et al*. 2017; Giribet *et al*. 2021*b*), with no phylogenetic ties to other nearby families, their highly divergent sister group inhabiting the Afrotropics and the Neotropics (Giribet *et al*. 2012; Oberski *et al*. 2018). The family Neopilionidae thus shows a different pattern from other families of Opiliones, making it extremely difficult to generalise anything with respect to the evolutionary origins of the New Caledonian opiliofauna. This harvestman fauna is certainly unlike most other arthropod groups that seem to have arrived relatively recently from Australia or New Zealand (Nattier *et al*. 2017) – it maintains an Australian–Zealandian connection, but does not require recent dispersal. Interestingly, neopilionids were not known from New Caledonia until its recent discovery by Giribet and Baker (2019) but are now known from multiple localities (Giribet *et al*. 2021*a*), some with dense rainforest and high-elevation maquis that have received relatively little faunistic attention.

The remaining samples in this Australian–Zealandian clade included members of the Australian genera *Megalopsalis* and *Neopantopsalis* as well as the New Zealand genera *Monoscutum*, *Templar*, the New Zealand *Megalopsalis* (for *M. triascuta* Forster, 1944 and *M. turneri*), *Mangatangi*, *Forsteropsalis* and *Pantopsalis*, i.e. the members of Enantiobuninae, excluding the South American *Thrasychirus*/*Thrasychiroides*. However, as stated above, relationships within this clade are unstable and analysis-dependent.

Australia

The Australian fauna of Neopilionidae was clearly non-monophyletic, as *Ballarra*, our only representative of the Australian Ballarrinae, diverged earlier than the remaining Australian species, all in Enantiobuninae. Our sampling included 11 specimens tentatively identified as *Megalopsalis* from Tasmania, Victoria and New South Wales, as well as one species of *Neopantopsalis*. We are therefore missing a substantial diversity of the group, including the monotypic Western Australian genus *Tercentenarium* (previously in *Megalopsalis*) (Taylor 2008, 2011) as well as much of the eastern Australian diversity. Nevertheless, what we identified as *Megalopsalis* were either resolved as multiple lineages (Fig. 3–5) or a single lineage (*Dataset 1*), depending on the analysis (see above). At this point, being conservative, we see 2–4 lineages of Australian Neopilionidae and 1–3 lineages of Australian Enantiobuninae. The fact that the Tasmanian samples, with three described species, all in the genus *Megalopsalis*, appeared in three distinct clades may seem uncharacteristic, but a much larger analysis based on *COI* data and including 44 Tasmanian samples and hundreds of other enantiobunines (mostly from New Zealand) also showed three distinct and not closely related Tasmanian clades (authors' unpublished data). One of these lineages seems to correspond to a small unsclerotised species that could indeed constitute a separate genus. The existence of multiple unrelated Opiliones lineages in Tasmania is also the case for the other main family, Triaenonychidae (Baker *et al*. 2020*b*; Derkarabetian *et al*. 2021*b*).

The enantiobunine fauna of Australia comprises 30 species in 4 genera: *Australiscutum* (3 species from eastern Australia) (Taylor 2009); *Megalopsalis* (with 20 species in Australia, and 2 not closely related ones from New Zealand), including species previously described in the now synonymised genera *Macropsalis*, *Spinicrus* and *Hypomegalopsalis* (see Taylor 2013*a*); *Neopantopsalis* (with 6 species from north-eastern Australia), including species previously assigned to *Pantopsalis* and *Spinicrus* (Taylor and Hunt 2009); and the monotypic *Tercentenarium*. The generic circumscriptions have therefore been in flux and our sampling suggests that the Australian *Megalopsalis*, as currently defined, may contain more than one genus. Alternatively, in one of the analyses *Megalopsalis* formed a (poorly supported) clade, but in this case *Neopantopsalis* still nested within *Megalopsalis*.

Admittedly, the resolution as well as our sampling and our knowledge of the Australian enantiobunines remain insufficient to properly address this undoubtedly interesting group of Neopilionidae. We hope to invest more effort in this group in the future as additional samples become available for molecular study.

New Zealand

Mangatangi, Monoscutum, Templar, etc.

As discussed above, monophyly of New Zealand taxa was supported in three analyses (*Datasets 1, 6, 8*), but others

suggested a division into multiple clades, some separating *Mangatangi* from all the remaining New Zealand species (*Dataset 2* and Fig. 5). The genus *Mangatangi* was erected for a species described from the Hunua Ranges, in the northern part of the North Island (Taylor 2013*b*), *M. parvum* Taylor, 2013. This is a small and unsclerotised neopilionid species with moderately enlarged chelicerae in the males (Fig. 1*H*). Females and juveniles have remained largely ignored in collections – in fact, the *M. parvum* specimens used for the description of the genus had been in a museum since 1977. Another specimen, originally identified as *M. parvum*, was later reported from Te Urewera National Park, also in the North Island, by Giribet *et al*. (2014). Here we included genetic data from specimens from the type locality (MCZ IZ-133381), the Te Urewera specimen (MCZ IZ-29238), and additional specimens of *Mangatangi* from the North and South Islands. Our results showed that the Te Urewera specimen represents a different species from *M. parvum*, and that additional species remain to be described, even though they all are morphologically very similar. Examination of additional samples will be needed to resolve the taxonomy of *Mangatangi*, a genus that began diversifying since *c*. 52 Ma (95% HPD: 32–78 Ma), in the Palaeogene to Late Cretaceous. This inferred date largely predates the 'Oligocene drowning', an episode of major marine transgression affecting much of the New Zealand landmass (Cooper and Cooper 1995) although, as discussed above, these dates are tentative given the lack of ingroup calibrations.

Some analyses supporting monophyly of the New Zealand neopilionids placed *Mangatangi* as the sister group to a clade of *Monoscutum*, *Templar*, *Megalopsalis triascuta* and a putative new species closely related to *M. triascuta*. *Monoscutum* and *Templar* are both monotypic genera from New Zealand. *Monoscutum titirangiensis* Forster, 1948 is known from its type locality of Titirangi, near Auckland, whereas our specimens of *Monoscutum* are from more distant places in the North Island, and for the time being are designated as *Monoscutum* sp., given the paucity of material for study. In addition, these specimens did not sequence well, and for two of them we have only *COI* data available whereas for the other specimen only the *28S* rRNA sequences are available, and thus *Monoscutum* artefactually appeared as non-monophyletic, yet both *28S* rRNA and *COI* placed them with the members of *Templar* and the New Zealand *Megalopsalis*. Focused sampling for *Monoscutum*, as well as the putatively related genus *Acihasta*, should help resolve relationships in this clade of New Zealand neopilionids. Our results suggest that a new genus may need to be erected for *Megalopsalis triascuta* (and its unnamed sister species), as this clade was not closely related to any of the Australian *Megalopsalis*, and the type locality of the type species of *Megalopsalis* is in New South Wales.

The remaining New Zealand samples included a diverse set of representatives from the genera *Forsteropsalis* and *Pantopsalis* plus *Megalopsalis turneri* – a species that had not been formally transferred to either of the New Zealand genera but which Taylor (2011) suggested might be a possible member of *Forsteropsalis*, and indeed has been referred to as *Forsteropsalis turneri* in previous studies (e.g. Vélez *et al*. 2014). Species within *Forsteropsalis* and *Pantopsalis* have been included in several different genera in the past. The diagnostic character for these genera is whether the pedipalpal coxa bears a distinct array of denticles prolaterally (in *Forsteropsalis*) or is unarmed prolaterally (in *Pantopsalis*). The generic circumscriptions based on this pedipalpal character were tested in a cladistic analysis that included two *Pantopsalis* species (*P. albipalpis* Pocock, 1903 and *P. listeri* (White, 1849) [as *P. luna* (Forster, 1944), now a junior synonym of *P. listeri*]) and four *Forsteropsalis* species (*F. chiltoni* (Hogg, 1909), *F. fabulosa* (Phillipps & Grimmett, 1932), *F. grimmetti* (Forster, 1944) and *F. inconstans* (Forster, 1944)) (see Taylor 2011). However, *F. grimmetti* differed from the other members of *Forsteropsalis* in several small details, and it has therefore been informally placed in *Pantopsalis* by C. K. Taylor (unpublished Key to New Zealand Palpatores). We did recover monophyly of *Pantopsalis* (excluding *F. grimmetti*) with 100% UFBS in all analyses, and found *F. grimmetti* as the sister group to *Pantopsalis* in six of the IQ-TREE analyses, with variable support (68–95% UFBS). However, no analysis supported monophyly of *Forsteropsalis*, which was often paraphyletic with respect to *Pantopsalis* and *Megalopsalis turneri*. Given the slight morphological differences between *Forsteropsalis* and *Pantopsalis*, the genus *Forsteropsalis* may seem unjustified at this point. However, in the absence of a more stable phylogenetic backbone we prefer not to take any taxonomic action other than transferring *M. turneri* to *Forsteropsalis*, as *Forsteropsalis turneri* (Marples, 1944), **comb. nov.**, recognising that in the future *Forsteropsalis* may need to be synonymised with *Pantopsalis*.

Pantopsalis

The genus *Pantopsalis* contains 10 valid species plus 5 synonymised species-group taxa. Among our samples, we were able to identify six species based on male morphology, but some of these morphospecies were contradicted by our results, and some males were unable to be assigned to species. In our analyses, *Pantopsalis* divided into two main clades. One clade comprised specimens from the North Island and the western side of the South Island, including samples identified as *P. listeri* and *P. cheliferoides* (Colenso, 1883), but specimens identified as *P. listeri* appeared in three distinct subclades. *Pantopsalis listeri* and *P. cheliferoides* have some very similar overall morphology but were found to be reciprocally monophyletic in earlier population-level analyses (Fernández *et al*. 2014). All our specimens identified as *P. listeri* came from or near Mount Aspiring National Park in the west coast of the South Island, while the specimens identified as *P. cheliferoides* were from the north of the South Island and appeared as sister group to two unidentified females from the North Island, from Tongariro National Park

The second clade comprised specimens from the east and southern region of the South Island, including Stewart Island, and included samples identified as *P. albipalpis*, *P. coronata* Pocock, 1903, *P. phocator* Taylor, 2004, and *P. pococki* Hogg,

1920. For the most part, these morphospecies were not recovered as monophyletic, though the chronogram did identify multiple clades that date to the Neogene, and which therefore probably correspond to species (Fig. 5). One example was the clade comprising samples CP0572 and CP0566 (identified as *P. phocator*), CP0656 (identified as *P. coronata*) and samples CP0337 and CP0372 (identified as *P. albipalpis*), dated to *c*. 7.3 Ma; another clade included two samples identified as *P. pococki* and *P. phocator* respectively (*c*. 5.5 Ma); a third clade included two specimens identified as *P.* cf. *coronata* and *P.* cf. *phocator* (*c*. 2.4 Ma); and yet a forth clade included a male identified as *P. phocator* and three unidentified female individuals (*c*. 4.7 Ma). The identified specimens included those neopilionids with distinctly pigmented supracheliceral lamellae, distinct palp colouration, and striking opisthosomal colouration, that goes from white (over the usual black background) to yellow and orange (e.g. Fig. 1*N*, *O*).

Pantopsalis has had a convoluted taxonomic history, and many of its species were described without fully appreciating the extent to which the group exhibits both sexual dimorphism and male polymorphism; as a result, it is plagued with synonymies (Taylor 2004). In addition, little is known about the variation in live colouration both within and among species, as even the most recently described species, *P. phocator*, from Stewart Island, was based on old museum specimens collected in 1981 whose colours had been largely washed away in ethanol. In the description of this species, Taylor (2004) recognised *P. phocator* as being very similar to *P. coronata* and *P. albipalpis*, distinguishing the new species by the presence of bright white articular membranes. He also noted that *P. phocator* has more denticulation on the carapace than *P. coronata*, and the 'grey abdominal areas' (probably depigmented) are restricted to the lateral sides, not extending medially in transverse stripes. But without a detailed examination of larger numbers of specimens to assess variability, and without information about the live colouration of the types, which can be striking in these species, it may be difficult to segregate these species.

The clade composed of male IZ-129583 and the three females IZ-129582, IZ-129585 and IZ-129586 included samples from Oban, Stewart Island | Rakiura, probably close to the type locality of *P. phocator*, which is from Codfish Island | Whenua Hou. The male specimen presents what is today considered the typical colouration of *P. phocator* (see images of the specimen in https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:129583). The immediate sister group to this clade included two specimens that originally were identified as different species: *P.* cf. *coronata* from Southland, which lacks bright colouration (see https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:133453); and *P.* cf. *phocator* from Stewart Island, with striking white membranes at the base of the chelicerae and red–white colouration on the abdomen (see https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:133437). Despite these drastic morphological differences, they formed a well-supported clade, clearly indicating that at least two species of *Pantopsalis* live on Stewart Island, one of which also inhabits the South Island. Other specimens originally identified as *P. phocator*, based on morphology, were from Lake Hauroko (Southland) (CP0483) and Catlins Forest Park (Otago) (CP0566 and CP0572), both localities in the southern part of the South Island, but they clearly belong to two different species. Both sets of localities are quite distant from the type locality of *Pantopsalis coronata*, which is Timaru (Pocock 1903*a*), but not too far from the type locality of *Pantopsalis albipalpis*, which is Maungatua, south of Dunedin (Pocock 1903*b*). Given the mixed identifications of specimens in multiple clades, it seems that external morphology and colour patterns are poor characters (or not sufficiently understood in terms of polymorphism) for identification of these species, and further work, including inspecting type specimens as well as new material from the type localities, will be needed to resolve the taxonomy of this clade of *Pantopsalis*. In addition, it is also worth noting that several localities have yielded specimens in more than one clade, including Stewart Island (see above) or Lake Hauroko, which, in addition to specimen CP0483, has also yielded specimen CP0491, a male from an unidentified species that appeared as the sister group to all the remaining members of this clade.

Forster (1964) described four *Pantopsalis* species from offshore islands of New Zealand (Snares, Auckland and Campbell Islands), and from these only *Pantopsalis snaresensis* Forster, 1964 was included in our study, although unfortunately only amplified for *COI*. This gene clearly placed this species within *Pantopsalis*, but it is unclear whether it was the sister species to all other *Pantopsalis* (*Datasets 1, 6*) or sister group to the southern clade (the *P. phocator* clade) (e.g. Fig. 3). Future sampling effort should target the other two valid species, *P. johnsi* Forster, 1964 (*P. mila* Forster, 1964 was synonymised with *P. johnsi* by Taylor 2004), from Auckland Island, and *P. rennelli* Forster, 1964 from Campbell Island.

The last remaining *Pantopsalis* species, not sampled here, is *P. halli* Hogg, 1920, the description of which was based on a female specimen from Mount Algidus, in Rakaia Gorge (South Island), and which is poorly preserved and considered of uncertain status (Taylor 2004).

Forsteropsalis

No matter the treatment, *Forsteropsalis* Taylor, 2001 was never recovered as monophyletic, in our analyses as in most cases it was paraphyletic with respect to *Pantopsalis* (see also Vélez *et al*. 2014), the whole clade (*Forsteropsalis* + *Pantopsalis*) originating between the Eocene and the Late Cretaceous (95% HPD: 52–82 Ma), long before the Oligocene drowning of New Zealand. *Forsteropsalis* was erected to accommodate the majority of the New Zealand species previously placed in *Megalopsalis* and *Pantopsalis*, and was diagnosed by (1) the small pointed apophysis present on the pedipalpal patella in both sexes (except for females of *Forsteropsalis grimmetti* and males of *F. distincta* (Forster, 1964)), and (2) by the array of denticles on the medial side of the pedipalpal coxa (Taylor 2011). In addition, *Forsteropsalis* can be distinguished from the Australian *Megalopsalis* by the penis, exhibiting a more elongate, narrower glans. Females,

including those of *F. grimmetti*, can be distinguished from *Megalopsalis* by possessing four rather than two seminal receptacles. However, at the time of the family's original description some species were left in *Megalopsalis* due to lack of study material, such as *Megalopsalis turneri*. This species, here transferred to *Forsteropsalis*, appears closely related to other *Forsteropsalis* specimens in all analyses, and never closely related to the other leftover New Zealand '*Megalopsalis*' – *M. triascuta* Forster, 1944.

Due to the instability of the backbone, relationships within *Forsteropsalis* presented different alternatives, but there were some trends that we would like to highlight here. Most analyses found a clade including the bulk of *Forsteropsalis* samples: *F. fabulosa*, *F. chiltoni*, *F. marplesi* (Forster, 1944), *F. inconstans*, *F. bona* Taylor & Probert, 2014, *F. photophaga* Taylor & Probert, 2014 and *F. turneri*. Another clade included *F. pureora* Taylor, 2013 and *F. wattsi* (Hogg, 1920), which sometimes grouped with *F. grimmetti* and *Pantopsalis*. Indeed, the only datasets providing high support values in this part of the tree recovered a clade including all the samples of *Forsteropsalis* plus *Pantopsalis* (*Datasets 1, 2, 6*).

Forsteropsalis pureora and *F. wattsi* were both represented by multiple specimens and together formed a well supported clade in all analyses. The type locality of *Forsteropsalis pureora* is Waipapa Reserve, in the Bay of Plenty (North Island), and our included specimens spaned the central part of the North Island, from near Waitomo in the west, to Te Urewera National Park and the Bay of Plenty. The type locality of *F. wattsi* is Hawera, also in the North Island, but farther south, and our specimens all came from the South Island. Two were from the Cook Strait area, but the other specimen, identified as *F.* cf. *wattsi*, was from the southern tip of the South Island, and given the divergence time (diverging from the other samples *c*. 11.4 Ma), it probably constitutes an undescribed species.

Forsteropsalis grimmetti was represented in our study by a single specimen from near Haast, in the west coast of the South Island, while its type locality is Waiho Gorge, near Franz Josef, also in Southland (https://collections.tepapa.govt.nz/object/127237). This species either clustered with *Pantopsalis* (Fig. 3, 4), as sister group to a clade composed of *F. pureora* and *F. wattsi* plus *Pantopsalis* (*Dataset 2*), or with *F. pureora* and *F. wattsi* alone (Fig. 5). This position near *Pantopsalis* is reflected in the characters discussed above where the females of *F. grimmetti* disagree with the diagnostic character of *Forsteropsalis*.

Another small but well supported clade across analyses was the one including *F. bona* and *F. photophaga*, two troglophilic species based on material from the Waitomo region of the North Island (Taylor and Probert 2014), plus two putative new species. We sampled a male and a female of *F. bona* from Waitomo (CP0237, CP0238) and a male of *F. photophaga* (CP0268) from a nearby locality, plus a male of a putative new species from Te Urewera National Park (MCZ IZ-29239; see images in https://mczbase.mcz.harvard.edu/guid/MCZ:IZ:29239) and a juvenile of another putative new species from Northland (CP0775). *Forsteropsalis grayi* (Hogg, 1920) was described based on a female from Waikeremoana, in Te Urewera National Park, but the holotype is poorly preserved and this taxon has been considered a *nomen dubium* by Taylor (2011). Although other species have been collected from the area, it is possible that the male MCZ IZ-29239 could correspond to this species. Using the new generation of ultraconserved elements that allow sequencing DNA from degraded Opiliones specimens (e.g. Derkarabetian *et al*. 2019), it could be possible to link the type to recent collections.

Another well supported but small clade, sometimes sister group to the *bona–photophaga* clade (*Datasets 2, 4*) or to that clade + a larger *Forsteropsalis* clade (see below; *Datasets 1, 5–8*), included all our specimens identified as *F. turneri*, plus two other unidentified specimens, a female (CP0581) from Catlins Forest Park, in Otago (south of the South Island), and another one from near Haast (Southland) (MCZ IZ-135579). All our specimens of *F. turneri* were from the Clifden Caves area, in Southland. The type material of *F. turneri* consists of a single dry male collected near Lake Manapouri (Marples 1944), but the locality is not precise and Clifden Caves are located ~60 km south of Manapouri.

Finally, a large well supported clade included a diversity of *Forsteropsalis* species: *F. fabulosa*, *F. marplesi*, *F. chiltoni*, *F. inconstans*, and a few additional individuals that were either unidentified or may constitute new species. *Forsteropsalis fabulosa* is a very distinctive species described from Wellington, and we have included a male and a female from Belmont Regional Park, north of Wellington. The status of *F. fabulosa* is unclear, as the type is lost and Forster (1944) designated a neotype that was later deemed a male of *F. inconstans* by Taylor (2011) (see Forster's neotype at https://collections.tepapa.govt.nz/object/127171), another species described from the Wellington area. In the latter publication, Taylor (2011, p. 51) stated that '[i]n order to stabilise the definition of *Macropsalis fabulosa*, a proposal will be submitted to the ICZN (in preparation) to set aside Forster's (1944) neotype and establish a new neotype in closer accord with the original description' but to our knowledge, such request has not been submitted. *Forsteropsalis fabulosa* was sister group to an unidentified specimen from the Akaroa Peninsula, in the South Island (MCZ IZ-129552).

Another subclade includes specimens identified as *F. chiltoni* and *F. marplesi*, plus several unidentified females and juveniles. *Macropsalis chiltoni* Hogg, 1910, from Stewart Island, is the type species of *Forsteropsalis* – an odd designation since the whereabouts of the type specimen of this species are unknown, but this decision was made based on the supposed presence of a single species of *Forsteropsalis* in Stewart Island (Taylor 2011). Likewise, a lectotype of *Megalopsalis marplesi* Forster, 1944, from Dunedin, was designated by Taylor (2011) after evaluating what was supposed to be a type series that only contained a female specimen; that female therefore was designated as the lectotype, but the lectotype designation is not valid, as there is no solid evidence of a syntype series, and Forster (1944) designated a type for it. *Forsteropsalis marplesi* and *F. chiltoni* are very similar, and according to Taylor (2011), both species can only be distinguished by the number of pseudosegments in the second tibia. However, this character has been shown to vary within species, as in one specimen of *F. marplesi*, where the pseudoarticulation in tibia IV on one side is only present dorsally, fading out ventrally, or in a female *F. chiltoni*, which

had six pseudosegments in tibia II on one side of the body and five on the other side, overlapping with the range of *F. marplesi* (Taylor 2011).

Our specimens of the *chiltoni–marplesi* clade came from the southern part of the South Island (Otago and Southland) and Stewart Island. They divided into two clades that originated *c*. 37 Ma and that each diversified during the Oligocene, perhaps suggesting a cladogenetic event coinciding with the Oligocene drowning, and that today may constitute two very similar sister species. One of these clades included our specimens identified as *F. chiltoni*, from Stewart Island (MCZ IZ-129526, 129581, 129584) (ID based on Fernández *et al*. 2014, which included a male) plus an unidentified female from Clifden caves (MCZ IZ-129525). The other clade included specimens ranging from Dunedin (CP0376), to the Catlins and Invercargill (Otago and Southland), but it also contained a female from Stewart Island (MCZ IZ-129527). Therefore, given the presence of two possible species in Stewart Island, the lack of male types for both species, and the nearly indistinguishable anatomy of the species, further work will be needed in this clade that may bear the signal of the Oligocene drowning event that has been so important in shaping New Zealand's biodiversity.

The Nelson–Marlborough region harbours a few specimens that we have identified as new species, one being a male from Mt Stokes (MCZ IZ-29252; Fig. 1*L*), which appeared as sister group to the *chiltoni–marplesi* clade in some analyses or as an independent lineage of a small, lightly sclerotised species for which little material is available. Two other specimens appeared as a clade, sister group to *F. inconstans*, a male and a female from the same locality, Mt Stokes (MCZ IZ-129511, IZ-29253).

The remaining samples included several *F. inconstans* specimens, a species described based on a female from Wellington (https://collections.tepapa.govt.nz/object/127263). Our samples included multiple specimens from the North Island (Manawatu–Wanganui, Wellington) and the South Island (Marlborough, Tasman, West Coast), as an earlier study (Vélez *et al*. 2014) found it to be one of the most widespread neopilionid species across New Zealand. The sampled specimens of this species started diversifying *c*. 29 Ma in the Oligocene (95% HPD: 19–39 Ma), and the earliest diverging specimens were all from the South Island except for one (MCZ IZ-129576); another terminal clade included four specimens from the North Island, two males from Karori Wildlife Sanctuary, in Wellington (MCZ IZ-129529, IZ-135904) and two other specimens from Tararua Forest Park (MCZ IZ-129575, IZ-129577).

Two additional species of *Forsteropsalis* were not included in this study: *F. distincta*, a species from Auckland Island, one of the sub-Antarctic islands of New Zealand not available for study; and *F. tumida* (Forster, 1944), a distinctive species from Khandallah, near Wellington (type illustrated here: https://collections.tepapa.govt.nz/object/127669) that has been considered of doubtful validity by Taylor (2011) and could be a synonym of *F. fabulosa*.

Our results clearly showed that *Forsteropsalis* (including *Pantopsalis*) consists of a large number of described species and several undescribed ones. They also illustrated that multiple species may be found in certain areas (e.g. Stewart Island, Mount Stokes, certain sites in Wellington) and, therefore, in the absence of careful examination of types, simply using the collecting locality to assign neotypes without additional information should be avoided.

Final remarks

This represents the first comprehensive molecular study of the family Neopilionidae with a broad sampling not restricted to New Zealand. Despite the lack of the type genus of the family and a suboptimal sampling of the Australian diversity, we were able to include key diversity from South America (largely undersampled in prior studies), New Caledonia (previously unsampled) and especially New Zealand. We also demonstrate the existence of a well-supported clade including all Enantiobuninae and the Australian Ballarrinae, though this excludes *Vibone*, a member of the South African Ballarrinae. While the monophyly of Enantiobuninae remains questionable, Ballarrinae is clearly diphyletic, even with only 2 of the 11 known species sampled. Our data also identified *Martensopsalis* as a clade of New Caledonian neopilionids related to, or nested within, the other Australian–Zealandian species, containing at least two unnamed species in an undescribed genus. The Australian Enantiobuninae need additional work, and currently the genus *Megalopsalis* looks like a catch-all genus that probably needs splitting into multiple genera, as the few species from Tasmania clearly do not form a clade. Finally, the question of whether the New Zealand neopilionids form a monophyletic group or not remains to be satisfactorily resolved. The New Zealand neopilionid fauna includes some deep diverging clades, such as *Mangatangi*, a genus so far monotypic but that has multiple undescribed species in both the North and South islands. The other groups probably include the *Templar*, *Monoscutum*, and '*Megalopsalis*' *triascuta* lineages on the one hand, and *Pantopsalis* and a paraphyletic *Forsteropsalis* on the other.

While Neopilionidae has emerged as an invaluable system to study the evolution of animal weapons and polymorphism (Painting *et al*. 2015; Powell *et al*. 2020), it has also begun to shed some light into the biogeographic history of Gondwana. A more stable basis will be needed before further biogeographic hypotheses that depend on time calibrations can be tested, though, probably requiring the use of much larger multigene approaches instead of a handful of Sanger-based markers. These approaches recently used for other Gondwanan harvestman families, including transcriptomics for Pettalidae (Baker *et al*. 2020*a*) and ultraconserved elements for Triaenonychidae (Derkarabetian *et al*. 2021*b*), have elucidated complex biogeographical patterns (see Derkarabetian *et al*. 2021*a*) that had not been satisfactorily resolved with Sanger-based approaches (i.e. Giribet *et al*. 2016; Baker *et al*. 2020*b*). Our phylogenetic knowledge of Neopilionidae also remains frustratingly incomplete given the contrasting results of morphological phylogenetic analyses (Hunt and Cokendolpher 1991; Taylor 2011, 2013*a*) and our molecular results (see also Vélez *et al*. 2014). However, some clades appear well resolved, and this study sets the roadmap towards providing a more comprehensive and stable resolution of the systematics of this group, including broader genomic data and a better characterisation of some

potential new clades. Finally, the New Zealand Neopilionidae include several clades that may be excellent examples to further study the effects of the Oligocene drowning episode.

Taxonomically, the family Neopilionidae will need to be substantially revised. First and foremost, it will require including *Neopilio*, the type genus of the family, for determining whether *Vibone* and *Hesperopilio* belong in the family. It will also require both assessing the validity of the South American genera and describing several new Chilean species. The generic status of multiple lineages of the Australian *Megalopsalis* may also require addressing, and the description of additional species of the recently described New Caledonian genus *Martensopsalis* will be necessary. And, finally, the description of a new genus for *Megalopsalis triascuta* and the related species reported above, the assessment of the possible paraphyly of *Forsteropsalis* with respect to *Pantopsalis*, as well as the description of a multitude of new New Zealand species will be required. We expect to contribute to some of these taxonomic changes in future work.

Conflicts of interest

G. Giribet is the Editor-in-Chief of *Invertebrate Systematics*. Despite this relationship, he did not at any stage have Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Invertebrate Systematics* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors declare that they have no further conflicts of interest.

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