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Molecular phylogeny and biogeography of the temperate Gondwanan family Triaenonychidae (Opiliones : Laniatores) reveals pre-Gondwanan regionalisation, common vicariance, and rare dispersal

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Abstract. Triaenonychidae Sørensen *in* L. Koch, 1886 is a large family of Opiliones with ~480 described species broadly distributed across temperate forests in the Southern Hemisphere. However, it remains poorly understood taxonomically, as no comprehensive phylogenetic work has ever been undertaken. In this study we capitalise on samples largely collected by us during the last two decades and use Sanger DNA-sequencing techniques to produce a large phylogenetic tree with 300 triaenonychid terminals representing nearly 50% of triaenonychid genera and including representatives from all the major geographic areas from which they are known. Phylogenetic analyses using maximum likelihood and Bayesian inference methods recover the family as diphyletic, placing *Lomanella* Pocock, 1903 as the sister group to the New Zealand endemic family Synthetonychiidae Forster, 1954. With the exception of the Laurasian representatives of the family, all landmasses contain non-monophyletic assemblages of taxa. To determine whether this non-monophyly was the result of Gondwanan vicariance, ancient cladogenesis due to habitat regionalisation, or more recent over-water dispersal, we inferred divergence times. We found that most divergence times between landmasses predate Gondwanan breakup, though there has been at least one instance of transoceanic dispersal – to New Caledonia. In all, we identify multiple places in the phylogeny where taxonomic revision is needed, and transfer *Lomanella* outside of Triaenonychidae in order to maintain monophyly of the family.

Additional keywords: Insidiatores, phylogeny, vicariance.

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Introduction

Triaenonychidae Sørensen *in* L. Koch, 1886, is the fourth most diverse family of Opiliones, with ~480 described species and subspecies (Kury *et al*. 2014). They can be readily identified by their trident-shaped tarsal claws of the third and fourth legs, and, as with most Laniatores, their robust, armoured pedipalps, which are much larger than the chelicerae. All triaenonychids have similar basic habitat requirements, living in cool, dark, humid environments such as leaf litter, rotting logs, and caves. They are nocturnal predators, and, like most harvestmen, are believed to be dispersal-limited. Despite sharing these characteristics, the family contains remarkable morphological and behavioural diversity, with body sizes that range from ~2 to 10 mm in length, variable levels of armature, striking colour pattern variation, both sexual dimorphism and male polymorphism, and even a documented instance of paternal care (Machado 2007) (Fig. 1).

Together with the New Zealand–endemic family Synthetonychiidae Forster, 1954 (14 species), Triaenonychidae is traditionally placed in the superfamily Triaenonychoidea. This group in turn is classified with the superfamily Travunioidea Absolon & Kratochvíl, 1932 (~78 species and subspecies) in the infraorder Insidiatores Loman, 1901, one of the two main lineages within Laniatores Thorell, 1876 (Kury *et al*. 2014; Derkarabetian *et al*. 2018). Despite this traditional classification scheme, the monophyly of

Fig. 1. Live habitus of members of Triaenonychidae. (*A*) *Fumontana deprehendor* MCZ IZ-46881; (*B*) *Pristobunus heterus* MCZ IZ-133243; (*C*) *Lomanella* sp. MCZ IZ-152652; (*D*) *Karamea lobata* MCZ IZ-152313; (*E*) *Glyptobunus ornatus*; (*F*) new genus MCZ IZ-138076; (*G*) *Hickmanoxyomma* sp.; (*H*) *Austromontia* sp. MCZ IZ-49523; (*I*) *Triconobunus horridus* MCZ IZ-151590; (*J*) *Nuncia* sp. MCZ IZ-152266; (*K*) *Larifuga* sp. MCZ IZ-132879; (*L*) '*Nuncia*' *verrucosa* MCZ IZ-138139. Photographs *A*, *B*, *F*, *H*, *K*, and *L* by Gonzalo Giribet; *C* by Shahan Derkarabetian; *D*, *I*, and *J* by Caitlin Baker; *E* and *G* by Marshal Hedin.

Insidiatores has been inconsistently recovered. While a recent phylogenetic analysis using transcriptomic data did find a monophyletic Insidiatores (Fernández *et al*. 2017), other phylogenies based on Sanger DNA-sequencing data (Giribet *et al*. 2010; Sharma and Giribet 2011) and UCE sequencing (Derkarabetian *et al*. 2018) instead found either Synthetonychiidae or Travunioidea to be the sister group to all other Laniatores, rendering Insidiatores paraphyletic. It has been postulated that the limited taxonomic sampling of Triaenonychidae in these previous studies (each included no more than eight exemplars of the family) may have contributed to the inability to resolve these phylogenetic relationships (Sharma and Giribet 2011).

In addition to the uncertain placement of Triaenonychidae within Insidiatores, the phylogenetic relationships within the family are also subject to debate. Genera within the family are traditionally classified in four subfamilies. Adaeinae Pocock, 1903 (40 species) is diagnosed by having a subtriangular or wedge-shaped sternum and primarily contains genera from South Africa, as well as a monotypic genus from Western Australia (*Dingupa* Forster, 1952). Members of the subfamily Sorensenellinae Forster, 1954 (16 species and subspecies) all have tarsal claws on the third and fourth legs in which the lateral prongs are longer than the median prong. Sorensenellinae is composed of two genera from New Zealand (*Sorensenella* Pocock, 1903 and *Karamea* Forster, 1954) and two monotypic genera from South Africa (*Lawrencella* Strand, 1932 and *Speleomontia* Lawrence, 1931), but the putative synapomorphy of the family is also found in the Tasmanian genus *Tasmanonyx* Hickman, 1958, classified in Triaenonychinae. The subfamily Triaenobuninae Pocock, 1903 (69 species and subspecies) is also diagnosed by

the shape of the sternum, which is wide and crescent-shaped on its posterior margin. It contains multiple genera from New Zealand and Australia, as well as two monotypic genera from Chile (*Americobunus* Muñoz-Cuevas, 1972 and *Araucanobunus* Muñoz-Cuevas, 1973) and the genus *Ankaratrix* Lawrence, 1959, from Madagascar. Finally, the bulk of diversity is classified in the subfamily Triaenonychinae Sørensen, 1886 (354 species and subspecies), all of which have a long, arrow-shaped sternum. However, this subfamily has been treated as a 'catch-all' clade and, as such, it demands phylogenetic investigation.

To date, only a few studies have addressed phylogenetic relationships within Triaenonychidae, most of which used morphological data only for a subset of species, and focused on specific landmasses (Hunt 1996; Mendes and Kury 2008). In an unpublished Ph.D. thesis, Mendes (2009) addressed the broader Insidiatores phylogeny using morphological data. Although none of the taxonomic actions proposed there have validity, she placed the Tasmanian–South Australian *Lomanella* Pocock, 1903 and the Tasmanian monotypic genus *Pyenganella* Hickman, 1958 in a 'new' family, Lomanellidae (*nomen nudum*), which then formed a clade with Synthetonychiidae, but this result was only obtained under implied weights; in other analyses they nested within Triaenonychidae. Hunt (1996) also found *Lomanella* (but not *Pyenganella*) to be the sister group to all other Australian triaenonychids, whether using equal weights or successive weighting, but as this analysis lacked representatives outside of Australia it is hard to compare with other analyses. Phylogenetic relationships in the family were also addressed using Sanger DNA sequencing in another unpublished thesis (Vélez 2011) that focused on the New Zealand taxa and provided a dated chronogram in order to test the Oligocene drowning hypothesis (Landis *et al*. 2008; Giribet and Boyer 2010).

Most triaenonychid diversity is found in the Southern Hemisphere, across South America, southern Africa, Madagascar, Australia, and New Zealand (Fig. 2). This geographic pattern reflects a classic temperate Gondwanan distribution, inviting biogeographic comparisons to other groups such as Pettalidae Shear, 1980 (Opiliones) (Shear 1980; Boyer and Giribet 2007; Giribet *et al*. 2016; Baker *et al*. 2020), Neopilionidae Lawrence, 1931 (Opiliones) (Taylor 2011; Vélez *et al*. 2014), Peripatopsidae Bouvier, 1907 (Onychophora) (Murienne *et al*. 2014; Giribet *et al*. 2018), Orsolobidae Cooke, 1965 (Araneae) (Chousou-Polydouri *et al*. 2019), and Bothriuridae Simon, 1880 (Scorpiones) (Sharma *et al*. 2018). However, along with its temperate Gondwanan members, the family also contains monotypic genera in eastern North America (*Fumontana deprehendor* Shear, 1977 (Thomas and Hedin 2008)), and Sardinia (*Buemarinoa patrizii* Roewer, 1956 (see Karaman 2019)), a species from the oceanic Crozet Islands in the Southern Ocean (*Promecostethus unifalculatus* Enderlein, 1909), and two species from Grande Terre in New Caledonia (*Triconobunus horridus* Roewer, 1914 and *Diaenobunus armatus* Roewer, 1915). Grande Terre's basement geology is derived from Gondwanan terranes, but subsequently experienced long periods of marine inundation, and is therefore more accurately thought of as a functionally Darwinian island (Grandcolas *et al*. 2008; though see discussion in Giribet and Baker 2019).

Given this largely temperate Gondwanan distribution, Triaenonychidae has been suggested as another example of a Gondwanan vicariant group, comparable to the examples listed above. Nevertheless, their presence in the Northern

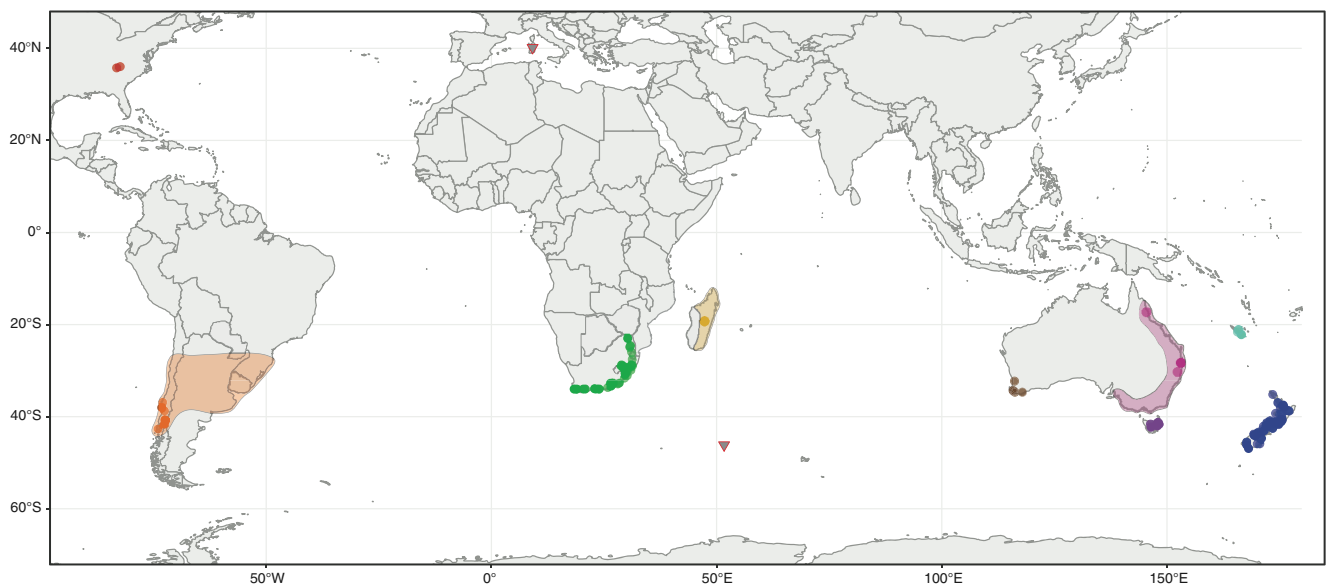

Fig. 2. The distribution of Triaenonychidae samples used in the present study, with points coloured by region. Outlined shapes in South America, Madagascar, and eastern Australia reflect the known distribution of Triaenonychidae on those landmasses that extends beyond our study's sampling. Triangles correspond to the phylogenetically and biogeographically important, but unsampled, lineages of *Buemarinoa patrizii* (Sardinia) and *Promecostethus unifalculatus* (Crozet Islands). For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

Hemisphere and the morphological affinities of those Northern Hemisphere species to the genus *Flavonuncia* Lawrence, 1959 from Madagascar (Karaman 2019) suggest either ancient relictualism or else more recent dispersal to these areas, as dispersal explains their occurrence on multiple Darwinian islands. It is also unknown whether the different continental landmasses contain monophyletic assemblages of taxa, as one might expect under a Gondwanan vicariant scenario. None of these biogeographic hypotheses have been interrogated using time-calibrated molecular phylogenetics. However, the limited triaenonychid sampling in the dated phylogenies of Giribet *et al*. (2010), Vélez (2011), Sharma and Giribet (2011), and Fernández *et al*. (2017) estimated the family's origin at some point between the Cretaceous and the Permian, suggesting an ancient origin for the group.

To address these gaps in our knowledge of a major lineage within Opiliones, we herein present a densely sampled time-calibrated molecular phylogeny of Triaenonychidae. This marks the first phylogeny focused on the family using broad molecular data, and allows us to evaluate both the taxonomy and major biogeographic patterns of the group.

Materials and methods

Taxon sampling

Specimens used in this study were collected mostly by the authors by leaf-litter sifting or direct hand collection between 2003 and 2018. Animals were immediately preserved in 95% ethanol and later stored at –20°C or –80°C. All specimens used in this work are stored at the Museum of Comparative Zoology (MCZ) or at Worcester State University (WSU), and locality data are available online through MCZBase (https://mczbase.mcz.harvard.edu, accessed March 2020) and Table 1. All specimens acquired by the authors for this project were collected under valid permits (New Zealand multiple permits [38002-RES]; Australia [NSW #SL101324; Qld #WITK00845202; WA Permits #OF000190, #CE000648, #SF004565]; New Caledonia [#609011-75/2018]; Chile [Autorización #026/2014]; South Africa [Easter Cape permits #CRO 108/11CR and CRO 109/11CR; KZN #OP 4085/2011; Western Cape Permit #AAA007-00344-0035]; USA [Great Smoky Mts N.P. Permit #GRSM-2014-SCI-02335]) or by donation from local collectors and museums.

Taxonomic identification was done using light microscopy examination of somatic and genitalic characters, and specimens were then selected for molecular work, focusing our sampling on representing as many genera and species as possible. We also used multiple specimens per genus and species whenever possible so as to test the monophyly of those groups. Our sampling spans ~50% of all currently accepted genera (50 of 108 genera, plus 1 undescribed genus) and includes representatives from all the major geographic areas from which triaenonychids are known, with the exception of Sardinia and the Crozet Islands. In total, our dataset includes 329 terminals, 300 of which are currently classified as triaenonychids. For our outgroup sampling, we included three Dyspnoi Hansen & Sørensen, 1904, three Eupnoi Hansen & Sørensen, 1904, eight Grassatores Kury *in* Giribet, Edgecombe, Wheeler & Babbitt, 2002, thirteen Travunioidea, and two *Synthetonychia* Forster, 1954, an endemic New Zealand genus classified as a separate family, Synthetonychiidae (Table 2).

Molecular data generation

DNA extractions were done using Qiagen's DNeasy Blood & Tissue kit with an overnight incubation. We sequenced three markers, including two conserved nuclear ribosomal genes (*18S* and *28S* rRNA) and the more variable mitochondrial gene cytochrome *c* oxidase subunit I (hereafter '*COI*'), totalling to almost 4 kb of sequence data. *18S* rRNA was amplified in three fragments using primer pairs 1F–5R, 3F–18Sbi, and 18Sa2.0–9R (Giribet *et al*. 1996; Whiting *et al*. 1997). *28S* rRNA was sequenced in two fragments using primer pairs 28Sa–28Srd5b and 28Srd4.8a–28Srd7bi. Some specimens were also amplified for the first fragment of *28S* rRNA using primer pair 28Srd1a and rd4b, but due to difficulty getting clean sequences for this fragment, these were excluded from the final analysis (for details on the *28S* rRNA primers see Giribet and Shear 2010). *COI* was amplified with the primer pair LCO1490–HCO2198 (Folmer *et al*. 1994). PCR reactions were carried out with 1–2 µL of DNA template, using either GoTaq DNA polymerase in a 25-µL reaction, Bioline Biolase in a 10-µL reaction, or with GE beads in a 25-µL reaction. Gel electrophoresis was used to visualise amplification reactions, and successful reactions were cleaned using ExoSAP in a 1 : 5 dilution. Cycle sequencing proceeded with 0.5 µL of BigDye, and final cycle sequencing products were sequenced on an ABI 3730 in the Bauer Core at Harvard University. New sequences are deposited in GenBank under accession numbers MT224318–MT224908 and MT240314–MT240477 (Table 1).

Sequence data were quality-checked, trimmed, and assembled in Geneious (ver. 10, see https://www.geneious.com), with additional outgroup sequences downloaded from GenBank. Each locus was then aligned in MAFFT using the Geneious plug-in (ver. 1.4.0, Biomatters Ltd, see https://mafft.cbrc.jp/alignment/software/; Katoh and Standley 2013), with automatic model selection. The *28S* rRNA alignment was further edited to remove long gaps at the ends of the alignment. Alignments were concatenated in SequenceMatrix (ver. 1.8, see https://code.google.com/p/sequencematrix/; Vaidya *et al*. 2011) and the concatenated dataset was then subjected to phylogenetic analysis.

Phylogenetic inference

Model testing and phylogenetic analysis was initially performed in W-IQ-TREE (ver. 1.6.9, see https://iqtree.cibiv.univie.ac.at/; Nguyen *et al*. 2015), implementing the ModelFinder function (Kalyaanamoorthy *et al*. 2017) and partitioning by locus (Chernomor *et al*. 2016). Nodal support was assessed with Shimodaira–Hasegawa approximate likelihood ratio testing (SH-aLRT) and ultrafast bootstrap analysis (UFBoot) (Hoang *et al*. 2018), specifying 1000 replications for each measure. We also inferred a tree with RAxML-HPC2 (ver. 8.2.10, see https://cme.h-its.org/exelixis/web/software/raxml/; Stamatakis 2014)

Table 1. Collection information and GenBank accession numbers for specimens used in this study
Sequences newly generated for this study are shown in bold

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Equitius doriae	MCZ-134630	Triaenonychinae	Australia (NSW)	U37003	GQ912788	EF108590	–	–
Holonuncia sp.	MCZ-134219	Triaenonychinae	Australia (Qld)	**MT224370**	**MT224762**	**MT240352**	–28.194	153.18692
Triaenobunus armstrongi	MCZ-134473	Triaenobuninae	Australia (NSW)	GQ912724	GQ912794	**MT240354**	–	–
Triaenobunus armstrongi	MCZ-58944	Triaenobuninae	Australia (Qld)	**MT224527**	**MT224671**		–17.3109	145.62625
Triaenobunus bicarinatus	MCZ-134879	Triaenobuninae	Australia (NSW)	GQ912724	GQ912795	GQ912878	–30.1475	152.44389
Triaenobunus minutus	MCZ-134218	Triaenobuninae	Australia (Qld)	**MT224369**	**MT224761**		–28.194	153.18692
Triaenobunus minutus	MCZ-134220	Triaenobuninae	Australia (Qld)	**MT224371**	**MT224763**	**MT240353**	–28.194	153.18692
Glyptobunus ornatus	WSU-10076	Triaenobuninae	Australia (Tas.)	**MT224610**	**MT224656**	**MT240476**	–41.6406	148.2417
Glyptobunus ornatus	WSU-10077	Triaenobuninae	Australia (Tas.)	**MT224611**	**MT224657**	**MT240477**	–41.6406	148.2417
Glyptobunus ornatus	WSU-10090	Triaenobuninae	Australia (Tas.)	**MT224614**	**MT224660**		–41.3223	148.1319
Glyptobunus signatus	WSU-10028	Triaenobuninae	Australia (Tas.)	**MT224598**	**MT224644**		–41.3083	147.9389
Glyptobunus signatus	WSU-10049	Triaenobuninae	Australia (Tas.)	**MT224605**	**MT224651**		–41.3214	147.9247
Glyptobunus signatus	WSU-10050	Triaenobuninae	Australia (Tas.)	**MT224606**	**MT224652**	**MT240472**	–41.3214	147.9247
Glyptobunus sp.	WSU-10008	Triaenobuninae	Australia (Tas.)	**MT224584**	**MT224630**		–41.2245	147.9689
Glyptobunus sp.	WSU-10026	Triaenobuninae	Australia (Tas.)	**MT224596**	**MT224642**		–41.9483	147.8742
Glyptobunus sp.	WSU-10044	Triaenobuninae	Australia (Tas.)	**MT224601**	**MT224647**	**MT240468**	–42.2867	146.4569
Rhynchobunus arrogans	WSU-10001	Triaenobuninae	Australia (Tas.)	**MT224580**	**MT224626**	**MT240457**	–41.624	148.2556
Triaenobunus asper	WSU-10006	Triaenobuninae	Australia (Tas.)	**MT224582**	**MT224628**	**MT240458**	–41.624	148.2556
Triaenobunus asper	WSU-10016	Triaenobuninae	Australia (Tas.)	**MT224589**	**MT224635**	**MT240460**	–41.9483	147.8742
Triaenobunus asper	WSU-10017	Triaenobuninae	Australia (Tas.)	**MT224590**	**MT224636**	**MT240461**	–41.9483	147.8742
Triaenobunus asper	WSU-10020	Triaenobuninae	Australia (Tas.)	**MT224592**	**MT224638**	**MT240462**	–41.9483	147.8742
Triaenobunus asper	WSU-10021	Triaenobuninae	Australia (Tas.)	**MT224593**	**MT224639**	**MT240463**	–41.9483	147.8742
Triaenobunus asper	WSU-10023	Triaenobuninae	Australia (Tas.)	**MT224594**	**MT224640**	**MT240464**	–41.9483	147.8742
Triaenobunus asper	WSU-10024	Triaenobuninae	Australia (Tas.)	**MT224595**	**MT224641**	**MT240465**	–41.9483	147.8742
Triaenobunus asper	WSU-10060	Triaenobuninae	Australia (Tas.)	**MT224607**	**MT224653**	**MT240473**	–42.0042	147.8517
Triaenobunus asper	WSU-10069	Triaenobuninae	Australia (Tas.)	**MT224608**	**MT224654**	**MT240474**	–41.6406	148.2417
Triaenobunus asper	WSU-10070	Triaenobuninae	Australia (Tas.)	**MT224609**	**MT224655**	**MT240475**	–41.6406	148.2417
Hickmanoxyomma gibbergunyar	MCZ-134907	Triaenonychinae	Australia (Tas.)	**MT224374**	**MT224767**		–41.5803	146.34389
Hickmanoxyomma gibbergunyar	MCZ-135687	Triaenonychinae	Australia (Tas.)	**MT224407**	**MT224800**		–41.5994	146.40528
Hickmanoxyomma cf. *tasmanicum*	WSU-10005	Triaenonychinae	Australia (Tas.)	**MT224581**	**MT224627**		–41.624	148.2556
Hickmanoxyomma cf. *tasmanicum*	WSU-10032	Triaenonychinae	Australia (Tas.)	**MT224599**	**MT224645**	**MT240466**	–41.5344	148.1756
Hickmanoxyomma cf. *tasmanicum*	WSU-10082	Triaenonychinae	Australia (Tas.)	**MT224612**	**MT224658**		–41.5608	148.095
Lomanella raniceps	WSU-10045	Triaenonychinae	Australia (Tas.)	**MT224602**	**MT224648**	**MT240469**	–42.2867	146.4569
Lomanella raniceps	WSU-10046	Triaenonychinae	Australia (Tas.)	**MT224603**	**MT224649**	**MT240470**	–42.2867	146.4569
Lomanella raniceps	WSU-10047	Triaenonychinae	Australia (Tas.)	**MT224604**	**MT224650**	**MT240471**	–42.2867	146.4569
Lomanella sp.	WSU-10011	Triaenonychinae	Australia (Tas.)	**MT224587**	**MT224633**		–41.2245	147.9689
Lomanella sp.	WSU-10038	Triaenonychinae	Australia (Tas.)	**MT224600**	**MT224646**	**MT240467**	–41.5344	148.1756
Lomanella sp.	WSU-10089	Triaenonychinae	Australia (Tas.)	**MT224613**	**MT224659**		–41.3223	148.1319
Nucina dispar	WSU-10018	Triaenonychinae	Australia (Tas.)	**MT224591**	**MT224637**		–41.9483	147.8742
Nunciella tasmaniensis	WSU-10009	Triaenonychinae	Australia (Tas.)	**MT224585**	**MT224631**		–41.2245	147.9689
Nunciella tasmaniensis	WSU-10010	Triaenonychinae	Australia (Tas.)	**MT224586**	**MT224632**		–41.2245	147.9689
Nunciella tasmaniensis	WSU-10027	Triaenonychinae	Australia (Tas.)	**MT224597**	**MT224643**		–41.3083	147.9389
Nunciella sp.	WSU-10014	Triaenonychinae	Australia (Tas.)	**MT224588**	**MT224634**		–41.2245	147.9689

(*continued next page*)

Table 1. (*continued*)

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Odontonuncia saltuensis	WSU-10007	Triaenonychinae	Australia (Tas.)	**MT224583**	**MT224629**	**MT240459**	–41.2245	147.9689
Calliuncus cf. *labyrinthus*	MCZ-132901	Triaenonychinae	Australia (WA)	**MT224352**	**MT224744**	**MT240343**	–34.3419	115.86191
Calliuncus cf. *labyrinthus*	MCZ-99185	Triaenonychinae	Australia (WA)	**MT224578**	**MT224721**	**MT240336**	–34.3419	115.86191
Calliuncus cf. *labyrinthus*	MCZ-99220	Triaenonychinae	Australia (WA)	**MT224579**	**MT224722**	**MT240337**	–34.3905	115.86077
Nunciella karriensis	MCZ-132904	Triaenonychinae	Australia (WA)	**MT224353**	**MT224745**	**MT240344**	–34.6759	117.8717
Nunciella sp.	MCZ-132908	Triaenonychinae	Australia (WA)	**MT224354**	**MT224746**	**MT240345**	–32.2711	116.16604
Nunciella sp.	MCZ-99182	Triaenonychinae	Australia (WA)	**MT224577**	**MT224720**		–34.7002	116.2223
Americobunus ringueleti	MCZ-138157	Triaenobuninae	Chile	**MT224504**	**MT224896**	**MT240440**	–38.7291	–72.59149
Diasia michaelsenii	MCZ-138126	Triaenonychinae	Chile	**MT224496**	**MT224888**		–40.7372	–72.31062
Diasia sp.	MCZ-138056	Triaenonychinae	Chile	**MT224480**	**MT224873**		–38.0126	–73.18517
Nuncia americana	MCZ-59011	Triaenonychinae	Chile	**MT224537**	**MT224681**	**MT240321**	–40.7372	–72.30647
Nuncia americana	MCZ-59016	Triaenonychinae	Chile	**MT224538**	**MT224682**	**MT240322**	–40.7372	–72.30647
Nuncia americana	MCZ-59020	Triaenonychinae	Chile	**MT224539**	**MT224683**	**MT240323**	–40.7372	–72.30647
Nuncia americana	MCZ-59021	Triaenonychinae	Chile	**MT224540**	**MT224684**	**MT240324**	–40.7372	–72.30647
Nuncia cf. *americana*	MCZ-138110	Triaenonychinae	Chile	**MT224490**	**MT224882**		–41.5935	–72.59359
Nuncia cf. *americana*	MCZ-138115	Triaenonychinae	Chile	**MT224491**	**MT224883**		–40.7355	–72.32894
Nuncia chilensis	MCZ-138133	Triaenonychinae	Chile	**MT224498**	**MT224890**	**MT240436**	–40.7135	–72.50297
Nuncia verrucosa	MCZ-138097	Triaenonychinae	Chile	**MT224488**	**MT224880**	**MT240432**	–41.5783	–72.55828
Nuncia verrucosa	MCZ-138122	Triaenonychinae	Chile	**MT224492**	**MT224884**	**MT240434**	–40.7372	–72.31062
Nuncia verrucosa	MCZ-138139	Triaenonychinae	Chile	**MT224500**	**MT224892**	**MT240437**	–40.7375	–72.30875
Nuncia sp.	MCZ-138091	Triaenonychinae	Chile	**MT224484**	**MT224877**	**MT240429**	–41.5881	–72.58122
Nuncia sp.	MCZ-138093	Triaenonychinae	Chile	**MT224485/MT224486**	**MT224878**	**MT240430**	–41.5785	–72.55692
Nuncia sp.	MCZ-59030	Triaenonychinae	Chile	**MT224541**	**MT224685**		–42.662	–74.01062
Triaenonyx chilensis	MCZ-138132	Triaenonychinae	Chile	**MT224497**	**MT224889**	**MT240435**	–40.7135	–72.50297
Triaenonyx dispersus	MCZ-138125	Triaenonychinae	Chile	**MT224495**	**MT224887**		–40.7372	–72.31062
Triaenonyx sp.	MCZ-138029	Triaenonychinae	Chile	**MT224479**	**MT224872**		–36.876	–72.99386
Triaenonyx sp.	MCZ-138074	Triaenonychinae	Chile	**MT224481**	**MT224874**	**MT240426**	–38.0163	–73.17902
Triaenonyx sp.	MCZ-138096	Triaenonychinae	Chile	**MT224487**	**MT224879**	**MT240431**	–41.5783	–72.55828
Triaenonyx sp.	MCZ-138109	Triaenonychinae	Chile	**MT224489**	**MT224881**	**MT240433**	–41.5935	–72.59359
Triaenonyx sp.	MCZ-138124	Triaenonychinae	Chile	**MT224494**	**MT224886**		–40.7372	–72.31062
Triaenonyx sp.	MCZ-138140	Triaenonychinae	Chile	**MT224501**	**MT224893**	**MT240438**	–40.7375	–72.30875
cf. *Triaenonyx arrogans*	MCZ-138077	Triaenonychinae	Chile	**MT224483**	**MT224876**	**MT240428**	–38.0163	–73.17902
Valdivionyx crassipes	MCZ-138123	Triaenonychinae	Chile	**MT224493**	**MT224885**		–40.7372	–72.31062
Valdivionyx crassipes	MCZ-138138	Triaenonychinae	Chile	**MT224499**	**MT224891**		–40.7375	–72.30875
Valdivionyx crassipes	MCZ-138150	Triaenonychinae	Chile	**MT224502**	**MT224894**		–40.7381	–72.31139
Valdivionyx sp.	MCZ-138151	Triaenonychinae	Chile	**MT224503**	**MT224895**	**MT240439**	–40.7381	–72.31139
Triaenonychidae n. gen.	MCZ-138076	Triaenonychinae	Chile	**MT224482**	**MT224875**	**MT240427**	–38.0163	–73.17902
Acumontia sp. 2		Triaenonychinae	Madagascar	**MT224322**	**MT224615**		–19.3546	47.31128
Acumontia sp. 3		Triaenonychinae	Madagascar	**MT224323**	**MT224616**	**MT240451**	–19.35062	47.30402
Acumontia sp. 4		Triaenonychinae	Madagascar	**MT224324**	**MT224617**	**MT240452**	–19.35217	47.30753
Acumontia sp. 5		Triaenonychinae	Madagascar	**MT224325**	**MT224618**	**MT240453**	–19.35062	47.30402
Acumontia sp. 6		Triaenonychinae	Madagascar	**MT224326**		**MT240454**	–19.35062	47.30402
Acumontia sp. 7		Triaenonychinae	Madagascar	**MT224327**	**MT224619**	**MT240455**	–19.35062	47.30402
Acumontia sp. 8		Triaenonychinae	Madagascar	**MT224328**	**MT224620**		–19.35062	47.30402
Flavonuncia sp. 9		Triaenonychinae	Madagascar	**MT224329/MT224330**	**MT224624**	**MT240456**	–19.3546	47.31128

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Table 1. (*continued*)

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Flavonuncia sp. 10		Triaenonychinae	Madagascar	**MT224319**	**MT224621**	**MT240450**	–19.3546	47.31128
Flavonuncia sp. 11		Triaenonychinae	Madagascar	**MT224320**	**MT224622**		–19.3546	47.31128
Flavonuncia sp. 12		Triaenonychinae	Madagascar	**MT224321**	**MT224623**		–19.35217	47.30753
Triaenonychidae sp. 1		Triaenonychinae	Madagascar	**MT224318**	**MT224625**	**MT240449**	–19.35217	47.30753
Diaenobunus armatus	MCZ-151609.1	Triaenonychinae	New Caledonia	**MT224512**	**MT224904**	**MT240444**	–22.1706	166.50861
Diaenobunus armatus	MCZ-151609.2	Triaenonychinae	New Caledonia	**MT224513**	**MT224905**	**MT240445**	–22.1706	166.50861
Diaenobunus armatus	MCZ-151609.3	Triaenonychinae	New Caledonia	**MT224514**	**MT224906**	**MT240446**	–22.1706	166.50861
Diaenobunus armatus	MCZ-151611.1	Triaenonychinae	New Caledonia	**MT224515**	**MT224907**	**MT240447**	–22.1708	166.50833
Diaenobunus armatus	MCZ-151611.2	Triaenonychinae	New Caledonia	**MT224516**	**MT224908**	**MT240448**	–22.1708	166.50833
Diaenobunus sp.	MCZ-134884	Triaenonychinae	New Caledonia	**MT224372**	**MT224765**	**MT240355**	–21.6167	165.88333
Triconobunus horridus	MCZ-151590.1	Triaenonychinae	New Caledonia	**MT224510**	**MT224902**	**MT240442**	–21.1116	165.87869
Triconobunus horridus	MCZ-151590.2	Triaenonychinae	New Caledonia	**MT224511**	**MT224903**	**MT240443**	–21.1116	165.87869
Karamea lobata australis	MCZ-136031	Sorensenellinae	New Zealand	**MT224431**	**MT224824**	**MT240391**	–42.0369	171.38972
Karamea lobata lobata	MCZ-136011	Sorensenellinae	New Zealand	**MT224428**	**MT224821**	**MT240389**	–41.7967	172.04944
Karamea lobata lobata	MCZ-136012	Sorensenellinae	New Zealand	**MT224429**	**MT224822**	**MT240390**	–41.7967	172.04944
Karamea tricerata	MCZ-135504	Sorensenellinae	New Zealand	**MT224397**	**MT224790**	**MT240365**	–40.883	172.81083
Karamea tricerata	MCZ-135507	Sorensenellinae	New Zealand	**MT224398**	**MT224791**	**MT240366**	–40.883	172.81083
Sorensenella prehensor prehensor	MCZ-133201	Sorensenellinae	New Zealand	**MT224364**	**MT224756**		–36.9466	174.61005
Sorensenella rotara	MCZ-148131	Sorensenellinae	New Zealand	**MT224508**	**MT224900**		–38.6474	176.90794
Sorensenella n. sp.	MCZ-133130	Sorensenellinae	New Zealand	**MT224362**	**MT224754**		–35.1904	173.45557
Sorensenella n. sp.	MCZ-133380	Sorensenellinae	New Zealand	**MT224367**	**MT224759**		–39.4654	175.09003
Sorensenella n. sp.	MCZ-133429	Sorensenellinae	New Zealand	**MT224368**	**MT224760**	**MT240350**	–38.26	175.0998
Cenefia cf. *adaeiformis*	MCZ-135771	Triaenobuninae	New Zealand	**MT224408**	**MT224801**		–41.0868	174.13811
Pristobonus henopoeus	MCZ-135974	Triaenobuninae	New Zealand	**MT224412**	**MT224805**		–41.3453	174.93167
Pristobunus acuminatus acantheis	MCZ-136194	Triaenobuninae	New Zealand	**MT224465**	**MT224858**	**MT240415**	–40.6388	175.32236
Pristobunus heterus	MCZ-133351	Triaenobuninae	New Zealand	**MT224366**	**MT224758**		–40.2445	175.54205
Pristobunus sp.	MCZ-133205	Triaenobuninae	New Zealand	**MT224365**	**MT224757**	**MT240349**	–39.2738	174.09365
Pristobunus sp.	MCZ-135678	Triaenobuninae	New Zealand	**MT224406**	**MT224799**	**MT240372**	–41.1377	173.51675
Pristobunus sp.	MCZ-148111	Triaenobuninae	New Zealand	**MT224506**	**MT224898**		–43.2859	170.401
Triaenonychidae sp.	MCZ-136244	Triaenobuninae	New Zealand	**MT224469**	**MT224862**	**MT240418**	–46.897	168.09228
Algidia chiltoni chiltoni	MCZ-135458	Triaenonychinae	New Zealand	**MT224383**	**MT224776**	**MT240358**	–38.6757	176.699
Algidia chiltoni chiltoni	MCZ-136192	Triaenonychinae	New Zealand	**MT224464**	**MT224857**	**MT240414**	–	–
Algidia chiltoni longispinosa	MCZ-135437	Triaenonychinae	New Zealand	**MT224379**	**MT224772**	**MT240356**	–41.1133	175.34944
Algidia cuspidata multispinosa	MCZ-136151	Triaenonychinae	New Zealand	**MT224453**	**MT224846**	**MT240407**	–42.5421	173.45244
Algidia homerica	MCZ-135537	Triaenonychinae	New Zealand	**MT224400**	**MT224793**	**MT240368**	–43.4126	170.17722
Algidia cf. *homerica*	MCZ-136061	Triaenonychinae	New Zealand	**MT224437**	**MT224830**	**MT240397**	–43.4882	170.03259
Algidia interrupta interrupta	MCZ-136008	Triaenonychinae	New Zealand	**MT224427**	**MT224820**	**MT240388**	–41.7967	172.04944
Algidia marplesi	MCZ-135672	Triaenonychinae	New Zealand	**MT224405**	**MT224798**	**MT240371**	–45.8803	170.61022
Algidia nigriflava	MCZ-136171	Triaenonychinae	New Zealand	**MT224457**	**MT224850**	**MT240410**	–41.1558	174.96519
Algidia cf. *nigriflava*	MCZ-136202	Triaenonychinae	New Zealand	**MT224467**	**MT224860**	**MT240417**	–40.7213	175.24561
Algidia sp.	MCZ-148126	Triaenonychinae	New Zealand	**MT224507**	**MT224899**	**MT240441**	–41.348	174.93093
Hedwiga manubriata	MCZ-135637	Triaenonychinae	New Zealand	**MT224404**	**MT224797**	**MT240370**	–46.897	168.09228
Hedwiga manubriata	MCZ-136129	Triaenonychinae	New Zealand	**MT224450**	**MT224843**	**MT240404**	–46.8942	168.10402
Hedwiga manubriata	MCZ-136258	Triaenonychinae	New Zealand	**MT224473**	**MT224866**	**MT240421**	–44.7006	170.96756
Hedwiga manubriata	MCZ-136259	Triaenonychinae	New Zealand	**MT224474**	**MT224867**	**MT240422**	–44.7006	170.96756

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Table 1. (*continued*)

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Hendea bucculenta	MCZ-136167	Triaenonychinae	New Zealand	**MT224454**	**MT224847**	**MT240408**	–41.1558	174.96519
Hendea maitaia	MCZ-135991	Triaenonychinae	New Zealand	**MT224421**	**MT224814**		–41.0867	174.13806
Hendea myersi	MCZ-135987	Triaenonychinae	New Zealand	**MT224418**	**MT224811**	**MT240380**	–41.7075	174.78611
Hendea myersi	MCZ-136170	Triaenonychinae	New Zealand	**MT224456**	**MT224849**	**MT240409**	–41.1558	174.96519
Hendea myersi	MCZ-136173	Triaenonychinae	New Zealand	**MT224459**	**MT224852**		–41.1558	174.96519
Hendea phillippsi	MCZ-136180	Triaenonychinae	New Zealand	**MT224460**	**MT224853**	**MT240411**	–41.0733	175.14631
Hendea sp.	MCZ-135543	Triaenonychinae	New Zealand	**MT224401**	**MT224794**		–43.7104	169.26714
Hendea sp.	MCZ-136005	Triaenonychinae	New Zealand	**MT224426**	**MT224819**	**MT240387**	–41.7956	172.59722
Hendea sp.	MCZ-136055	Triaenonychinae	New Zealand	**MT224436**	**MT224829**	**MT240396**	–43.4235	170.168
Nuncia arcuata aorangiensis	MCZ-136113	Triaenonychinae	New Zealand	**MT224447**	**MT224840**	**MT240402**	–46.1095	167.69026
Nuncia coriacea coriacea	MCZ-135438	Triaenonychinae	New Zealand	**MT224380**	**MT224773**		–41.065	175.35283
Nuncia coriacea coriacea	MCZ-135486	Triaenonychinae	New Zealand	**MT224394**	**MT224787**		–41.065	175.35283
Nuncia coriacea coriacea	MCZ-136041	Triaenonychinae	New Zealand	**MT224433**	**MT224826**	**MT240393**	–43.0211	171.595
Nuncia coriacea coriacea	MCZ-136043	Triaenonychinae	New Zealand	**MT224434**	**MT224827**	**MT240394**	–43.0211	171.595
Nuncia coriacea coriacea	MCZ-136091	Triaenonychinae	New Zealand	**MT224443**	**MT224836**		–44.0769	169.38656
Nuncia coriacea coriacea	MCZ-58942	Triaenonychinae	New Zealand	**MT224525**	**MT224669**	**MT240316**	–42.5421	173.45244
Nuncia coriacea ovata	MCZ-136038	Triaenonychinae	New Zealand	**MT224432**	**MT224825**	**MT240392**	–43.0211	171.595
Nuncia dentifera	MCZ-135460	Triaenonychinae	New Zealand	**MT224384**	**MT224777**	**MT240359**	–37.5974	175.86158
Nuncia heteromorpha	MCZ-136049	Triaenonychinae	New Zealand	**MT224435**	**MT224828**	**MT240395**	–42.7145	171.24502
Nuncia levis	MCZ-136022	Triaenonychinae	New Zealand	**MT224430**	**MT224823**		–41.4244	172.10556
Nuncia nigriflava parva	MCZ-135989	Triaenonychinae	New Zealand	**MT224419**	**MT224812**	**MT240381**	–41.0867	174.13806
Nuncia obesa grimmetti	MCZ-135970	Triaenonychinae	New Zealand	**MT224410**	**MT224803**	**MT240374**	–41.3475	174.92694
Nuncia obesa grimmetti	MCZ-135975	Triaenonychinae	New Zealand	**MT224413**	**MT224806**	**MT240376**	–41.2944	174.75132
Nuncia obesa grimmetti	MCZ-135980	Triaenonychinae	New Zealand	**MT224414**	**MT224807**	**MT240377**	–41.2656	174.7575
Nuncia obesa grimmetti	MCZ-135984	Triaenonychinae	New Zealand	**MT224416**	**MT224809**	**MT240378**	–41.2667	174.75833
Nuncia obesa grimmetti	MCZ-136198	Triaenonychinae	New Zealand	**MT224466**	**MT224859**	**MT240416**	–40.6388	175.32236
Nuncia obesa grimmetti	MCZ-136206	Triaenonychinae	New Zealand	**MT224468**	**MT224861**		–40.5755	175.48147
Nuncia obesa grimmetti	MCZ-136265	Triaenonychinae	New Zealand	**MT224476**	**MT224869**	**MT240423**	–41.2944	174.75132
Nuncia obesa obesa	MCZ-136076	Triaenonychinae	New Zealand	**MT224438**	**MT224831**	**MT240398**	–43.9381	169.28824
Nuncia obesa obesa	MCZ-136137	Triaenonychinae	New Zealand	**MT224451**	**MT224844**	**MT240405**	–45.9047	169.98778
Nuncia obesa obesa	MCZ-136169	Triaenonychinae	New Zealand	**MT224455**	**MT224848**		–41.1558	174.96519
Nuncia obesa rotunda	MCZ-136172	Triaenonychinae	New Zealand	**MT224458**	**MT224851**		–41.1558	174.96519
Nuncia cf. *obesa rotunda*	MCZ-149353	Triaenonychinae	New Zealand	**MT224509**	**MT224901**		–46.8985	168.10016
Nuncia oconnori paucispinosa	MCZ-135469	Triaenonychinae	New Zealand	**MT224388**	**MT224781**	**MT240362**	–37.4668	175.77125
Nuncia pallida	MCZ-136099	Triaenonychinae	New Zealand	**MT224444**	**MT224837**		–45.5733	167.61987
Nuncia roeweri demissa	MCZ-135439	Triaenonychinae	New Zealand	**MT224381**	**MT224774**		–41.065	175.35283
Nuncia roeweri gelida	MCZ-135468	Triaenonychinae	New Zealand	**MT224387**	**MT224780**		–37.4668	175.77125
Nuncia roeweri humilis	MCZ-135463	Triaenonychinae	New Zealand	**MT224385**	**MT224778**	**MT240360**	–37.5974	175.86158
Nuncia roeweri humilis	MCZ-135487	Triaenonychinae	New Zealand	**MT224395**	**MT224788**	**MT240364**	–37.5974	175.86158
Nuncia roeweri roeweri	MCZ-136116	Triaenonychinae	New Zealand	**MT224448**	**MT224841**		–46.8942	168.10402
Nuncia roeweri roeweri	MCZ-136147	Triaenonychinae	New Zealand	**MT224452**	**MT224845**	**MT240406**	–44.7006	170.9675
Nuncia roeweri seditiosa	MCZ-136112	Triaenonychinae	New Zealand	**MT224446**	**MT224839**		–46.1095	167.69026
Nuncia smithi	MCZ-135436	Triaenonychinae	New Zealand	**MT224378**	**MT224771**		–41.065	175.35283
Nuncia smithi	MCZ-135479	Triaenonychinae	New Zealand	**MT224390**	**MT224783**		–40.722	175.64019
Nuncia smithi	MCZ-135484	Triaenonychinae	New Zealand	**MT224392**	**MT224785**	**MT240363**	–37.4668	175.77125

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Table 1. (*continued*)

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Nuncia stewartia stewartia	MCZ-136086	Triaenonychinae	New Zealand	**MT224440**	**MT224833**	**MT240399**	–43.9381	169.28824
Nuncia stewartia stewartia	MCZ-136087	Triaenonychinae	New Zealand	**MT224441**	**MT224834**	**MT240400**	–44.0769	169.38656
Nuncia stewartia stewartia	MCZ-136127	Triaenonychinae	New Zealand	**MT224449**	**MT224842**	**MT240403**	–46.8942	168.10402
Nuncia stewartia tumosa	MCZ-136088	Triaenonychinae	New Zealand	**MT224442**	**MT224835**	**MT240401**	–44.0769	169.38656
Nuncia sublaevis	MCZ-135481	Triaenonychinae	New Zealand	**MT224391**	**MT224784**		–37.5974	175.86158
Nuncia sublaevis	MCZ-135485	Triaenonychinae	New Zealand	**MT224393**	**MT224786**		–37.4668	175.77125
Nuncia variegata delli	MCZ-135985	Triaenonychinae	New Zealand	**MT224417**	**MT224810**	**MT240379**	–41.2667	174.75833
Nuncia sp.	MCZ-134924	Triaenonychinae	New Zealand	**MT224375**	**MT224768**		–43.9381	169.28824
Nuncia sp.	MCZ-135475	Triaenonychinae	New Zealand	**MT224389**	**MT224782**		–40.6388	175.32236
Nuncia sp.	MCZ-135515	Triaenonychinae	New Zealand	**MT224399**	**MT224792**	**MT240367**	–41.27	172.13325
Nuncia sp.	MCZ-135610	Triaenonychinae	New Zealand	**MT224402**	**MT224795**	**MT240369**	–45.4511	167.68042
Nuncia sp.	MCZ-135973	Triaenonychinae	New Zealand	**MT224411**	**MT224804**	**MT240375**	–41.3478	174.92583
Nuncia sp.	MCZ-135983	Triaenonychinae	New Zealand	**MT224415**	**MT224808**		–41.2667	174.75833
Nuncia sp.	MCZ-135990	Triaenonychinae	New Zealand	**MT224420**	**MT224813**	**MT240382**	–41.0867	174.13806
Nuncia sp.	MCZ-135994	Triaenonychinae	New Zealand	**MT224422**	**MT224815**	**MT240383**	–41.0867	174.13806
Nuncia sp.	MCZ-135998	Triaenonychinae	New Zealand	**MT224423**	**MT224816**	**MT240384**	–41.3003	173.57111
Nuncia sp.	MCZ-135999	Triaenonychinae	New Zealand	**MT224424**	**MT224817**	**MT240385**	–41.1892	172.74222
Nuncia sp.	MCZ-136000	Triaenonychinae	New Zealand	**MT224425**	**MT224818**	**MT240386**	–41.1892	172.74222
Nuncia sp.	MCZ-136079	Triaenonychinae	New Zealand	**MT224439**	**MT224832**		–43.9381	169.28824
Nuncia sp.	MCZ-136111	Triaenonychinae	New Zealand	**MT224445**	**MT224838**		–46.1095	167.69026
Nuncia sp.	MCZ-136182	Triaenonychinae	New Zealand	**MT224461**	**MT224854**		–41.0752	175.14672
Nuncia sp.	MCZ-136183	Triaenonychinae	New Zealand	**MT224462**	**MT224855**	**MT240412**	–41.0752	175.14672
Nuncia sp.	MCZ-136250	Triaenonychinae	New Zealand	**MT224470**	**MT224863**	**MT240419**	–43.0211	171.595
Nuncia sp.	MCZ-136251	Triaenonychinae	New Zealand	**MT224471**	**MT224864**		–44.0769	169.38656
Nuncia sp.	MCZ-136252	Triaenonychinae	New Zealand	**MT224472**	**MT224865**	**MT240420**	–42.5421	173.45244
Nuncia sp.	MCZ-136261	Triaenonychinae	New Zealand	**MT224475**	**MT224868**		–46.1095	167.69026
Prasma tuberculata mearosa	MCZ-136190	Triaenonychinae	New Zealand	**MT224463**	**MT224856**	**MT240413**	–40.6388	175.32236
Prasma sp.	MCZ-117475	Triaenonychinae	New Zealand	**MT224331**	**MT224723**	**MT240338**	–46.1106	167.68966
Prasma sp.	MCZ-133199	Triaenonychinae	New Zealand	**MT224363**	**MT224755**	**MT240348**	–36.9466	174.61005
Prasma sp.	MCZ-135491	Triaenonychinae	New Zealand	**MT224396**	**MT224789**		–41.1856	173.48772
Prasma sp.	MCZ-135614	Triaenonychinae	New Zealand	**MT224403**	**MT224796**		–45.4511	167.68042
Prasma sp.	MCZ-147580	Triaenonychinae	New Zealand	**MT224505**	**MT224897**		–39.3561	175.47643
Triregia fairburni fairburni	MCZ-135467	Triaenonychinae	New Zealand	**MT224386**	**MT224779**	**MT240361**	–37.4668	175.77125
Triregia fairburni fairburni	MCZ-135963	Triaenonychinae	New Zealand	**MT224409**	**MT224802**	**MT240373**	–37.8809	175.91147
Triregia fairburni grata	MCZ-135450	Triaenonychinae	New Zealand	**MT224382**	**MT224775**	**MT240357**	–38.7979	177.12372
Adaeulum areolatum	MCZ-30072.1	Adaeinae	South Africa	**MT224518**	**MT224662**	**MT240314**	–32.6823	26.49135
Adaeulum bicolor	MCZ-126991.2	Adaeinae	South Africa	**MT224332**	**MT224724**		–28.745	31.13596
Adaeulum godfreyi	MCZ-138019	Adaeinae	South Africa	**MT224478**	**MT224871**	**MT240425**	–32.889	28.05258
Adaeulum humifer	MCZ-59004	Adaeinae	South Africa	**MT224532**	**MT224676**		–22.996	30.26447
Adaeulum moruliferum	MCZ-138016	Adaeinae	South Africa	**MT224477**	**MT224870**	**MT240424**	–28.7117	28.9342
Adaeulum robustum	MCZ-132883	Adaeinae	South Africa	**MT224350**	**MT224742**	**MT240342**	–29.3221	30.26258
Adaeulum supervidens	MCZ-127214	Adaeinae	South Africa	**MT224336**	**MT224728**	**MT240340**	–30.6311	29.71596
Adaeum sp.	MCZ-73548.1	Adaeinae	South Africa	**MT224561**	**MT224705**	**MT240328**	–32.5704	26.9403
Adaeum sp.	MCZ-73548.2	Adaeinae	South Africa	**MT224562**	**MT224706**	**MT240329**	–32.5704	26.9403
Larifuga capensis	MCZ-133938	Adaeinae	South Africa		GQ912792	**MT240351**	–33.9792	18.45

(*continued next page*)

Table 1. (*continued*)

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Larifuga sp.	MCZ-127211.3	Adaeinae	South Africa	**MT224335**	**MT224727**	**MT240339**	–33.9521	22.91155
Larifuga sp.	MCZ-132879	Adaeinae	South Africa	**MT224347**	**MT224739**	**MT240341**	–33.9942	20.45868
Larifuga sp.	MCZ-132909.2	Adaeinae	South Africa	**MT224355**	**MT224747**		–33.9749	23.14712
Larifuga sp.	MCZ-49519	Adaeinae	South Africa	**MT224524**	**MT224668**	**MT240315**	–34.0424	18.87395
Larifuga sp.	MCZ-98386	Adaeinae	South Africa	**MT224574**	**MT224718**	**MT240335**	–34.0424	18.87395
Larifugella cf. *afra*	MCZ-132913	Adaeinae	South Africa	**MT224358**	**MT224750**	**MT240347**	–30.5326	29.68318
Larifugella cf. *afra*	MCZ-98385	Adaeinae	South Africa	**MT224573**	**MT224717**	**MT240334**	–30.5326	29.68318
Larifugella zuluana	MCZ-98906.5	Adaeinae	South Africa	**MT224575/ MT224576**	**MT224719**		–28.745	31.13596
cf. *Larifugella* sp.	MCZ-132921.1	Adaeinae	South Africa	**MT224361**	**MT224753**		–24.5697	30.86031
cf. *Larifugella* sp.	MCZ-30078	Adaeinae	South Africa	**MT224521**	**MT224665**		–32.6871	26.4937
Paradaeum sp.	MCZ-73504	Adaeinae	South Africa	**MT224551**	**MT224695**		–33.9839	20.82532
Speleomontia sp.	MCZ-132910.1	Sorensenellinae	South Africa	**MT224356**	**MT224748**	**MT240346**	–33.9856	18.40128
Amatola sp.	MCZ-127202	Triaenonychinae	South Africa	**MT224334**	**MT224726**		–29.6028	30.3464
Amatola sp.	MCZ-128699	Triaenonychinae	South Africa	**MT224346**	**MT224738**		–30.5326	29.68318
Amatola sp.	MCZ-132881	Triaenonychinae	South Africa	**MT224348**	**MT224740**		–29.8635	30.98691
Amatola sp.	MCZ-132882	Triaenonychinae	South Africa	**MT224349**	**MT224741**		–29.3221	30.26258
Amatola sp.	MCZ-73541.2	Triaenonychinae	South Africa	**MT224557**	**MT224701**		–32.6823	26.49135
Austromontia sp.	MCZ-127281.1	Triaenonychinae	South Africa	**MT224338**	**MT224730**		–33.9521	22.91155
Austromontia sp.	MCZ-127282.2	Triaenonychinae	South Africa	**MT224339**	**MT224731**		–33.9521	22.91155
Austromontia sp.	MCZ-127678	Triaenonychinae	South Africa	**MT224343**	**MT224735**		–33.9262	22.93821
Austromontia sp.	MCZ-134926	Triaenonychinae	South Africa	**MT224376**	**MT224769**		–33.6858	25.8342
Austromontia sp.	MCZ-73450.3	Triaenonychinae	South Africa	**MT224545**	**MT224689**		–33.9673	18.94315
Austromontia sp.	MCZ-73484.3	Triaenonychinae	South Africa	**MT224547**	**MT224691**		–33.9749	23.14712
Austromontia sp.	MCZ-73488	Triaenonychinae	South Africa	**MT224549**	**MT224693**		–33.9876	18.40547
Austromontia sp.	MCZ-73505.2	Triaenonychinae	South Africa	**MT224552**	**MT224696**		–33.9839	20.82532
Austromontia sp.	MCZ-73525.3	Triaenonychinae	South Africa	**MT224555**	**MT224699**		–33.9657	23.9286
Austromontia sp.	MCZ-88579.1	Triaenonychinae	South Africa	**MT224571**	**MT224715**	**MT240332**	–34.0042	18.38316
Austromontia sp.	MCZ-88580	Triaenonychinae	South Africa	**MT224572**	**MT224716**	**MT240333**	–34.0042	18.38316
Biacumontia sp.	MCZ-127587	Triaenonychinae	South Africa	**MT224342**	**MT224734**		–34.0235	23.89033
Biacumontia sp.	MCZ-132917	Triaenonychinae	South Africa	**MT224359**	**MT224751**		–31.6061	29.5385
Biacumontia sp.	MCZ-73478.1	Triaenonychinae	South Africa	**MT224546**	**MT224690**		–33.9262	22.93821
Biacumontia sp.	MCZ-73512	Triaenonychinae	South Africa	**MT224554**	**MT224698**		–33.966	23.66401
Biacumontia sp.	MCZ-73544	Triaenonychinae	South Africa	**MT224560**	**MT224704**		–33.9749	23.14712
Biacumontia sp.	MCZ-87095.2	Triaenonychinae	South Africa	**MT224564**	**MT224708**		–33.9749	23.14712
Ceratomontia sp.	MCZ-127009	Triaenonychinae	South Africa	**MT224333**	**MT224725**		–31.0629	30.17422
Ceratomontia sp.	MCZ-135001.1	Triaenonychinae	South Africa	**MT224377**	**MT224770**		–33.3399	26.58824
Ceratomontia sp.	MCZ-30077.2	Triaenonychinae	South Africa	**MT224520**	**MT224664**		–32.6871	26.4937
Ceratomontia sp.	MCZ-58943.2	Triaenonychinae	South Africa	**MT224526**	**MT224670**	**MT240317**	–34.0235	23.89033
Ceratomontia sp.	MCZ-73543.1	Triaenonychinae	South Africa	**MT224559**	**MT224703**	**MT240327**	–32.6871	26.4937
Ceratomontia sp.	MCZ-88282	Triaenonychinae	South Africa	**MT224568**	**MT224712**		–33.3399	26.58824
cf. *Ceratomontia* sp.	MCZ-58945.1	Triaenonychinae	South Africa	**MT224528**	**MT224672**		–32.6868	28.37712
cf. *Ceratomontia* sp.	MCZ-58945.2	Triaenonychinae	South Africa	**MT224529**	**MT224673**	**MT240318**	–32.6868	28.37712
Graemontia sp.	MCZ-73486.1	Triaenonychinae	South Africa	**MT224548**	**MT224692**		–33.9749	23.14712
Graemontia sp.	MCZ-73506.2	Triaenonychinae	South Africa	**MT224553**	**MT224697**	**MT240326**	–33.9839	20.82532
Graemontia sp.	MCZ-73526	Triaenonychinae	South Africa	**MT224556**	**MT224700**		–33.9749	23.14712

(*continued next page*)

Table 1. (*continued*)

Species	Accession number	'Subfamily'	Region	*18S* rRNA	*28S* rRNA	*COI*	Latitude	Longitude
Lizamontia sp.	MCZ-132885	Triaenonychinae	South Africa	**MT224351**	**MT224743**		–28.9602	29.22588
Mensamontia sp.	MCZ-127856	Triaenonychinae	South Africa	**MT224344**	**MT224736**		–33.9942	20.45868
Mensamontia sp.	MCZ-73445.1	Triaenonychinae	South Africa	**MT224544**	**MT224688**		–33.9679	18.94161
Micromontia sp.	MCZ-73542.2	Triaenonychinae	South Africa	**MT224558**	**MT224702**		–29.0535	29.38516
Monomontia sp.	MCZ-127314	Triaenonychinae	South Africa	**MT224340**	**MT224732**		–28.7435	31.13804
Monomontia sp.	MCZ-127324	Triaenonychinae	South Africa	**MT224341**	**MT224733**		–28.7316	28.91859
Monomontia sp.	MCZ-128564	Triaenonychinae	South Africa	**MT224345**	**MT224737**		–28.9602	29.22588
Monomontia sp.	MCZ-132918	Triaenonychinae	South Africa	**MT224360**	**MT224752**		–28.8882	31.37523
Monomontia sp.	MCZ-30065.2	Triaenonychinae	South Africa	**MT224517**	**MT224661**		–32.5704	26.9403
Monomontia sp.	MCZ-35537	Triaenonychinae	South Africa	**MT224522**	**MT224666**		–27.545	31.28185
Monomontia sp.	MCZ-58975.3	Triaenonychinae	South Africa	**MT224531**	**MT224675**		–22.996	30.26447
Monomontia sp.	MCZ-73245.2	Triaenonychinae	South Africa	**MT224542**	**MT224686**		–22.996	30.26447
Monomontia sp.	MCZ-73250	Triaenonychinae	South Africa	**MT224543**	**MT224687**		–22.996	30.26447
Monomontia sp.	MCZ-87149.3	Triaenonychinae	South Africa	**MT224565**	**MT224709**		–24.5697	30.86031
Monomontia sp.	MCZ-87608	Triaenonychinae	South Africa	**MT224567**	**MT224711**	**MT240331**	–30.5326	29.68318
Monomontia sp.	MCZ-88573.1	Triaenonychinae	South Africa	**MT224570**	**MT224714**		–25.997	31.11646
Planimontia sp.	MCZ-134889	Triaenonychinae	South Africa	**MT224373**	**MT224766**		–34.0042	18.38316
Planimontia sp.	MCZ-73493.3	Triaenonychinae	South Africa	**MT224550**	**MT224694**	**MT240325**	–29.0535	29.38516
Planimontia sp.	MCZ-88571	Triaenonychinae	South Africa	**MT224569**	**MT224713**		–34.0042	18.38316
Roewerania sp.	MCZ-127275.2	Triaenonychinae	South Africa	**MT224337**	**MT224729**		–28.7316	28.91859
Roewerania sp.	MCZ-30076.2	Triaenonychinae	South Africa	**MT224519**	**MT224663**		–32.6823	26.49135
Roewerania sp.	MCZ-84507.2	Triaenonychinae	South Africa	**MT224563**	**MT224707**		–32.6823	26.49135
Roewerania sp.	MCZ-87385.1	Triaenonychinae	South Africa	**MT224566**	**MT224710**	**MT240330**	–28.9602	29.22588
Rostromontia capensis	MCZ-133944	Triaenonychinae	South Africa	GQ912723	GQ912793		–33.9792	18.45
Rostromontia sp.	MCZ-132911	Triaenonychinae	South Africa	**MT224357**	**MT224749**		–33.9854	18.40135
Triaenonychidae sp.	MCZ-58974	Triaenonychinae	South Africa	**MT224530**	**MT224674**	**MT240319**	–24.8742	30.71744
Triaenonychidae sp.	MCZ-59007.1	Triaenonychinae	South Africa	**MT224533**	**MT224677**		–33.3399	26.58824
Triaenonychidae sp.	MCZ-59007.2	Triaenonychinae	South Africa	**MT224534**	**MT224678**		–33.3399	26.58824
Triaenonychidae sp.	MCZ-59008.1	Triaenonychinae	South Africa	**MT224535**	**MT224679**	**MT240320**	–33.3399	26.58824
Triaenonychidae sp.	MCZ-59008.2	Triaenonychinae	South Africa	**MT224536**	**MT224680**		–33.3399	26.58824
Fumontana deprehendor	MCZ-134565	Triaenonychinae	United States	GQ912721	GQ912790/**MT224764**	EU162780	36.04833	–82.4
Fumontana deprehendor	MCZ-46881	Triaenonychinae	United States	**MT224523**	**MT224667**	EU162788	35.75681	–83.21165

Table 2. GenBank accession numbers for outgroup taxa used in this study

Species	Family	Higher group	*18S* rRNA	*28S* rRNA	*COI*
Acropsopilio chilensis	Acropsopilionidae	Dyspnoi	KF963305	KF955592	GQ912899
Ceratolasma tricantha	Ischyropsalididae	Dyspnoi	AF124943	GQ912764	GQ912865
Hesperonemastoma modestum	Taracidae	Dyspnoi	AF124942	EF108577	KU875193
Caddo agilis	Caddidae	Eupnoi	KF963310	KF955597	MF816271
Eurybunus brunneus	Sclerosomatidae	Eupnoi	JQ437010	JQ437102	
Alloepedanus sp.	Epedanidae	Grassatores	JF786480	JF786572	
Euepedanus sp.	Epedanidae	Grassatores	JF786479	JF786571	
Pseudobiantes japonicus	Epedanidae	Grassatores		LC176242	LC176240
Pseudoepedanus dolensis	Epedanidae	Grassatores	GQ912731	GQ912807	
Acutisoma longipes	Gonyleptidae	Grassatores	GQ912736	GQ912815	JF786441
Pachyloides thorellii	Gonyleptidae	Grassatores	PTU37007	U91508	KF726794
Remyus sp.	Phalangodidae	Grassatores	JF786470	JF786608	JF786431
Zalmoxis cardwellensis	Zalmoxidae	Grassatores	JN885755	JN885734	JN885769
Synthetonychia sp.	Synthetonychiidae		GQ912720	GQ912787	GQ912875
Synthetonychia sp.	Synthetonychiidae		KT302218	KT302254	KT302305
Briggsus flavescens	Cladonychiidae	Travunioidea		HM056643	HM056726
Erebomaster flavescens	Cladonychiidae	Travunioidea	GQ912716	GQ912781	HM056722
Holoscotolemon jaqueti	Cladonychiidae	Travunioidea	GQ912717	GQ912783	GQ912873
Peltonychia clavigera	Cladonychiidae	Travunioidea	FJ796479	GQ912785	FJ796491
Speleonychia sengeri	Cladonychiidae	Travunioidea		GQ205667	HM056727
Theromaster brunnea	Cladonychiidae	Travunioidea	GQ912718	GQ912784	HM056723
Cryptomaster leviathan	Cryptomastridae	Travunioidea		HM056641	HM056724
Speleomaster lexi	Cryptomastridae	Travunioidea		HM056642	HM056725
Metanonychus setulus	Paranonychidae	Travunioidea		HM056649	HM056732
Paranonychus brunneus	Paranonychidae	Travunioidea		HM056645	HM056728
Sclerobunus nondimorphicus	Paranonychidae	Travunioidea		HM056659	GQ870663
Zuma acuta	Paranonychidae	Travunioidea	AF124951	AF124978	EU162817
Trojanella serbica	Travuniidae	Travunioidea	GQ912719	GQ912786	GQ912874

using the CIPRES Science Gateway (ver. 3.3, see https://www.phylo.org), partitioning by locus and using the GTR+Γ substitution model for all partitions. Nodal support in RAxML was assessed using both standard non-parametric bootstrapping (–b) and rapid bootstrapping (–x) mapped onto the best tree. Finally, we analysed our dataset in BEAST (ver. 2.4.6, see https://www.beast2.org; Bouckaert *et al*. 2014), using the results of IQ-TREE's ModelFinder to define substitution models for each partition independently. In order to determine the best clock model and tree prior for our dataset, we used an iterative strategy using the stepping-stone Path sampler application (ver. 1.3.4, see https://github.com/BEAST2-Dev/model-selection; Xie *et al*. 2011) in BEAST (ver. 2.4.6). First, we ran three path sampling analyses, all under a Yule tree prior with 100 steps of 1 million generations, corresponding to a strict clock, an exponential relaxed clock, and a lognormal relaxed clock. Marginal likelihood estimates were compared using Bayes Factors to select the optimal clock model. We then ran another path sampling analysis under the optimal clock model, but using a birth–death tree prior. Again, marginal likelihood estimates for the two analysed tree priors were compared using Bayes Factors, and the optimal clock model and tree prior combination was used for lineage age inference.

BEAST chronograms were calibrated using known Opiliones fossils to constrain crown-group ages of specified nodes, all under uniform distributions with a maximum age for each calibration set to 514 million years (Ma), corresponding to the age of the oldest fossil chelicerate, *Wisangocaris barbarahardyae* Jago, García-Bellido & Gehling, 2016, from the Emu Bay Shale (Wolfe *et al*. 2016). The following nodes were calibrated: (1) Dyspnoi was constrained to a minimum age of 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); (2) The age of Eupnoi was constrained to a minimum of 305 Ma, reflecting the age of *Macrogyion cronus* Garwood, Dunlop, Giribet & Sutton, 2011, also from the Montceau-les-Mines Lagerstätte (Garwood *et al*. 2011); (3) Epedanidae Sørensen, 1886, was constrained to a minimum age of 105 Ma, reflecting the age of *Petrobunoides sharmai* Selden, Dunlop, Giribet, Zhang & Ren, 2016, from Burmese amber from the lowermost Cenomanian (*c*. 100 Ma) (Selden *et al*. 2016). While the placement of this fossil in Epedanidae has not been verified in the context of a total-evidence phylogeny, unlike the other fossils used in our calibrations (Garwood *et al*. 2014; Sharma and Giribet 2014), its assignment to Epedanidae is based on multiple morphological characters such as its elongate, raptorial pedipalps, the tarsal formula, and the shape of the ocularium (Selden *et al*. 2016); (4) The root age of all Opiliones was constrained to a minimum of 405 Ma, corresponding to the age of the oldest known Opiliones fossil, *Eophalangium sheari* Dunlop, Anderson, Kerp & Hass, 2003 (Dunlop *et al*. 2003; Garwood *et al*. 2014). Four different BEAST analyses were run for 200 million

generations each and combined after burn-in. Stationarity was confirmed in Tracer (ver.1.6, see https://tree.bio.ed.ac.uk/software/tracer/), with all ESS values >200.

All individual gene alignments (in phylip format), concatenated trees and trees inferred from individual loci (in Newick format), and the BEAST xml file are available as supplementary information in the Harvard Dataverse (https://doi.org/10.7910/DVN/ULZIHT).

Results and discussion

Composition of Triaenonychidae and its position within Insidiatores

Analysis of our partitioned dataset recovered a non-monophyletic Triaenonychidae (Fig. 3–6). Across all analyses with maximal support, we instead found a sister-group relationship between the Australian triaenonychid genus *Lomanella* and the New Zealand–endemic *Synthetonychia*, the only genus in the family Synthetonychiidae (red star in Fig. 3–5). *Lomanella* and *Synthetonychia* share several morphological affinities, specifically in terms of their penis structure (both have reduced dorsolateral plates along the truncus) and tarsal claws (many *Lomanella* species and all *Synthetonychia* species have a complex branching peltonychium rather than the typical triaenonychid trident claw), as previously discussed by Hunt and Hickman (1993), and in part supported by the work of Mendes (2009) (although she also included *Pyenganella* in this clade). However, Hunt (1996) did not place *Pyenganella* with *Lomanella*, instead finding *Lomanella* as the sister

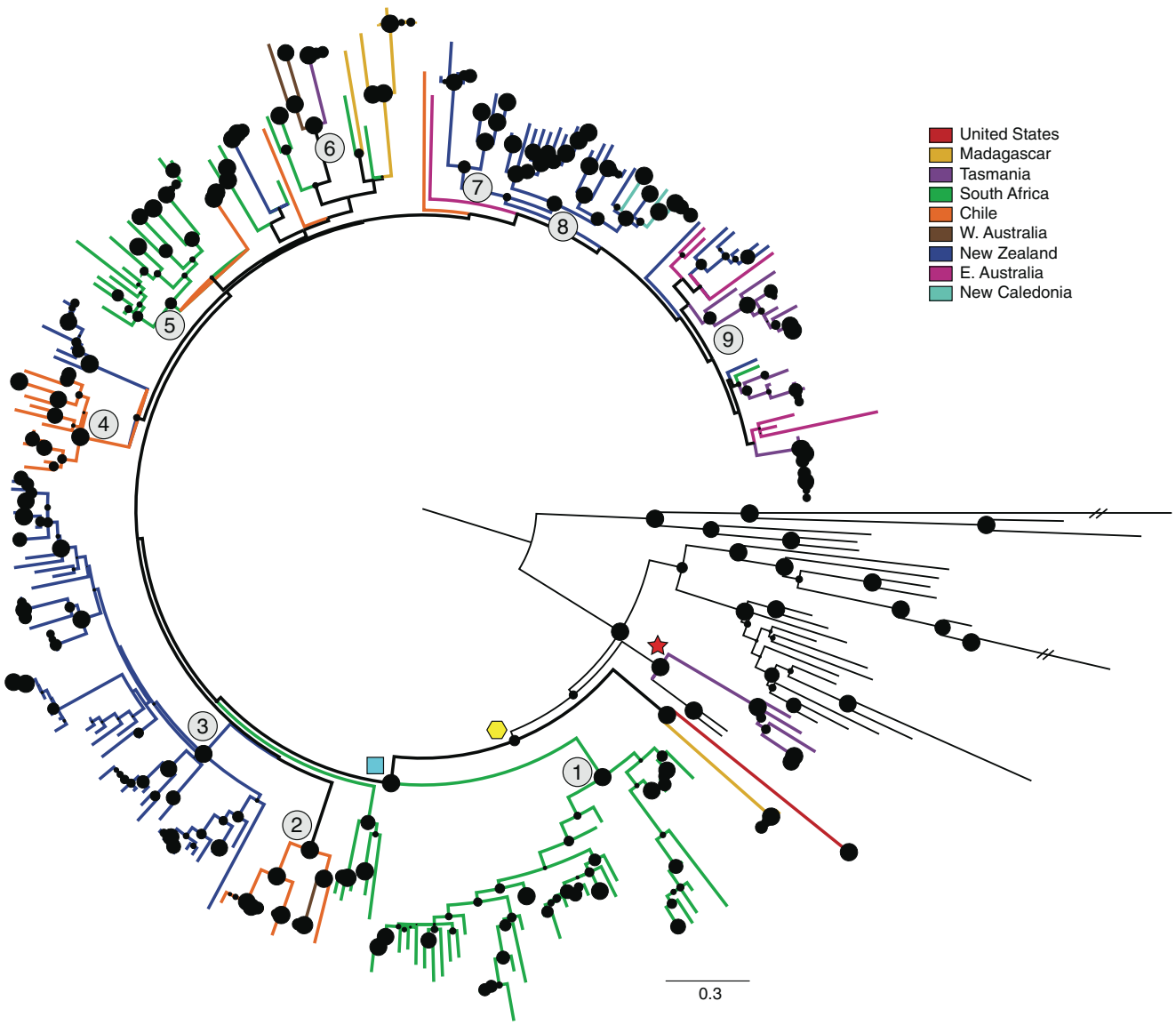

Fig. 3. Result of RAxML analysis, partitioned by locus. Branches are coloured by landmass as shown in the key and in Fig. 2. Circles at nodes are scaled according to rapid bootstrap support values. Star denotes the clade of *Lomanella* + *Synthetonychia*. Hexagon denotes Triaenonychidae including *Fumontana* + *Flavonuncia*. Square shows Southern Hemisphere Triaenonychidae. Numbered nodes correspond to well-supported clades across all analyses (see Results and Discussion for details). For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

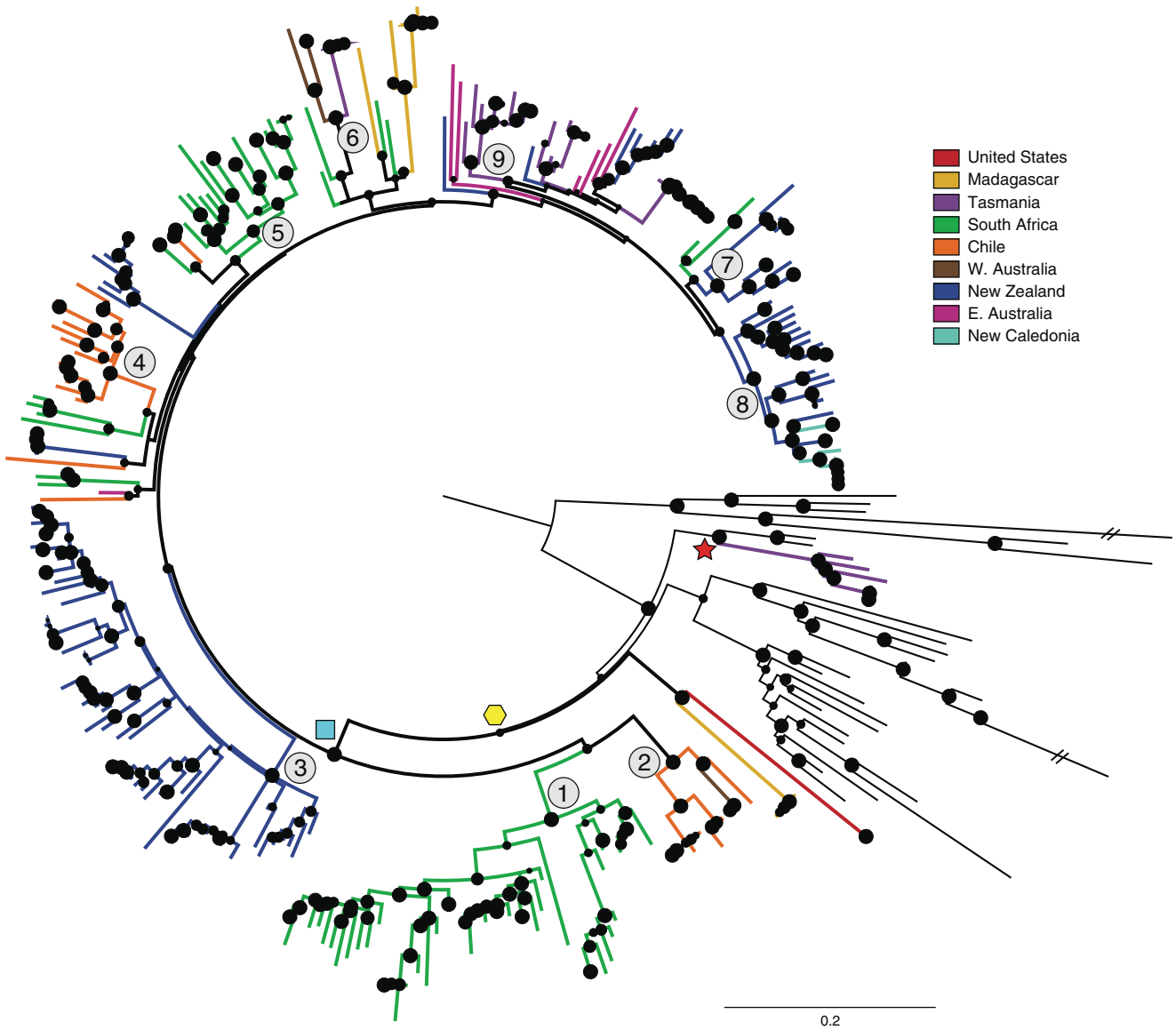

Fig. 4. Result of IQ-TREE analysis, partitioned by locus. Branches are coloured by landmass as indicated in the key, and in Fig. 2 and 3. Circles at nodes are scaled according to ultrafast bootstrap support values. Star corresponds to *Synthetonychia* + *Lomanella*, hexagon corresponds to Triaenonychidae, and square corresponds to Southern Hemisphere Triaenonychidae. Numbered nodes correspond to well-supported clades across all analyses, as in Fig. 3. For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

group to all remaining Australian triaenonychids. The placement of this clade of *Lomanella* + *Synthetonychia*, however, was inconsistent across analyses (Fig. 6). In our RAxML tree, it was recovered as the sister group to all other triaenonychids, albeit without support (47% rapid bootstrap support, RBS, and 30% standard bootstrap support, BS, in RAxML). In our BEAST tree, it was recovered as the sister group to Travunioidea, again without support (posterior probability (PP) 0.91) but consistent with the results of Fernández *et al*. (2017) (though that study did not include *Lomanella*). Finally, our IQ-TREE phylogeny placed the group as the sister lineage to all other Laniatores (100% SH-aLRT and 100% UFBoot), in line with the results of Giribet *et al*. (2010) and Sharma and Giribet (2011), who found *Synthetonychia* (*Lomanella* was not sampled) to be the sister group to the remaining Laniatores. Given this low and inconsistent support for the relationship of *Lomanella* + *Synthetonychia* to other triaenonychid genera, and the fact that other studies have found *Synthetonychia* not to be related to other triaenonychids, even when using phylogenomics (Fernández *et al*. 2017), we believe this constitutes a unique and distinct evolutionary lineage, as proposed earlier by Mendes (2009). However, until *Pyenganella* is examined, we refrain from erecting new taxa, yet recognise that *Lomanella* should be moved out of Triaenonychidae.

We also failed to recover a monophyletic Insidiatores in two of three analyses, and instead found a sister group relationship between Grassatores and Travunioidea with

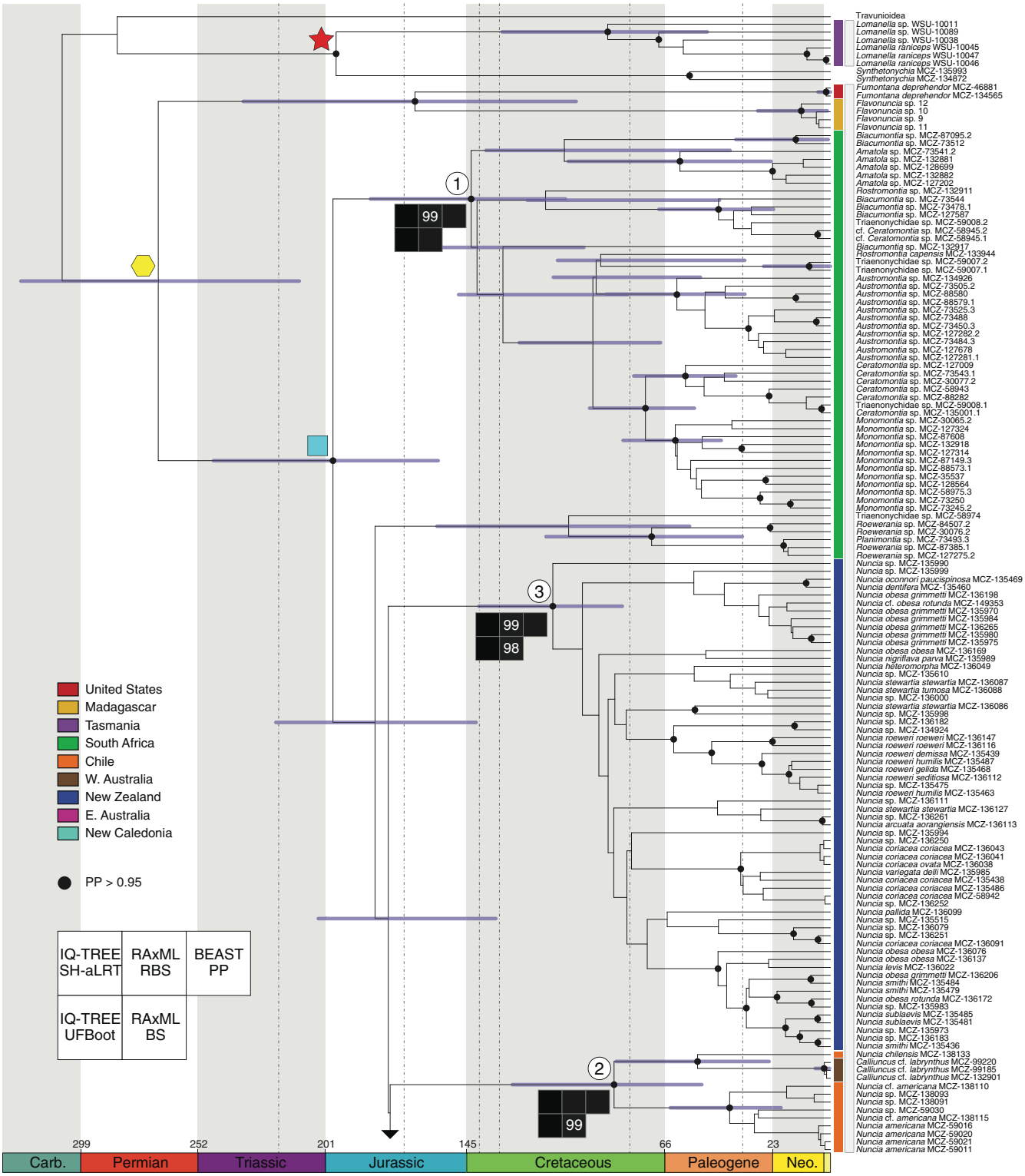

Fig. 5. BEAST chronogram showing divergence time estimates for Triaenonychidae. Error bars at nodes show 95% highest probability densities of estimated divergence times. Left column next to terminals is coloured by geographic area, as shown in the key and in Fig. 2–4. Right column is coloured by subfamily (white, Triaenonychinae; black, Sorensenellinae; light grey, Triaenobuninae; dark grey, Adaeinae). Star corresponds to *Synthetonychia* + *Lomanella*, hexagon corresponds to Triaenonychidae, and square corresponds to Southern Hemisphere Triaenonychidae. Nodes with black circles correspond to well-supported clades (posterior probability >0.95). Numbered nodes correspond to well-supported clades across all analyses, as in Fig. 3 and 4. For these nodes, sensitivity plots showing support values for all analyses are included. Dotted vertical lines correspond to major tectonic events in the breakup of Gondwana: 220 Ma (Pangaea splits into Gondwana and Laurasia); 170 Ma (East–West Gondwana split); 140 Ma (South Atlantic ocean starts opening); 132 Ma (Madagascar–India separates from Australia–Antarctica–Zealandia); 80 Ma (Zealandia separates from Australia–Antarctica); 35 Ma (Antarctica disconnects from Australia and South America, New Caledonia re-emerges after marine transgression). Carb., Carboniferous; Neo., Neogene. For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this article.

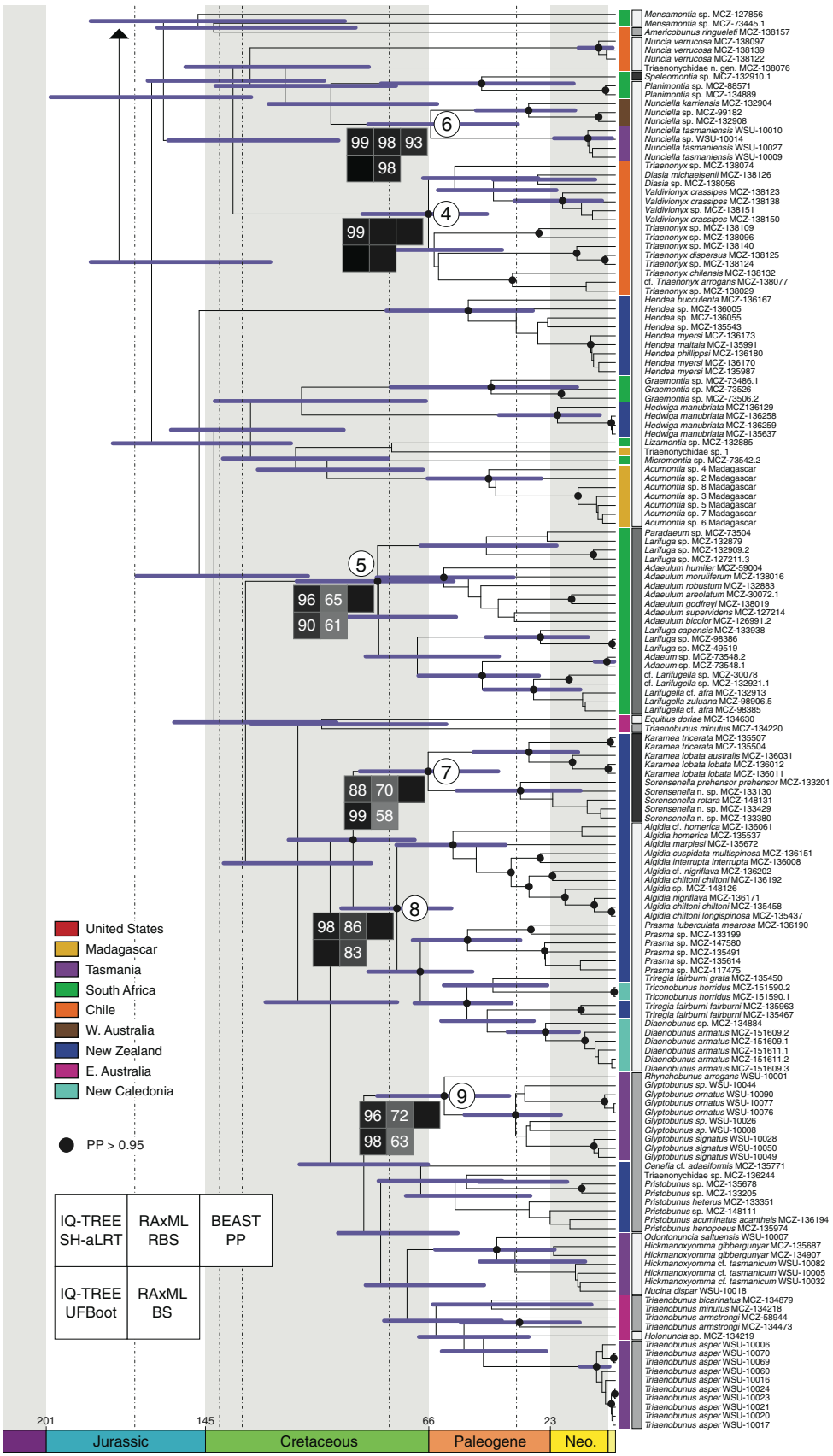

Fig. 5. *Continued.*

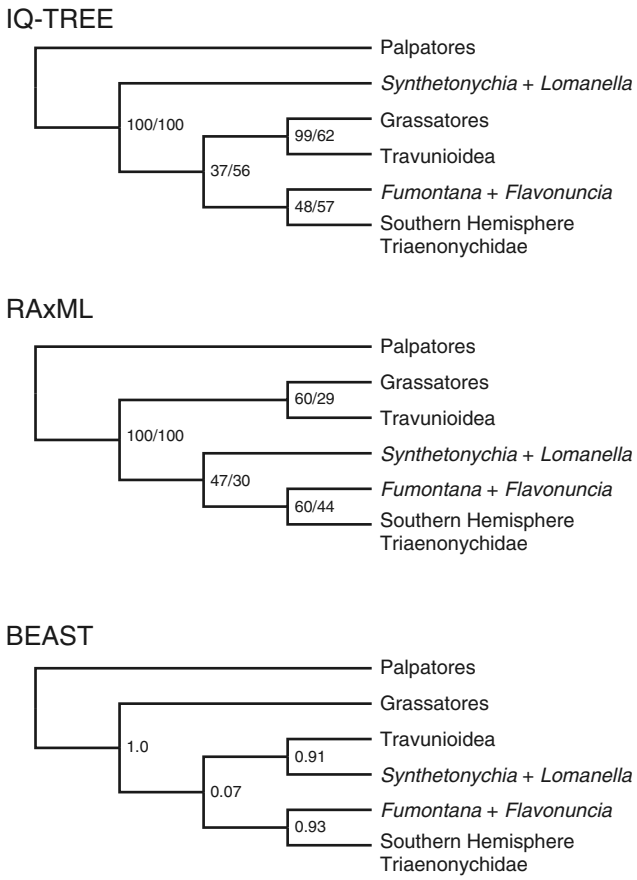

Fig. 6. Summary of major relationships of Laniatores from three phylogenetic analyses. Numbers at nodes show support values for depicted relationships (IQ-TREE: SH-aLRT/UFBoot; RAxML: RBS/BS; BEAST: PP).

variable levels of support in IQ-TREE (99% SH-aLRT, 62% UFBoot) and RAxML (60% RBS, 29% BS). This relationship contrasts with the results of previous analyses to include Travunioidea, Grassatores, and Triaenonychidae. For example, Derkarabetian *et al*. (2018) found a relationship of Grassatores + Triaenonychidae to the exclusion of Travunioidea in most analyses, and Sharma and Giribet (2011) found monophyly of Insidiatores except for *Synthetonychia*. Our BEAST analysis did recover a monophyletic Insidiatores, but with extremely low support (0.07 PP). This result was, however, recovered by Fernández *et al*. (2017) using transcriptomic data. Given the generally low nodal supports of our analyses and the limited number of loci used in our study, we prefer to leave this issue aside until additional data become available.

Triaenonychidae (excepting *Lomanella*, which we now consider to be the sister group of Synthetonychiidae) was monophyletic in all analyses, though with low support (IQ-TREE: 47% SH-aLRT, 57% UFBoot; RAxML: 60% RBS, 44% BS; BEAST: 0.93 PP). This poorly supported bipartition corresponds to a split between two monotypic genera, the eastern North American *Fumontana deprehendor* and *Flavonuncia pupilla* Lawrence, 1959, from Madagascar, and all other triaenonychids (herein 'Southern Hemisphere Triaenonychidae'). The relationship of *Fumontana* + *Flavonuncia* received high support in all analyses, and together with the Sardinian monotypic genus *Buemarinoa* Roewer, 1956, has been proposed as a tribe of Triaenonychinae, Buemarinoini Karaman, 2019, on the basis of their similar male genital morphology (Karaman 2019). While our data supported the clade Buemarinoini, they did not support its status as a tribe within Triaenonychinae. Likewise, the clade of the Southern Hemisphere Triaenonychidae received strong support in all analyses. We therefore accept the placement of *Fumontana* as a *bona fide* member of Triaenonychidae despite its geographic isolation. However, we acknowledge that given the low support for this relationship, *Fumontana* + *Flavonuncia* (=Buemarinoini) may represent a distinct evolutionary lineage, and its placement within the family should be further tested using more robust high-throughput sequencing methods, since the divergence between these two main lineages occurred between the Carboniferous and the Triassic (Fig. 5).

Phylogenetic relationships within Southern Hemisphere Triaenonychidae

Within the Southern Hemisphere Triaenonychidae, nodal supports along the backbone of the phylogeny were uniformly low, though some smaller clades were recovered consistently with high support (Fig. 3–5). These included (1) a clade of several South African genera classified in the subfamily Triaenonychinae (*Amatola* Lawrence, 1931, *Austromontia* Staręga, 1992, *Biacumontia* Staręga, 1992, *Ceratomontia* Roewer, 1915, *Monomontia* Staręga, 1992, and *Rostromontia* Staręga, 1992); (2) a clade of Chilean and Western Australian taxa (*Calliuncus* Roewer, 1931 and some *Nuncia* Loman, 1902 spp. with few spines – the South American *Nuncia* bear little morphological resemblance nor are closely phylogenetically related to the real *Nuncia* from New Zealand, as discussed below); (3) The New Zealand *Nuncia*; (4) a clade of some South American Triaenonychinae (*Diasia* Sørensen, 1902, *Triaenonyx* Sørensen, 1886, *Valdivionyx* Maury, 1988); (5) the South African genera in the subfamily Adaeinae (*Adaeulum* Roewer, 1915, *Adaeum* Karsch, 1880, *Larifuga* Loman, 1898, *Larifugella* Staręga, 1992, *Paradeum* Lawrence, 1931); (6) the genus *Nunciella* Roewer, 1931, from both Western Australia and Tasmania; (7) the New Zealand Sorensenellinae genera *Sorensenella* and *Karamea*; (8) a clade of several spiny Triaenonychinae genera from New Zealand (*Algidia* Hogg, 1920, *Prasma* Roewer, 1931, *Triregia* Forster, 1948) and the two genera from New Caledonia (*Triconobunus* and *Diaenobunus*); and (9) a clade comprising two Tasmanian Triaenobuninae genera, *Glyptobunus* Roewer, 1915 and *Rhynchobunus* Hickman, 1958.

Regarding the subfamilies of Triaenonychidae, our results confirmed the polyphyletic 'catch-all' status of Triaenonychinae, as well as the polyphyly of Triaenobuninae and Sorensenellinae. While we did recover a monophyletic Adaeinae in our trees, we were unable to

include the Western Australian genus *Dingupa*, the only member of that subfamily found outside of South Africa. Mendes (2009) previously identified the inconsistency of these subfamilial classifications, instead proposing a division of the family into two subfamilies, Adaeinae and Triaenonychinae. However, the constituent taxa in her emended subfamilies were either not sampled by us or else not closely related to each other in our phylogenies, making comparison and reconciliation difficult, and indeed the most recent catalogue of Opiliones still uses the traditional subfamilies (Kury *et al*. 2014). All told, we find the current categorisation of the four subfamilies to be uninformative at best and evolutionarily misleading at worst, and therefore recommend that their use be discontinued. However, we refrain from proposing any new classification scheme here given the low nodal support and inconsistent topology along the backbone of the tree.

New Zealand–New Caledonia

Wherever possible, we sequenced multiple individuals per genus in order to test their validity (i.e. monophyly). Of these, most genera from New Zealand were found to be monophyletic with high support in all analyses (*Hendea* Roewer, 1931, *Hedwiga* Roewer, 1931, *Algidia*, *Sorensenella*, *Karamea*, and *Prasma*). The New Zealand genus *Pristobunus* Roewer, 1931, was monophyletic in both IQ-TREE (96% SH-aLRT, 99% UFBoot) and RAxML (61% RBS, 49% BS) phylogenies, but potentially not in the BEAST tree, where one juvenile that could only be confidently identified to the subfamily 'Triaenobuninae' (MCZ-136244) fell within the clade (0.72 PP). In contrast to the ambiguous monophyly of *Pristobunus*, the New Zealand genus *Triregia* was paraphyletic with respect to the two genera from New Caledonia (*Triconobunus* and *Diaenobunus*) in all cases. Furthermore, *Triconobunus* and *Diaenobunus* were never found to be sister taxa, though support values for these internal relationships are generally low. It is clear, however, that this clade requires a thorough revision, including the incorporation of the type species *Triregia monstrosa* Forster, 1948, from Three Kings Islands.

Nuncia *and* Ceratomontia – *transoceanic genera?*

Currently, *Nuncia* and *Ceratomontia* are the only genera in Triaenonychidae known from multiple landmasses. *Ceratomontia* has previously been shown to be non-monophyletic, with one clade in South America and a possible grade in South Africa that also includes other genera (*Austromontia*, *Monomontia*) (Mendes and Kury 2008). We were not able to include South American *Ceratomontia* specimens in our study, so this hypothesis remains untested with molecular data, but our analyses showed that the South African *Ceratomontia* were deeply nested within a South African clade of triaenonychids.

Likewise, *Nuncia* was found in both New Zealand (which is home to the type species, *Nuncia sperata* Loman, 1902, junior synonym of *Triaenonyx obesus* Simon, 1899) and South America, in Chile and Argentina. *Nuncia* is by far the most diverse genus in the family, with 63 accepted species and subspecies (Kury *et al*. 2014), and it is characterised by a smooth carapace and a relative lack of spines and tubercles (see Fig. 1*J*). Despite being defined more by a lack of features than by the presence of any character in particular, all *Nuncia* from New Zealand constituted a clade with full support in all our analyses, unlike in the unpublished thesis of Vélez (2011). Lower-level relationships within the New Zealand *Nuncia*, though, indicate that many morphological species and subspecies are not valid, and this group requires substantial taxonomic revision.

The included *Nuncia* from South America were not at all closely related to the true New Zealand *Nuncia*, as suggested by a recent study of their genitalia (Porto and Pérez-González 2019), and indeed the South American species were found in two distinct places in the phylogeny. One of these clades corresponded to the species *Nuncia verrucosa* Maury, 1990 (and, based on morphology, presumably *N. spinulosa* Maury, 1990, though this species was not available for this study), the 'grupo *spinulosa*' of Maury (1990). As implied by their specific epithets, both of these species are replete with spines and tubercles (see Fig. 1*L* and fig. I, III in Maury 1990), and in his original descriptions Maury (1990) noted that perhaps they should not be placed in *Nuncia* at all given their morphological dissimilarity to both the New Zealand *Nuncia* and the other South American *Nuncia* species. Our phylogenetic results validate this scepticism, and while redescribing these species under a new genus name is outside the scope of this paper, we recommend such a transfer. The other clade of *Nuncia* from South America contained the species *Nuncia americana* Roewer, 1961 and *Nuncia chilensis* (H. Soares, 1968), as well as the species *Calliuncus* cf. *labyrinthus*, from Western Australia. While the members of this clade do lack spines and large tubercles and therefore superficially look similar to *Nuncia* from New Zealand, this clearly also constitutes a distinct evolutionary lineage. Again, without a thorough morphological examination of both *Calliuncus* (including its type species, *Calliuncus ferrugineus* Roewer, 1931) and the smooth-bodied South American *Nuncia* species, we refrain from taking any nomenclatorial action here, but our phylogenetic results highlight the need for revision.

Chile

Apart from the *Nuncia* from South America in our tree, we also recovered a clade of several other genera from Chile. The genus *Valdivionyx* was monophyletic in all analyses with high support. The closely related genus *Diasia* was monophyletic in both the RAxML and BEAST trees, but paraphyletic with respect to *Valdivionyx* in the IQ-TREE result. These two genera were closely related to the genus *Triaenonyx* in all analyses, which was recovered as monophyletic in the IQ-TREE and RAxML phylogenies, but was paraphyletic with respect to *Valdivionyx* and *Diasia* in the BEAST tree. The monotypic genus *Americobunus* does appear to be a distinct evolutionary lineage in the family, as it sat on a long branch and resolved in different locations in each of the three trees. Furthermore, we included an exemplar of an animal that morphologically does not correspond to any described

species (MCZ IZ-138076: Fig. 1*F*). It, too, was recovered as a distinct evolutionary lineage and, together with its unique morphology, corroborates its status as a new genus that will need to be described.

South Africa

Within South Africa, some genera were recovered as monophyletic in all analyses (e.g. *Adaeum*, *Adaeulum*, *Amatola*, *Austromontia*, *Graemontia* Staręga, 1992, *Larifugella*, and *Monomontia*), but just as many were not (e.g. *Biacumontia*, *Ceratomontia*, *Larifuga*, *Mensamontia* Staręga, 1992, *Planimontia* Kauri, 1961, *Roewerania* Lawrence, 1934, and *Rostromontia*). In addition, South African members appeared in 7–10 independent clades, some of them connected to Madagascar. Many genera as they are currently defined are extremely hard to distinguish on the basis of morphology, and diagnostic characters at the genus level show overlapping variability between genera. Future taxonomic work will certainly be needed to revise those genera, including looking for morphological characters that correspond to phylogenetic groups.

Madagascar

Our taxonomic sampling in Madagascar was restricted due to the limited availability of molecular-grade specimens from these landmasses in our collections. We therefore are unable to say much about the validity of those taxa, especially since its 35 species include several genera with only one or two species each (*Ankaratrix*, *Antogila* Roewer, 1931, *Decarynella* Fage, 1945, *Flavonuncia*, *Hovanuncia* Lawrence, 1959, *Ivohibea* Lawrence, 1959, *Millomontia* Lawrence, 1959, *Millotonyx* Lawrence, 1959, and *Paulianyx* Lawrence, 1959) plus the more diverse *Acumontia* Loman, 1898, with 22 described species (Kury *et al*. 2014). Even more unfortunately, the animals from Madagascar used in this study were consumed during DNA extraction and no vouchers remain for morphological analysis. However, we did recover multiple distinct lineages on the island, including the relictual *Flavonuncia*, a clade of specimens corresponding to *Acumontia*, and an unidentified species that groups with *Lizamontia* Kury, 2004 from South Africa in all analyses. Further sampling of Madagascar species with techniques that allow using historical museum samples (e.g. Derkarabetian *et al*. 2019) should help resolve this mystery.

Australia

We similarly had few exemplars from mainland Australia, which reflects the relatively unexamined triaenonychid diversity of the continent. Most of our specimens, and indeed most of the described species in the country, came from Tasmania, which we treated as a separate region. (While we often discuss Tasmania as a distinct region, it cannot be considered a separate landmass from Australia given continental land bridge connections during the Quaternary: Lambeck and Chappell 2001). Given the large part of Australia without suitable recent habitat, we also treated Western Australia as separate from the east, a distributional pattern that is not uncommon in short-range saproxylic animals (Giribet and Edgecombe 2006; Rix *et al*. 2015).

Here, we recovered a monophyletic *Glyptobunus* and found as its sister group the genus *Rhynchobunus*, also from Tasmania. However, some of our morphospecies were not monophyletic or had very old divergences, probably reflecting the poor taxonomy of the group. We also recovered a monophyletic *Nunciella*, which contained two reciprocally monophyletic lineages that corresponded to a group in Western Australia and a group in Tasmania. In contrast, we did not recover the monophyly of the genus *Triaenobunus* Sørensen, 1886, which is known from eastern and south-eastern mainland Australia as well as Tasmania. Similarly, the charismatic Tasmanian genus *Hickmanoxyomma* Hunt, 1990, which is easily identified by its extremely tall and pointed ocularium (Fig. 1*G*), was not recovered as a monophyletic group. Instead, we found two other Tasmanian species nested within the genus, *Nucina dispar* Hickman, 1958 and *Odontonuncia saltuensis* Hickman, 1958, neither of which have especially large spines on their ocularia (though in the BEAST tree *O. salutensis* formed the sister group to this clade rather than nesting within it). The close relationship between *Hickmanoxyomma* and *Odontonuncia* was previously hypothesised by Hunt (1990). Lastly, as discussed above, the Western Australian genus *Calliuncus* was monophyletic in all analyses, and nested within the smooth-bodied clade of South American *Nuncia*.

Clearly, many different lineages within Triaenonychidae are in need of revision. Future work must focus on areas with significant taxonomic and phylogenetic discrepancies, such as the South American *Nuncia*, the many para- and polyphyletic South African genera, the clade containing *Triregia* plus the New Caledonian triaenonychids, and the genus *Triaenobunus* in Australia. Furthermore, given the low nodal support along the backbone of our trees, future work should focus on resolving higher-level phylogenetic relationships using high-throughput sequencing techniques, including more genera, and, whenever possible, the type species of such genera.

Biogeographic results

With the exception of North America, which contains only the monotypic genus *Fumontana*, and Sardinia, with *Buemarinoa*, no major landmass on which triaenonychids are found contains a monophyletic assemblage of taxa. This result holds even accounting for the low nodal support values along the backbone of our tree. Indeed, even the two genera from New Caledonia were not recovered as sister taxa; instead, both nested within the New Zealand genus *Triregia*, as discussed above. In order to determine whether the non-monophyly of taxa in these Southern Hemisphere landmasses was attributable to ancient cladogenesis before Gondwanan breakup or more recent transoceanic dispersal, and to look for possible instances of Gondwanan vicariance, we performed a divergence dating analysis.

Comparison of marginal *L* estimates with Bayes Factors identified an exponential relaxed clock and a Yule tree prior as the optimal model for the dataset, with decisive support from Bayes Factors (BF = 15.59 compared to the next-highest

model's marginal *L* estimate). 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 ours, where most nodes correspond to interspecies divergences, estimates of node times were robust to tree prior choice, and that model selection procedures such as ours were effective in rejecting models likely to cause highly inaccurate node time estimates (Ritchie *et al*. 2017).

Initial diversification of Triaenonychidae predates Pangaean breakup

Our divergence dating results recovered an ancient origin for Triaenonychidae, with a mean age in the Permian, at 268 Ma (95% confidence interval, CI: 323–212 Ma) (Fig. 5). While the lower limit of the 95% CI did not quite predate the initial breakup of Pangaea *c*. 220 Ma (Ali and Aitchison 2008), for the most part these dates suggest that the family was diversifying before Pangaea began breaking up into the northern landmass of Laurasia and the southern landmass of Gondwana. The estimated age of the North America–Madagascar divergence, corresponding to the split between *Fumontana* and *Flavonuncia*, ranged from 234 to 101 Ma, with a mean age of 166 Ma, in the Jurassic. This age range approximately coincides with the timing of separation between Laurasia and Gondwana, and therefore implies that *Fumontana* is a relictual lineage in North America, just as *Buemarinoa* remains a relict in Western Europe. This parallels a similar pattern seen in other groups of arachnids, such as the oribatid mite family Malaconothridae Berlese, 1916, which has a cosmopolitan distribution and an estimated age of 333 Ma (Colloff 2013), as well as the dispersal-limited pseudoscorpion families Pseudotyrannochthoniidae Beier, 1932 and Pseudogarypidae Chamberlin, 1923, which have representatives in both temperate Australia and the Holarctic (though the ages of these families have not been estimated using molecular dating methods, their divergence from their sister group are Palaeozoic for the first and early Mesozoic for the latter) (Harvey *et al*. 2017; Benavides *et al*. 2019). Similar signatures of Pangaean breakup have also been detected in multiple groups of plants (Mao *et al*. 2012; Beaulieu *et al*. 2013) and amphibians (Pyron 2014).

The mean age of the Southern Hemisphere Triaenonychidae was estimated to be 198 Ma (95% CI: 246–156 Ma), in the Early Jurassic. Again, these dates suggest that the family was already diversifying well before Gondwana began breaking apart (initial rifting started in the Middle Jurassic, *c*. 170 Ma) (Ali and Aitchison 2008), and allows for the possibility that triaenonychids were able to colonise extensive continental areas via overland dispersal before continents separated. Palynological and isotopic records from this period suggest that during the Triassic and Jurassic, southern Gondwana experienced less climatic differentiation and a greater floristic uniformity dominated by lycophytes, ferns, and tree ferns (McLoughlin 2001; Cantrill and Poole 2012). Given the large-scale biotic turnovers that followed the end-Permian extinction and the subsequent expansion of continuous stretches of suitable vegetation, overland expansion of Triaenonychidae during this period seems highly plausible, and would therefore follow a pattern seen in other saproxylic taxa such as pettalid harvestmen (Baker *et al*. 2020) and peripatopsid velvet worms (Murienne *et al*. 2014; Giribet *et al*. 2018).

Relationships of taxa from disjunct landmasses

The Cretaceous period saw major rifting events, including the opening of the southern Atlantic Ocean, the separation of Madagascar–India from Australia–Antarctica–Zealandia, and the start of Zealandia's isolation (McLoughlin 2001; Ali and Aitchison 2008). Coinciding with this increased tectonism was the rise of angiosperms, and with it large-scale floristic turnovers and increased provincialism (McLoughlin 2001; McLoughlin and Kear 2010). All of these factors likely contributed to the inferred increase in cladogenesis of triaenonychids starting in the Cretaceous and continuing into the Paleogene (Fig. 5), as suitable forest habitat became more fragmented and populations in turn became more isolated. This may also have contributed to our difficulty resolving relationships between many clades in our phylogeny.

Because there was limited support for relationships between genera from different landmasses, we refrained from employing any explicit biogeographic models of range evolution. Despite those limitations, we still found a few places in the tree that were well supported and that corresponded to divergences between taxa from different landmasses. For example, *Calliuncus* (Western Australia) and *Nuncia chilensis* (Chile) (Clade 2 in Fig. 3–5) had an estimated divergence time of 25–85 Ma, with a mean date of 53 Ma. As Australia and Chile were connected via Antarctica until *c*. 35–40 Ma, when Tasmania and Antarctica separated (McLoughlin 2001; Wei 2004), this divergence time is consistent with the process of Gondwanan vicariance, though we cannot rule out transoceanic dispersal, as its lower age estimate postdates continental separation by *c*. 10 Ma. Interestingly, *Nuncia chilensis* was originally described as *Parattahia chilensis* H. Soares, 1968, making it the second species in the genus erected for the Tasmanian species *Parattahia usignata* Roewer, 1915. The similarity between *Parattahia* and *Calliuncus* was recognised by Hunt (1996), who suspected *Calliuncus* to be a junior synonym of *Parattahia* (though without explicit morphological justification). While *Parattahia chilensis* was later transferred to *Nuncia* by Maury (1990), our results bolster the hypothesis of Soares (1968), who recognised the affiliation between the species from Chile and Tasmania. Sampling *P. usignata* and *Calliuncus ferrugineus* Roewer 1931 (the type species of *Calliuncus*) will be useful in further clarifying the potential trans-Antarctic nature of this clade.

Nearly all divergences between taxa from different landmasses in the family were estimated to have occurred

before the end of the Mesozoic (66 Ma), though the lower limits of several 95% CIs postdated this boundary. Similarly, most Gondwanan rifting events took place during the Mesozoic, from the initial split into East and West Gondwana *c*. 170 Ma to the separation of Zealandia from East Gondwana *c*. 80 Ma. The only major separation events that occurred in the Cainozoic were the disconnection of Australia and South America from Antarctica, which occurred *c*. 35–40 Ma and *c*. 30–35 Ma respectively (McLoughlin 2001; Wei 2004). This underscores the idea that the common mode of range expansion and diversification in Triaenonychidae was overland dispersal followed by subsequent isolation as continental blocks separated.

A well-known biogeographic debate exists surrounding the source of New Zealand's terrestrial biota. Briefly, the controversy suggests that following the separation of Zealandia (i.e. the small continent that contains New Zealand and New Caledonia (Mortimer *et al*. 2017)) from Australia–Antarctica *c*. 80 Ma, New Zealand experienced a prolonged marine transgression (often called the 'Oligocene drowning') (see Giribet and Boyer 2010). This period lasted from *c*. 36 to *c*. 23 Ma, and at its peak (23 Ma) land area was reduced to ~18% of its current area (Cooper and Cooper 1995; Wallis and Jorge 2018). However, some authors have gone so far as to say the archipelago was completely inundated, which extirpated any relicts of Gondwanan origin; the implication then is that all of New Zealand's modern biota is the result of more recent dispersals that postdate 23 Ma (Trewick *et al*. 2007). We find at least three clades of taxa from New Zealand whose 95% CIs completely predate the peak of the Oligocene drowning period: (1) the New Zealand *Nuncia* (mean age: 110 Ma; 95% CI: 83–140 Ma), (2) *Hendea* (mean age: 52 Ma; 95% CI: 29–81 Ma), and (3) a clade composed of *Sorensenella*, *Karamea*, *Algidia*, *Prasma*, *Triregia*, and the New Caledonian *Diaenobunus* and *Triconobunus* (mean age: 93 Ma; 95% CI: 71–116 Ma). Triaenonychids therefore serve as yet another source of examples refuting the hypothesis of New Zealand's total submersion during the Oligocene, as suspected by earlier workers (Giribet and Boyer 2010).

While most divergences in the family concorded with Gondwanan vicariance or potentially pre-Gondwanan cladogenesis, there is at least one likely case of dispersal in the family: to New Caledonia. As stated previously, New Caledonia (specifically the main island of Grande Terre) is part of the small continent Zealandia, which separated from the eastern margin of Gondwana *c*. 80 Ma (McLoughlin 2001). Despite being part of the same crustal block, New Zealand and New Caledonia have never shared a terrestrial connection with each other. Unlike in New Zealand, where the geologic evidence for total submersion is inconclusive at best, there is strong geologic evidence that New Caledonia was submerged thousands of metres underwater during the Palaeocene, and subsequently thrust under oceanic crust during the Eocene, finally re-emerging *c*. 37 Ma (Grandcolas *et al*. 2008; Cluzel *et al*. 2012; Sutherland *et al*. 2020). New Caledonia is therefore functionally a Darwinian island and, accordingly, most endemic taxa that have been studied using time-calibrated molecular phylogenetics are found to have arrived to the island no earlier than 37 Ma (Nattier *et al*. 2017; though see Giribet and Baker 2019). In the case of Triaenonychidae, we found both New Caledonian genera (*Diaenobunus* and *Triconobunus*) to be clearly nested within the New Zealand genus *Triregia*, which was in turn a part of a larger clade of New Zealand-endemic taxa (Clade 8 in Fig. 3–5). While we only had specimens of *Triconobunus* from a single locality and therefore cannot make any inferences about its origination and diversification time on the island, we did have sequence data for *Diaenobunus* from two different localities, separated by a linear distance of 16 km and constituting two putative species (although the genus remains monotypic). The estimated diversification time of *Diaenobunus* was 25 Ma (95% CI: 13–38 Ma), consistent with the idea that the genus dispersed from New Zealand and started diversifying on the island after its re-emergence *c*. 37 Ma. While nodal supports within this clade were relatively low across all analyses, they were consistent, so if these results do reflect the true topology it implies that triaenonychids dispersed from New Zealand to New Caledonia twice. It is also worth noting that the upper limit of the 95% CI for this diversification at 38 Ma allows us to reject the hypothesis that these animals are a Gondwanan relict, as this postdates Zealandia's split from Gondwana in the Late Cretaceous, *c*. 80 Ma.

Conclusions

We generated the first molecular phylogeny focused on Triaenonychidae, the fourth most speciose family of Opiliones, and inferred divergence times using fossil-derived calibrations. We found that the family, as traditionally defined, is not monophyletic, and transferred *Lomanella* out of Triaenonychidae, as it is the sister group to Synthetonychiidae, and this clade is not always related to the other triaenonychids. We also support *Fumontana* and *Flavonuncia* as a clade (*Buemarinoa* would be related to these, but was not sampled), which is the sister group to all other temperate Gondwanan triaenonychids. Despite low nodal support for relationships between many taxa, our results do highlight many places in which taxonomy does not reflect phylogeny, and which should therefore be revised. Complementary work by our group is already underway to resolve higher-level relationships using UCE (ultraconserved elements) sequencing (Faircloth *et al*. 2012). A well resolved phylogeny of this nature will be critical for further addressing evolutionary questions in the family, such as those about morphological stasis and disparity, sexual and male dimorphism, parental care strategies, niche conservatism, and diversification dynamics through time.

Through our divergence dating analysis, we also found that Triaenonychidae is an ancient family that predates Pangaean and Gondwanan rifting, therein explaining their widespread but disjunct distribution across the Southern Hemisphere and North America and Western Europe. Indeed, nearly all divergences of taxa from different landmasses predate or coincide with Gondwanan tectonic events. However, we find at least one irrefutable case of dispersal, to the island of Grande Terre in New Caledonia. We suggest this is another

example of 'common vicariance and rare dispersal' in Opiliones (Hedin and McCormack 2017). There have likely been multiple dispersal events in the family, as evidenced by their presence in the oceanic Crozet Islands and on far offshore islands in New Zealand, such as the Chatham and Auckland Islands (Forster 1954). Future work will also be necessary to incorporate specimens from these islands into a phylogenetic framework so as to understand their biogeographic history and the capacity for dispersal within the family.

Conflicts of interest

G. Giribet is the Editor-in-Chief of *Invertebrate Systematics*. Despite this relationship, he took no part in the review and acceptance of this manuscript. The authors declare that they have no further conflicts of interest.

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