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Phylogenomic re-evaluation of Triaenonychoidea (Opiliones : Laniatores), and systematics of Triaenonychidae, including new families, genera and species

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Abstract. The Opiliones superfamily Triaenonychoidea currently includes two families, the monogeneric New Zealand–endemic Synthetonychiidae Forster, 1954 and Triaenonychidae Sørensen, 1886, a diverse family distributed mostly throughout the temperate Gondwanan terranes, with ~110 genera and ~500 species and subspecies currently described. Traditionally, Triaenonychidae has been divided into subfamilies diagnosed by very few morphological characters largely derived from the troublesome 'Roewerian system' of morphology, and classifications based on this system led to many complications. Recent research within Triaenonychoidea using morphology and traditional multilocus data has shown multiple deeply divergent lineages, non-monophyly of Triaenonychidae, and non-monophyly of subfamilies, necessitating a revision based on phylogenomic data. We used sequence capture of ultraconserved elements across 164 samples to create a 50% taxon occupancy matrix with 704 loci. Using phylogenomic and morphological examinations, we explored family-level relationships within Triaenonychoidea, including describing two new families: (1) Lomanellidae Mendes & Derkarabetian, fam. nov., consisting of *Lomanella* Pocock, 1903, and a newly described genus *Abaddon* Derkarabetian & Baker, gen. nov. with one species, *A. despoliator* Derkarabetian, sp. nov.; and (2) the elevation to family of Buemarinoidae Karaman, 2019, consisting of *Buemarinoa* Roewer, 1956, *Fumontana* Shear, 1977, *Flavonuncia* Lawrence, 1959, and a newly described genus *Turonychus* Derkarabetian, Prieto & Giribet, gen. nov., with one species, *T. fadriquei* Derkarabetian, Prieto & Giribet, sp. nov. With our dataset we also explored phylogenomic relationships within Triaenonychidae with an extensive taxon set including samples representing ~80% of the genus-level diversity. Based on our results we (1) discuss systematics of this family including the historical use of subfamilies, (2) reassess morphology in the context of our phylogeny, (3) hypothesise placement for all unsampled genera, (4) highlight lineages most in need of taxonomic revision, and (5) provide an updated species-level checklist. Aside from describing new taxa, our study provides the phylogenomic context necessary for future evolutionary and systematic research across this diverse lineage.

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Introduction

Phylogenomic analyses have led to strongly supported relationships in Opiliones, resulting in more stable classifications. Whereas early phylogenomic studies focused on relationships across all Opiliones (e.g. Hedin *et al*. 2012; Sharma *et al*. 2014; Fernández *et al*. 2017), more recent studies are exploring relationships at shallower levels within suborders (e.g. Baker *et al*. 2020*a*), particularly within the most diverse of the four suborders, Laniatores (Derkarabetian *et al*. 2018; Aharon *et al*. 2019). Historically within Laniatores there

have been three main lineages, the two superfamilies Travunioidea and Triaenonychoidea (historically grouped together and called Insidiatores, although not always forming a clade), and the highly diverse and largely tropical Grassatores. Currently, Triaenonychoidea includes two families, Synthetonychiidae Forster, 1954 and Triaenonychidae Sørensen, 1886 (Fig. 1). Synthetonychiidae is a morphologically unique and monogeneric family endemic to New Zealand. Triaenonychidae is a largely Gondwanan lineage with ~500 species and subspecies in ~110 genera found throughout the temperate forests of South America, southern Africa, Madagascar, Crozet Islands, Australia, New Zealand, and New Caledonia, with the enigmatic *Fumontana deprehendor* Shear, 1977 found in the southern Appalachians of the south-eastern United States and the recently transferred *Buemarinoa patrizii* Roewer, 1956 known from a single cave in Sardinia (Fig. 2). Like many Laniatores, Triaenonychoidea includes taxa with generally low dispersal ability and high microhabitat specificity – with many typical examples of short-range endemics (*sensu* Harvey 2002). They are nocturnal and often confined to dense dark forests, but can be typically found in moist microhabitats resting under woody debris, rocks or in caves, although some are associated with more specific microhabitats like moss.

Early multilocus studies and more recent transcriptome-based studies have shown paraphyly of Triaenonychoidea, largely due to the placement of Synthetonychiidae (Giribet *et al*. 2010; Sharma and Giribet 2011; Fernández *et al*. 2017). However, the most recent analysis using sequence capture methods showed monophyly of the lineages Travunioidea, Triaenonychoidea and Grassatores across multiple types of phylogenetic analyses (Derkarabetian *et al*. 2018), except for an ASTRAL analysis. Although these relatively deeper relationships are becoming more stable and consistent across studies, multiple factors hinder stable classifications within these groups. The most obvious issue is the morphological characters that are traditionally used to define and diagnose lineages, which were largely derived from the 'Roewerian system' of morphology, relying on trivial characters to diagnose taxa outside of a phylogenetic context, while also ignoring the most potentially useful characters. Within Triaenonychidae, multiple tribes and subfamilies have been proposed, largely defined by the shape of the sternum or hind tarsal claw structure. In the case of tarsal claws, this structure has been shown to be highly homoplastic at all taxonomic levels and therefore not suitable as a defining character (e.g. Hunt and Hickman 1993; Shear and Derkarabetian 2008), a situation most evident in Travunioidea (Derkarabetian *et al*. 2018). Other problems preventing stable classifications stem from rare taxa, some of which were poorly described, and taxa that may be difficult to identify because of poor taxonomic work. For example, the cave-obligate species *Buemarinoa patrizii* Roewer, 1956, which is endemic to Sardinia. This species was placed in the Travunioidea family Travuniidae Absolon & Kratochvíl, 1932 based on superficial morphological similarities resulting from obligate cave life. Derkarabetian *et al*. (2018) conducted a revision of Travunioidea based on phylogenomic results, but were unable to acquire specimens of this genus because of its rarity. As such, the authors retained *Buemarinoa* in Travunioidea largely based on historical classifications and previous studies based on those classifications (e.g. Kury and Mendes 2007), stating that the final status of these genera will require more thorough re-examination of specimens.

Modern studies within Triaenonychoidea have been alleviating uncertainty associated with the above issues. More recent morphology-based phylogenetic studies (e.g. Mendes and Kury 2008; Mendes 2009) were critical in Triaenonychidae because they provided support for the failure of the 'Roewerian system' of morphology, identified more useful characters for modern systematic work in Triaenonychidae, and provided more stable and reliable phylogenetic hypotheses. Karaman (2019), through examination of the type specimens of *Buemarinoa patrizii* and comparative study of genitalic morphology, showed that *Buemarinoa* Roewer, 1956 is actually a triaenonychid most closely related to the other Northern Hemisphere triaenonychid, *Fumontana* Shear, 1977. Additionally, Karaman (2019) suggested a close similarity of these two genera to *Flavonuncia* Lawrence, 1959, a small triaenonychid endemic to Madagascar. Given the unique morphological similarities of these three genera, he established and diagnosed the new tribe Buemarinoini Karaman, 2019 within Triaenonychidae. A recent multilocus study by Baker *et al*. (2020*b*) explored the systematics and biogeography of Triaenonychidae using a Sanger-based sequencing approach including a large number of species across most of the range where the family occurs. At the familial level, Baker *et al*. (2020*b*) found that no subfamily was monophyletic, and recovered the Australian endemic triaenonychid genus *Lomanella* Pocock, 1902 as sister group to *Synthetonychia* Forster, 1954, and as such, removed *Lomanella* from Triaenonychidae to maintain monophyly of the family. Additionally, Baker *et al*. (2020*b*) confirmed the monophyly of Buemarinoini with genetic data, recovering a sister group relationship between *Flavonuncia* and *Fumontana*, which form the earliest-diverging lineage with respect to all other Triaenonychidae, but the study lacked data for *Buemarinoa*. The authors noted the potential for a distinct family, but refrained from formal taxonomic changes until more detailed analyses could be conducted, specifically including the Tasmanian genus *Pyenganella* Hickman, 1958, which was previously recovered with Synthetonychiidae and *Lomanella* in some morphological analyses (Mendes 2009). Although Baker *et al*. (2020*b*) provided a preliminary exploration demonstrating the unsuitability of current subfamilies, classification was not addressed because of many weakly supported nodes.

Our ongoing work on the systematics of Triaenonychidae (e.g. Baker *et al*. 2020*b*), and the recent findings of Karaman (2019) necessitated a re-evaluation of the family-level classification of Triaenonychoidea in order to provide stable phylogenetic context for future research into this diverse lineage. Using a phylogenomics-based approach, Derkarabetian *et al*. (2018) proposed a stable family-level classification for Travunioidea, and further demonstrated the failure of many historical morphological classification systems to reflect the actual phylogenetic relationships. Phylogenomic

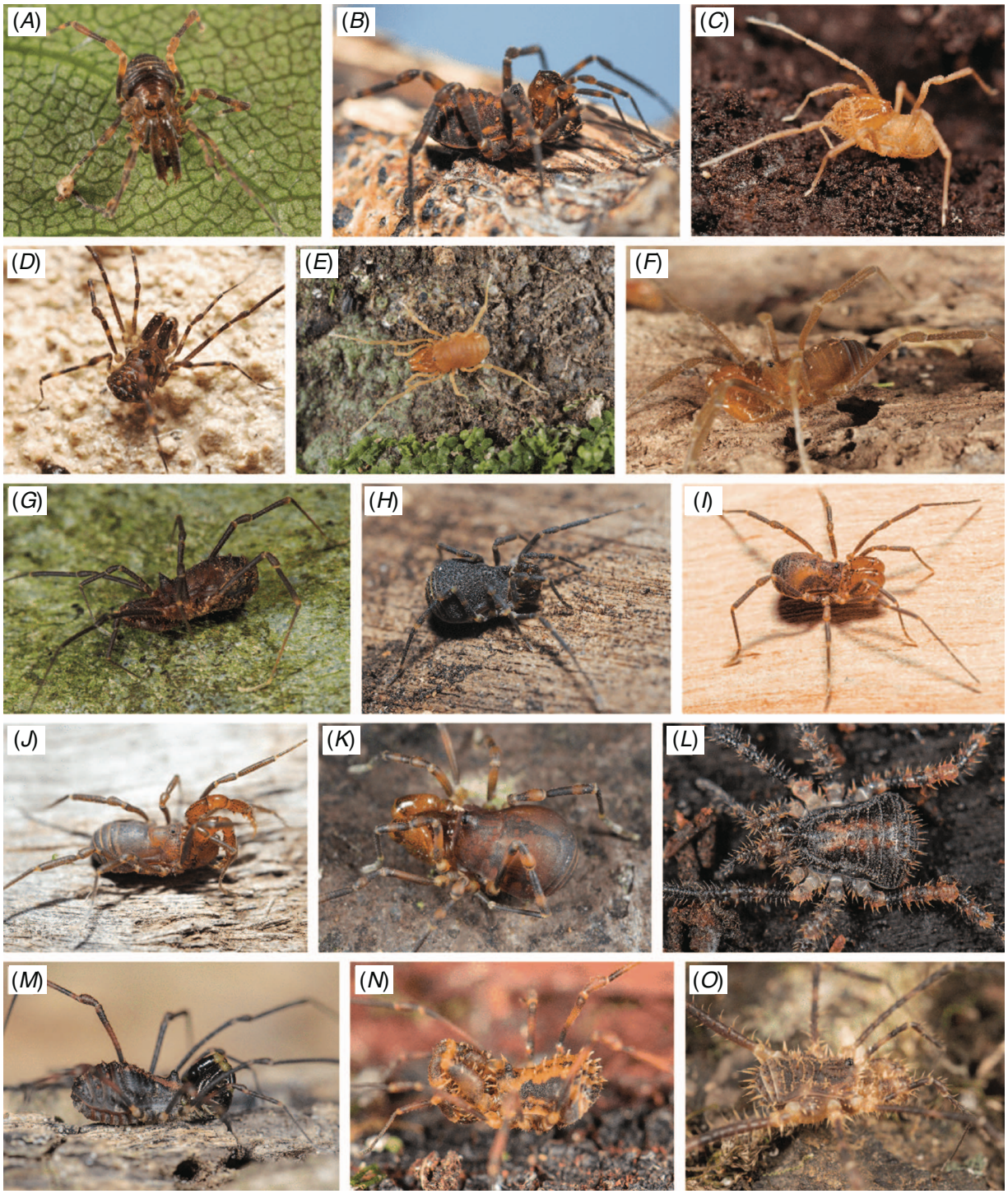

Fig. 1. Photographs of live Triaenonychoidea. (*A*) Synthetonychiidae: *Synthetonychia oliveae*, MCZ:IZ:144638. (*B*) Lomanellidae: *Lomanella* sp., MCZ:IZ:152652. (*C*) Buemarinoidae: *Fumontana deprehendor*. (*D–O*): Triaenonychidae. (*D*) *Hendea myersi cavernicola* [Clade A]. (*E*) *Austromontia* sp. [Clade B], MCZ:IZ:49523. (*F*) *Triaenonyx chilensis* [Clade C], MCZ:IZ:138132. (*G*) *Larifuga* sp. [Clade D1], MCZ:IZ:132879. (*H*) *Yatala aspera* [Clade D4], MCZ:IZ:152561. (*I*) *Calliuncus* sp. [Clade E1], MCZ:IZ:152607. (*J*) 'new genus B Australia' [Clade D5], MCZ:IZ:152679. (*K*) *Nuncia* sp. [Clade E2], MCZ:IZ:133374. (*L*) *Triaenobunus asper* [Clade E4]. (*M*) *Glyptobunus ornatus* [Clade E5]. (*N*) *Phanerobunus saxatilis* [Clade E5]. (*O*) *Diaenobunus armatus* [Clade E5], MCZ:IZ:151609. Photographs copyright of Gonzalo Giribet (*A*, *E–G*, *K*, *O*), Marshal Hedin (*C*, *L–N*), Shahan Derkarabetian (*B*, *H–J*). (*D*) copyright and courtesy of Erin Powell.

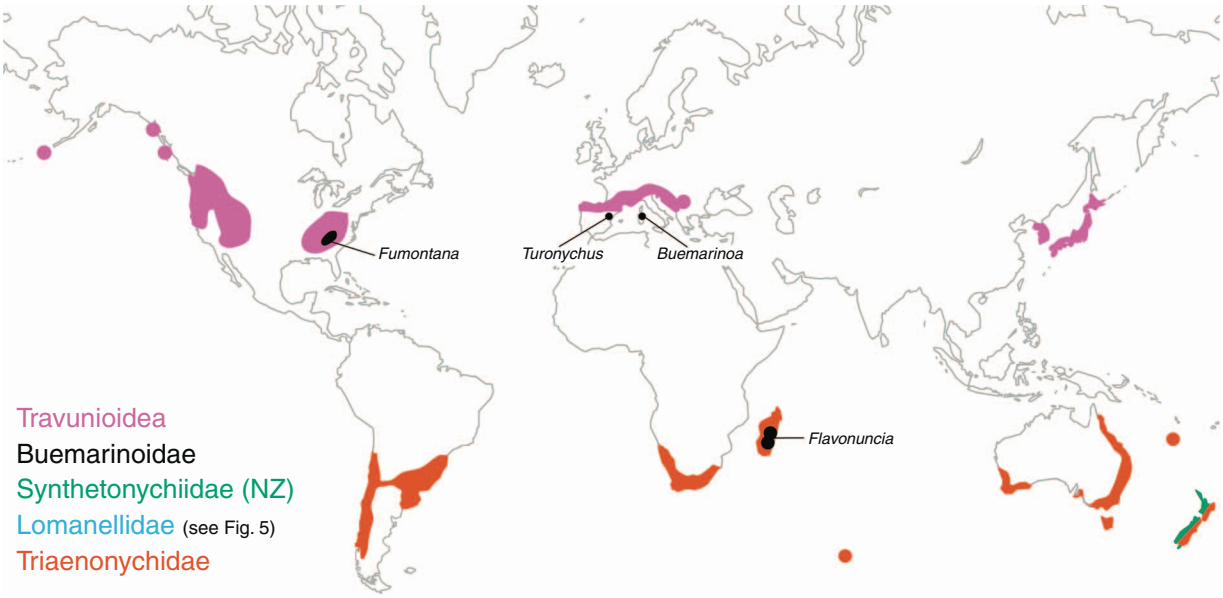

Fig. 2. Geographic distribution of Triaenonychoidea. Travunioidea is included for comparative purposes. Family names correspond to those proposed in this study. See Fig. 5 for distribution of Lomanellidae, fam. nov. Note: Synthetonychiidae and Triaenonychidae are broadly sympatric across New Zealand.

approaches have also provided strong support for many other clades, including Grassatores (Fernández *et al*. 2017). However, Triaenonychidae remained poorly sampled in earlier phylogenomic work. In this study, we conduct phylogenomic analyses using newly acquired and published data to examine the classification of Triaenonychoidea. Using sequence capture of ultraconserved elements (UCEs), we confirm the relationship between *Lomanella* and *Synthetonychia*, creating a new family for the lineage containing *Lomanella*. We also confirm that *Fumontana* and *Flavonuncia* are sister taxa and form a deeply divergent monophyletic lineage, and we elevate this clade to family rank. We describe two new monotypic genera, one each within these two newly described families. We also fully explore the systematics of Triaenonychidae with a dataset including ~80% of the 108 genera currently classified in the family. Finally, we discuss the taxonomic implications of this study relating to the use of subfamilies, provide an updated checklist of Triaenonychoidea species, discuss morphological patterns in a phylogenomic context, and highlight those lineages in greatest need of taxonomic revision and with the highest potential for new species discovery.

Materials and methods

Taxon sample

Specimens from multiple collections were used for this study, including the Invertebrate Zoology collections at the Museum of Comparative Zoology (vouchers labelled MCZ:IZ), the San Diego State University Terrestrial Arthropod Collection (SDSU_TAC:OP), the Natural History Museum of Denmark – University of Copenhagen (NHMUC), the California Academy of Sciences (CASENT), the Worcester State University collection (WSU), the Arachnological Collection of the Departamento de Zoología y Biología Celular Animal de la Universidad del País Vasco (ZUPV·ARACH), the Museo Nacional de Ciencias Naturales (MNCN), and the personal collection of the first author (some Tasmanian taxa, vouchers labelled as TAS).

Our final taxon set included 164 samples: 105 were newly sequenced for this study, and 59 were taken from previously published UCE studies (Table S1). Outgroups included 23 samples of Travunioidea, 4 Grassatores, and 1 sample from each of the 3 other Opiliones suborders. Previously published UCE samples are derived from Starrett *et al*. (2017) and Derkarabetian *et al*. (2018, 2019). The species-level checklist of all currently described Triaenonychoidea created by Kury *et al*. (2014) was used to guide our sampling at the genus level. Within Triaenonychidae we sampled at least one specimen from 84 of 108 (78%) currently recognised genera, with additional inclusion of samples from several potentially undescribed and new genera. Importantly, the majority of missing genera are monotypic, and largely single-site endemics.

We briefly mention several sampled taxa here to highlight their importance in confirming hypotheses of previous studies based on morphology (Shear 1977; Mendes 2009; Karaman 2019). Our dataset included two specimens of *Flavonuncia*, two specimens of the Australian-endemic genus *Lomanella*, and two specimens each of two new genera described below. Fresh tissue of *Buemarinoa* for molecular work could not be acquired. However, a specimen of *Buemarinoa* was available for morphological work. Given the detailed morphological work of Karaman (2019) showing its similarity to *Fumontana* and *Flavonuncia*, this genus can be included in our resulting classification with certainty. We also included a single specimen of the monotypic Tasmanian genus *Pyenganella*, which was recovered as the sister group to *Lomanella* in some morphological analyses and placed in a new family

Lomanellidae (*nomen nudum*) in an unpublished Ph.D. dissertation by Mendes (2009). On the basis of genitalic morphology, Shear (1977) hypothesised that *Fumontana* was most similar to *Monomontia* Staręga, 1992 from South Africa and *Hendea* Roewer, 1931 from New Zealand. Similarly, on the basis of genitalic morphology, Karaman (2019) hypothesised that the Buemarninoini is most similar to the South African group that includes *Monomontia*, *Austromontia* Staręga, 1992, and *Ceratomontia* Roewer, 1915. As such, the dataset included one newly sequenced sample each of *Monomontia* and *Austromontia*, and two samples each of *Ceratomontia* and *Hendea*.

Two transcontinental genera are known within Triaenonychidae: *Ceratomontia* from South America and South Africa, and *Nuncia* Loman, 1902 from South America, New Zealand, and one species endemic to the Crozet Islands. *Ceratomontia* is represented by two samples: one sample of *C. argentina* Canals, 1939 from South America and one sample of *Ceratomontia* sp. from South Africa. The polyphyletic genus *Nuncia* is represented by six samples: three from New Zealand, and three samples from South America (*N. americana* Roewer, 1961, *N. chilensis* (Soares, 1968), and *N. verrucosa* Maury, 1990, representing the unrelated clades identified by Baker *et al*. 2020*b*). Specimens of *Nuncia unifalculata* (Enderlein, 1909) from the Crozet Islands could not be acquired for this study.

Sequence capture and phylogenomic analyses

For newly sequenced samples, protocols for sequence capture of UCEs were identical to Derkarabetian *et al*. (2019) using the Arachnida probe set (Arbor Biosciences, Ann Arbor, MI, USA) developed and tested by Faircloth (2017) and Starrett *et al*. (2017). Several historical museum samples preserved in 70–80% ethanol (not preserved for genetic work) were used in this study; DNA extraction and sequence capture from these specimens were conducted with the modified protocols outlined in Derkarabetian *et al*. (2019). Samples were sequenced at the Bauer Core Facility at Harvard University on either an Illumina HiSeq 2500 with 125-bp paired-end reads or an Illumina NovaSeq with 150-bp paired-end reads. Raw read data were processed using Phyluce (ver. 1.6, B. C. Faircloth, see https://github.com/faircloth-lab/phyluce; Faircloth 2016), with an Illumiprocessor wrapper used for quality control (B. C. Faircloth, see https://github.com/faircloth-lab/illumiprocessor). Contigs were assembled using Velvet (ver. 1.2.10, see https://www.ebi.ac.uk/~zerbino/velvet/; Zerbino and Birney 2008) and Trinity (ver. 2.1.1, https://github.com/trinityrnaseq/trinityrnaseq/; Grabherr *et al*. 2011) and the two resulting contig assembly files were combined into a single file. To match contigs to probes, we used minimum occupancy and minimum identity thresholds of 65. UCE loci were then aligned using Mafft (ver. 7.407, see https://mafft.cbrc.jp/alignment/software/; Katoh and Standley 2013) at default settings and trimmed using Gblocks (ver. 0.91b, see http://molevol.cmima.csic.es/castresana/Gblocks.html; Castresana 2000; Talavera and Castresana 2007) with conservative settings of –b1 0.5 –b2 0.85 –b3 4 –b4 8. Individual alignments were imported into Geneious (Kearse *et al*. 2012) for visual inspection, and following inspection we created a matrix including all loci with at least 50% taxon occupancy.

Phylogenetic analyses were run using a partitioned maximum likelihood analysis in IQ-TREE (ver. 1.6, see http://www.iqtree.org/release/v1.6.12; Nguyen *et al*. 2015), with tree reconstruction using the optimal partitioning strategy estimated with ModelFinder (MFP+MERGE) (Kalyaanamoorthy *et al*. 2017), the fast relaxed clustering algorithm (rclusterf), and 1000 ultrafast bootstrap replicates (Hoang *et al*. 2018). Following this, gene concordance factors (gCF) and site concordance factors (sCF) were calculated for the resulting phylogeny using IQ-TREE (ver. 2, see http://www.iqtree.org/; Minh *et al*. 2020*a*, 2020*b*). A concatenated unpartitioned Bayesian analysis was run using the BEAST package (ver. 2.6, https://www.beast2.org/; Bouckaert *et al*. 2014). Analyses used GTR+I+G and Yule models, and were run for 40 million generations logging every 1000 with 10% burn-in removed. Convergence was assessed using Tracer (ver. 1.7, A. Rambaut, A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard, see http://beast.community/tracer) and to confirm that all Effective Sample Size (ESS) values were >200. We also ran SVDQuartets (Chifman and Kubatko 2014) implemented in PAUP* (ver. 4.0a167, see https://paup.phylosolutions.com/; Swofford 2003) using default settings and 100 bootstrap replicates. Preliminary analyses found that placement of the historical museum sample ‘cf. *Triaenobunus* NHMUC:21B’ (from Derkarabetian *et al*. 2019) was unstable across analyses, leading to associated weakly supported nodes.

Morphology

Three taxa underwent detailed morphological study including *Buemarinoa*, a new genus from Spain, and a new genus from Western Australia. During the course of this study, Karaman (2019) published a detailed morphological comparison of *Buemarinoa* and *Fumontana*, clearly showing the close relationship between the two. Despite this, we still include our morphological analyses of *Buemarinoa* here to compare to the new genus from Spain and because the specimens were acquired from a different cave in Sardinia ~18 km away from the type (and only) locality of *B. patrizii*, indicating a more widespread distribution on the island.

Scanning electron microscopy (SEM) examination for *Buemarinoa* and the new genus from Spain were conducted through the Biomedical and High Resolution Analytical Microscopy Service at UPV/EHU (Leioa, Spain). The specimen was mounted on an SEM stub and coated with 15 nm gold in an Emitech K550X and imaged using a Hitachi S-3400N. SEM analyses of the new genus from Western Australia were conducted at the Center for Nanoscale Systems at Harvard. In this case, the penis was mounted on a SEM stub using a carbon adhesive tab (Electron Microscopy Sciences) and coated with 10 nm Pt/Pd (80 : 20) in a HAR 050 EMS 300T D dual head sputter coater. The specimen was then imaged using an Ultra FESEM using an SE2 detector with an EHT target of 10 kV.

Scanning electron micrographs were processed and edited in Adobe Photoshop CC 2018–2020 (Adobe Systems Corporation). Additional photographs were taken with a Keyence VHX 6000 digital microscope (Keyence Corp. Osaka, Japan), which can recognise focus information automatically and create a depth composition image. Line drawings were done in Adobe Illustrator 2020 (Adobe Systems Corporation) based on SEM and Keyence images. Genitalia for other taxa were examined on a Leica MZ 12.5 dissecting microscope.

Results

Phylogenomic analyses

Sequence Read Archive accession numbers for newly sequenced samples (SRA BioProject PRJNA649588) are in Table S1. The final 50% taxon occupancy matrix contained 704 loci, had a total length of 94 702 bp, and an average locus length of 135 bp. The average number of loci per sample in the final matrix across all samples was 526 (range = 49–678), with an average of 535 loci for Triaenonychoidea. The samples representing both the minimum and maximum number of loci across all samples were historical samples. The 12 historical museum specimens had an average of 412 loci in the final matrix, with collection dates ranging from 1914 to 2011. The IQ-TREE phylogeny had generally highly supported nodes, with all but 12 nodes having bootstrap support values >95% within Triaenonychoidea, only three of which were <80% (Fig. 3, 4). Six of the twelve nodes with <95% support within Triaenonychidae are associated with two highly derived lineages with very short internodes, and have no effect on the taxonomic conclusions discussed in this paper. For concordance factors, gCF values are typically lower than sCF for any given bipartition, even accounting for sCF values typically bottoming out at 33% given uninformative quartets (Fig. S1*A*). This suggests that individual loci have limited ability to resolve bipartitions, which is expected from relatively short UCE loci, and many loci have conflicting signal. Additionally, these short loci are even further limited at short internodes, as the shortest nodes typically had the lowest concordance values (Fig. S1*B*). The BEAST analyses had only four nodes with posterior probability below 0.95 (Fig. S2), whereas the SVDQuartets had many nodes with weak support (Fig. S3).

Three main early-diverging Laniatores lineages were found to be monophyletic with full bootstrap and posterior probability support across analyses: Travunioidea, Triaenonychoidea, and Grassatores. As in previous UCE studies (Derkarabetian *et al*. 2018, 2019), Travunioidea was recovered as the sister group to all remaining Laniatores

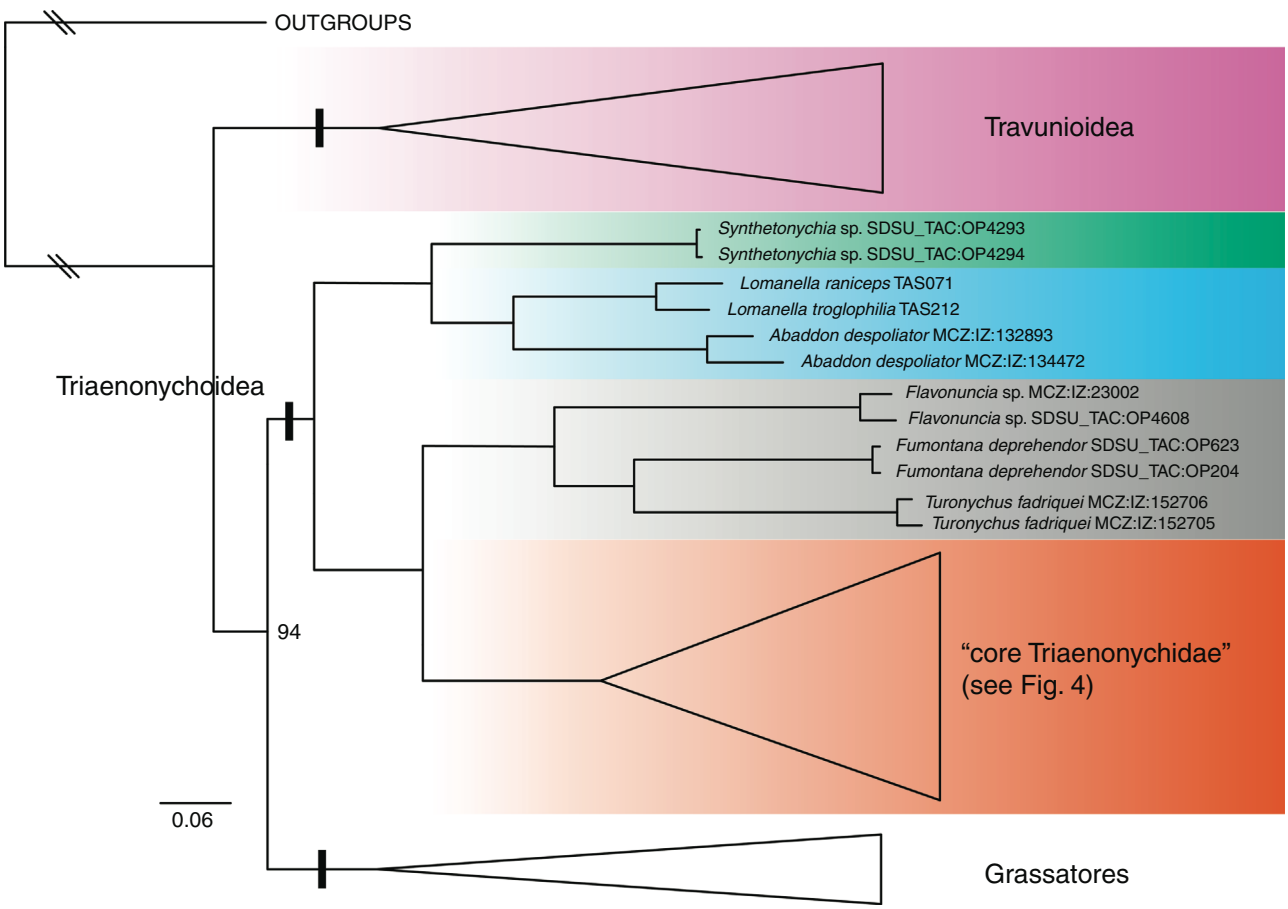

Fig. 3. Phylogenomic relationships among major laniatorean lineages, with emphasis on family-level divergences within Triaenonychoidea. Phylogeny is derived from the IQ-TREE analysis. Represented nodes are fully supported with 100% bootstrap support, unless indicated otherwise.

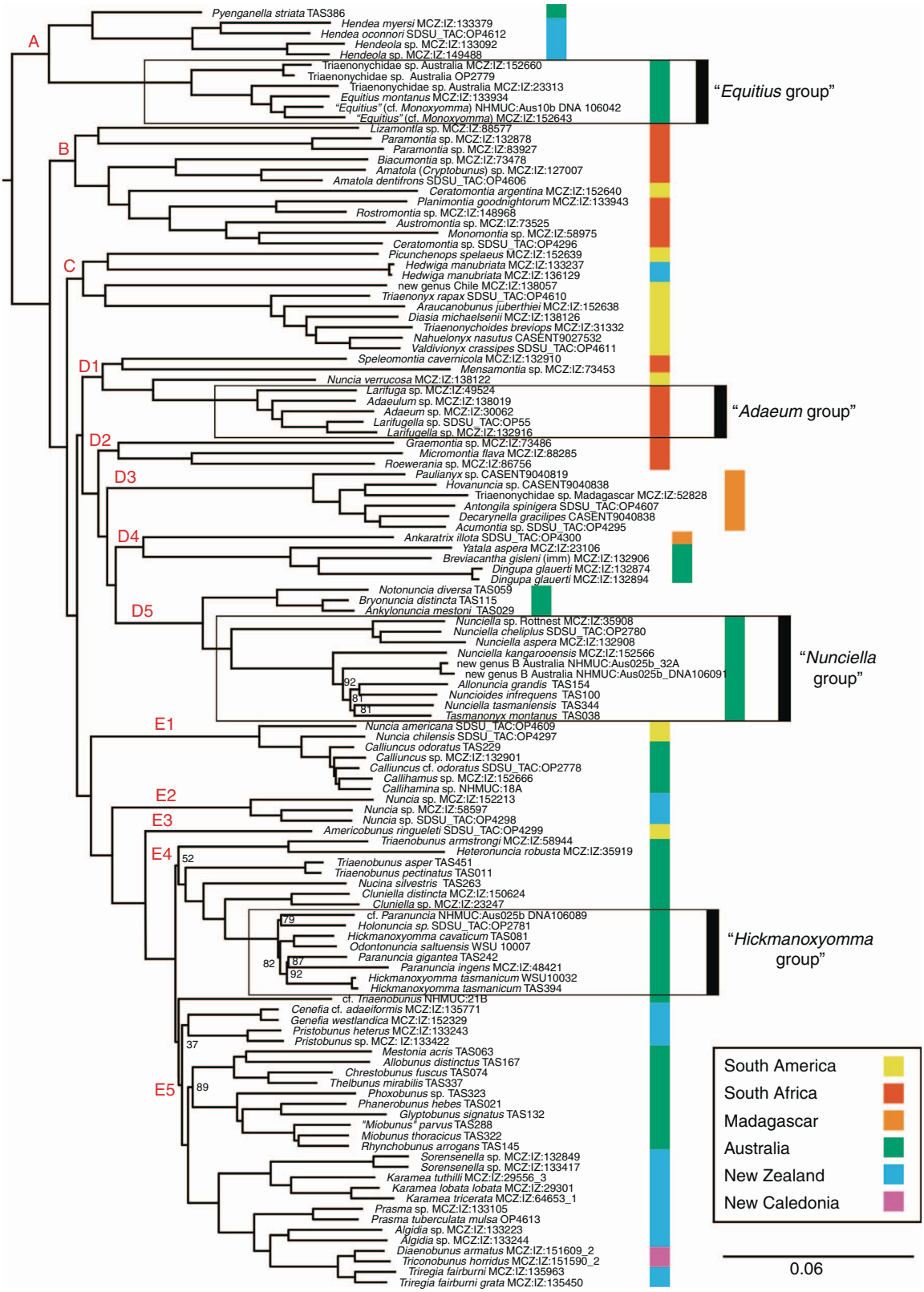

Fig. 4. Phylogenomic relationships of Triaenonychidae, with clade names as discussed in the main text. Phylogeny is derived from the IQ-TREE analysis. All nodes have 95% or higher bootstrap support, unless indicated otherwise. Coloured bars indicate geographic distribution of sampled taxa.

(Triaenonychoidea + Grassatores) across all analyses. Within Triaenonychoidea, three deeply divergent lineages were strongly supported (Fig. 3). The first lineage contained the New Zealand genus *Synthetonychia*, the Australian genus *Lomanella*, and a newly described genus from Western Australia, *Abaddon*, gen. nov. (see Taxonomy below). Second, we recovered Buemarinoini, including *Fumontana*, *Flavonuncia*, and a newly described genus from Spain, *Turonychus*, gen. nov. (see Taxonomy). The third lineage corresponded to the 'core Triaenonychidae', which includes all Southern Hemisphere triaenonychids (except for *Flavonuncia*, *Lomanella*, and the new genus from Western Australia). Notably, the genus *Pyenganella* is recovered within the 'core Triaenonychidae' with full support, and not as sister group to *Lomanella*, as was suggested by Mendes (2009). Within 'core Triaenonychidae' we define five major clades (A–E), some of which can be further subdivided into subclades (Fig. 4) (see Discussion for greater detail).

Within 'core Triaenonychidae', there are a few differences between the IQ-TREE and BEAST analyses (Fig. 4, S1, S2). The 'cf. *Triaenobunus* NHMUC:21B' specimen was found as sister group to *T. armstrongi* + *Heteronuncia* Roewer, 1920. The rest of the differences are largely associated with Clade D: the placement of subclade D1 sister group to Clade E, the placement of *Mensamontia* either in Clade C or sister group to all remaining 'core Triaenonychidae', and paraphyly of D2 with respect to D3. Relative to the IQ-TREE analysis, SVDQuartets showed a sister relationship between Clades A and B, *Mensamontia* in Clade C, *Ankaratrix* Lawrence, 1959 as sister group to subclade D2, *Heteronuncia* as sister group to E3 + E4 + E5, and non-monophyly of E5 with respect to E4.

Taxonomy

On the basis of our phylogenomic results, we formally establish the family name **Lomanellidae**, fam. nov. for the Australian genera *Lomanella* and the new monotypic genus from Western Australia, which we name ***Abaddon***, gen. nov., including ***A. despoliator***, sp. nov. We establish the family rank **Buemarinoidae** Karaman, 2019, stat. nov. to include *Buemarinoa*, *Fumontana*, *Flavonuncia*, and the new monotypic genus from Spain, which we name ***Turonychus***, gen. nov., including ***T. fadriquei***, sp. nov. All remaining triaenonychoid taxa, except Synthetonychiidae, are considered Triaenonychidae ('core Triaenonychidae' mentioned above). A checklist of all described Triaenonychoidea species is provided in Table S2. Type specimens for the new species are deposited in either the Museum of Comparative Zoology, USA (MCZ), the Museo Nacional de Ciencias Naturales, Spain (MNCN), or the Western Australian Museum, Australia (WAM), as noted below. Authorship varies for the newly described taxa and author(s) are associated with specific taxonomic names below. All measurements are in millimetres.

Superfamily **TRIAENONYCHOIDEA** Sørensen 1886

Included families: Triaenonychidae Sørensen 1886, Synthetonychiidae Forster 1954, Lomanellidae Mendes & Derkarabetian, fam. nov., Buemarinoidae Karaman 2019, stat. nov.

Family **LOMANELLIDAE** Mendes & Derkarabetian, fam. nov.

ZooBank LSID: urn:lsid:zoobank.org:act:B2825A44-1616-4103-91F1-A2BFF07BBC3F

Included genera: *Lomanella* Pocock, 1903, *Abaddon* Derkarabetian & Baker, gen. nov.

Type genus: *Lomanella* Pocock, 1903.

Type species: *Lomanella raniceps* Pocock, 1903, by original designation

Diagnosis

This Australian family (Fig. 5) is most closely related to the morphologically unique Synthetonychiidae from New Zealand, but differs from the family-level diagnosis of Forster (1954) by the presence of an obvious eye mound and shorter pedipalps bearing tubercles, which are sometimes more robust. Synthetonychiidae are diagnosed by their lack of an eye mound and elongate pedipalps that are slender and without tubercles (e.g. Forster 1954, fig. 708). Lomanellidae can be distinguished from Triaenonychidae by their relatively simple palps with weak spination (Fig. 6*E*) (Hunt and Hickman 1993, fig. 1), a process on the dorsal surface of coxae II, and lateral projections on the carapace above coxae II associated with the ozopore. Additionally, compared to male triaenonychid genitalia, which typically possess the full complement of plates (dorsal, dorsolateral, and ventral), the male genitalia of lomanellids are extremely attenuated and show a complete loss of the dorsal plate (Fig. 7*A*) (Hunt and Hickman 1993, fig. 3).

Distribution

Lomanellids are restricted to Australia (Fig. 5). The genus *Lomanella* is widespread in the temperate forests of southern New South Wales, Victoria and Tasmania, with a single species that is restricted to a small region of south-western Western Australia. The new genus *Abaddon*, gen. nov. is extremely restricted in distribution, known only from two localities in south-western Western Australia, an area where other arthropod taxa inhabiting these temperate rainforests show similar species distribution patterns (e.g. Rix *et al*. 2015; Sato *et al*. 2018; Schwentner and Giribet 2018).

Remarks

Amanda Mendes is included as a taxon author for this family to acknowledge her previous work, being the first to identify, recognise, and name this family in her unpublished dissertation. Although the morphological analyses of Mendes (2009) recovered *Pyenganella* in Lomanellidae, she expressed caution about the recovered relationship of *Pyenganella* with *Lomanella* and *Synthetonychia*. Simultaneously, she was certain that *Lomanella* represented a new family-level lineage as it was the only new name

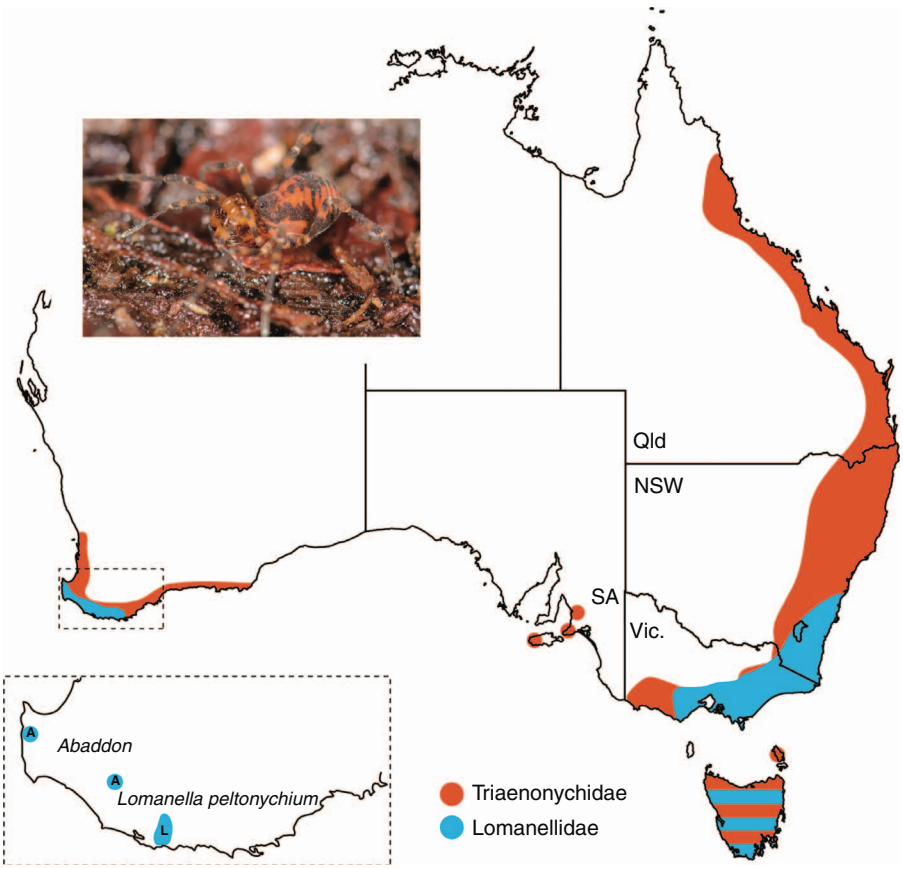

Fig. 5. Geographic distribution of Lomanellidae, fam. nov. and Triaenonychidae in Australia. Inset shows detailed distribution of lomanellid genera in Western Australia (with Triaenonychidae removed): A, *Abaddon despoliator*, gen. nov., sp. nov.: L, *Lomanella peltonychium*. Photograph is of a live *Lomanella raniceps* (photograph by Marshal Hedin). Note: Lomanellidae, fam. nov. is broadly sympatric with Triaenonychidae throughout its distribution range.

proposed based on her extensive morphological phylogenetic analyses. She approved the family diagnosis and agreed to authorship.

Genus ***Abaddon*** Derkarabetian & Baker, gen. nov.

(Fig. 6, 7*A*, S4)

ZooBank LSID: urn:lsid:zoobank.org:act:3575B6CE-740A-45AB-8892-31195A50F4A0

Type species: *Abaddon despoliator* Derkarabetian, sp. nov., by monotypy.

Diagnosis

This genus is very distinctive and can be easily distinguished from *Lomanella*, and all triaenonychids known from Western Australia, based on its highly tuberculate–spiny body (Fig. 6, S4). Compared to *Lomanella*, it has a penis with large lateral wing-like laminae, an elongate and tubular stylus rising directly from the sensillar region (sensillenträger of Martens 1986), without dorsal or ventral plates.

Description

Eye mound recessed from the anterior margin of the carapace, tuberculate and heavily pigmented (Fig. 6*A*, *B*). Anterior margin of carapace with large anteriorly directed spines, the medial spine being the largest (Fig. 6*A*, *B*). Dorsal scutum outline in dorsal view outline Eta η of Kury and Medrano (2016), with a slight widening at the midline. Body densely covered in brown pigmented tubercles except along lateral margins, with lateral projections above coxae II associated with ozopores (Fig. 6*A*, *B*). Each scutal segment with a row of large spines, generally increasing in number posteriorly. Coxae II with an elongate dorsal tubercle associated with ozopore; coxae IV with a small pigmented area dorsally (Fig. 6*A*, *B*). Ventral surface of body tuberculate; leg I coxae with a series of elongate tubercles along prolateral margin; sternum long and narrow (Fig. S4*B*). Genital operculum subtriangular and tuberculate. Pedipalps without heavy spination, one spine-bearing tubercle ventrally on the femur, tarsus with an elongate claw and elongate spines terminally (Fig. 6*E*). Leg I femur with a series of elongate dorsal and ventral tubercles bearing setae (Fig. 6*C*, *D*). Leg

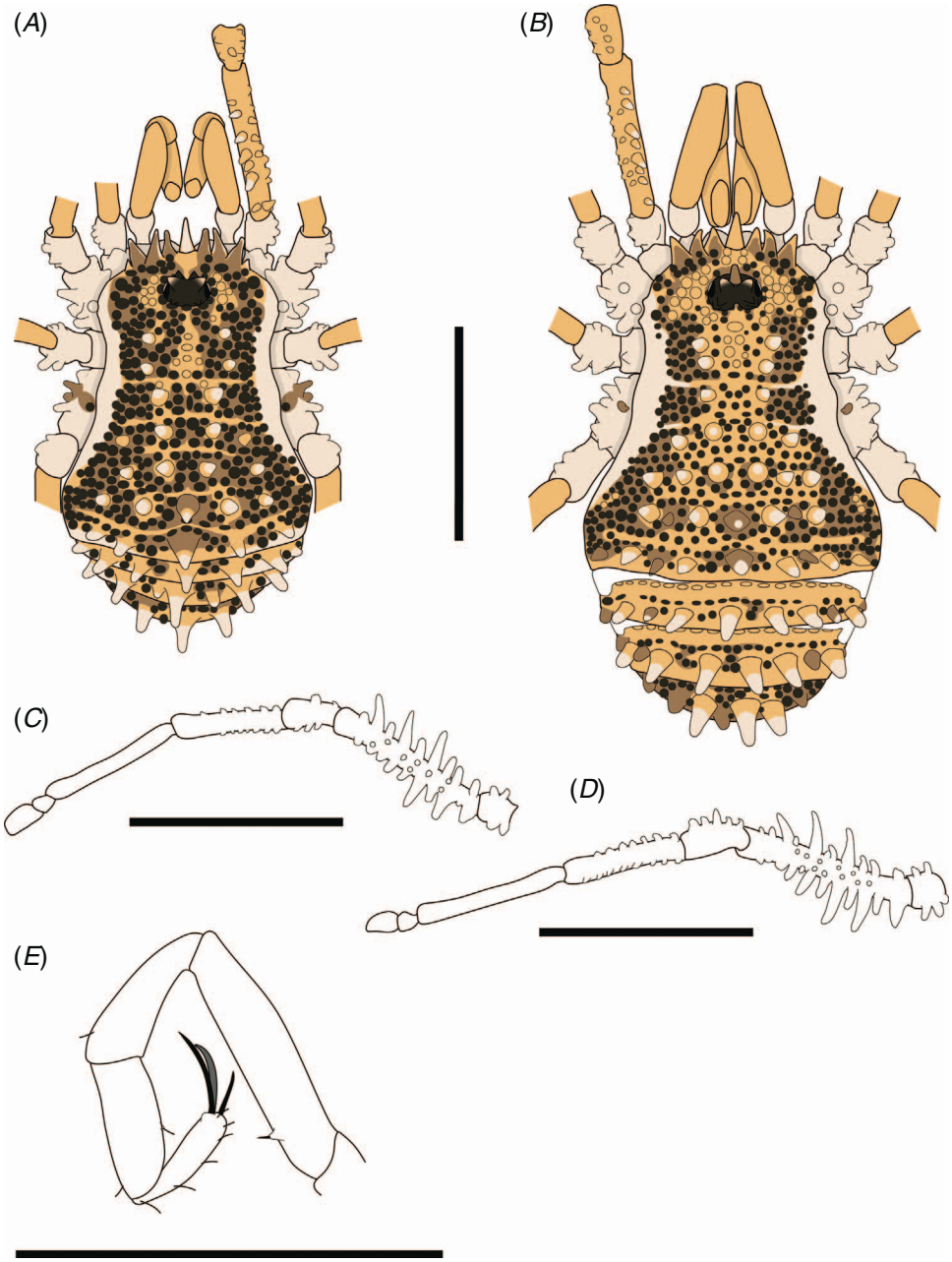

Fig. 6. General morphology of *Abaddon despoliator*, gen. nov., sp. nov. (*A*, *B*) Dorsal habitus: (*A*) male holotype (MCZ:IZ:134472_3), (*B*) female paratype (MCZ:IZ:134472_1). (*C*, *D*) Retrolateal view of leg I: (C) male holotype, (*D*) female paratype (MCZ:IZ:134472_1). (*E*) Retrolateral view of pedialp of male holotype. All scale bars: 1 mm; (*A*)–(*D*) at same scale. Note: (*C*) and (*D*) drawn without colour.

coxae tuberculate, legs with rows of longitudinal tubercles. Tarsal formula 2,2,3,3. Penis without dorsal or lateral plates; with large lateral wing-like laminae; stylus elongate, thin, and tubular, arising directly from the sensillar region (Fig. 7*A*).

Etymology

The genus name is in reference to the fictional character 'Abaddon the Despoiler' from the Warhammer 40 000 tabletop miniature game and science fiction universe developed by Games Workshop, which is a favourite hobby of the first author. The character is typically portrayed adorned with spikes and various sharp things. The name should be treated as masculine.

Abaddon despoliator Derkarabetian, sp. nov.

(Fig. 6, 7*A*, S4)

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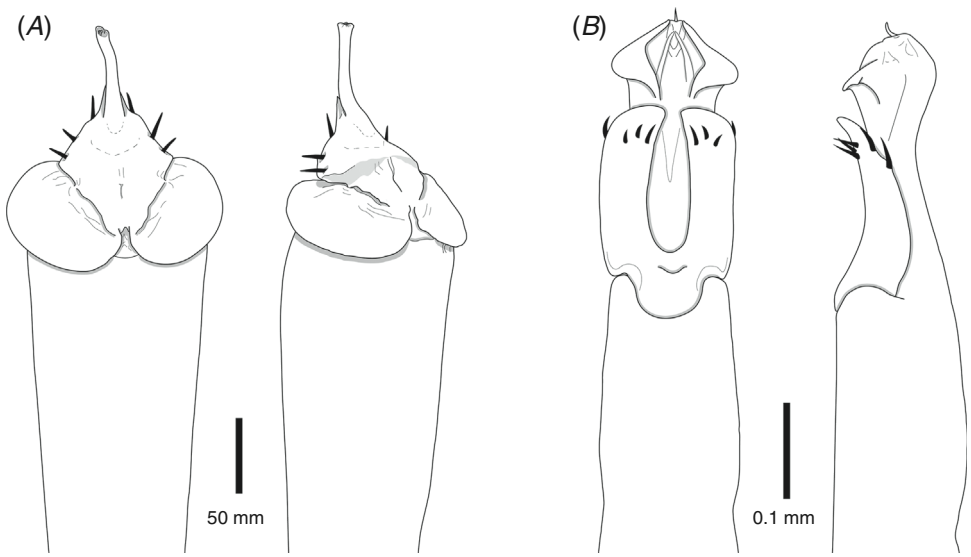

Fig. 7. Morphology of male genitalia. (*A*) *Abaddon despoliator*, gen. nov., sp. nov., ventral and ventrolateral views of male paratype (MCZ:IZ:132893_3). (*B*) *Turonychus fadriquei*, gen. nov., sp. nov., ventral and lateral views of male holotype.

Type material: Holotype male, one female paratype, and one male paratype from Australia: Western Australia: Glenbourne Farm, south of Gracetown, 33.9139°S, 115.01587°E, elevation ~40 m, collected by Julianne M. Waldock and S. Hill on 21 October 2001, dry pitfall traps (deposited in MCZ and WAM; genetic voucher MCZ:IZ:134472). Two male paratypes from Australia: Western Australia: Crowea forest along Crowea Road, 34.5399°S, 116.041°E, elevation ~230 m, collected by Gonzalo Giribet, Stephanie W. Aktipis, and Michele K. Nishiguchi on 10 July 2004 (deposited in MCZ; genetic voucher MCZ: IZ:132893).

Diagnosis

As per genus.

Description

Male holotype (MCZ:IZ:134472_3) (average of all males in parentheses, $n = 4$). Scutum length 1.5 (1.6), width at widest point 1.2 (1.3), width at narrowest point 0.83 (0.85). Integument colour light brown and tan, with patterning of dark brown pigment (Fig. 6*A*, S4*A*). Anterior margin of carapace with a large medial spine directed anteriorly, with four anteriorly directed spines on either side (three large and one small). Pedipalps smooth, except a single small spine-bearing tubercle basally on the ventral surface of the femur, with little or no brown pigmentation (Fig. 6*E*). Coxae IV with a pigmented area dorsally with dorsally directed tubercles (Fig. 6*A*). Genital operculum of males with tubercles at the anterior margin. Legs tuberculate, tan in colour, with brown pigmentation particularly on the femurs. Leg I femur with a series of elongate spine-bearing tubercles on the dorsal and ventral surface (Fig. 6*C*). Leg II length 4.6. Penis: glans without ventral or dorsal plates, with large lateral wing-like lamellae (Fig. 7*A*); each side of the sensillar region with two inferior setae placed ventrolaterally and one superior seta dorsally; with very reduced dorsolateral plates; stylus arising directly from the sensillar region, elongate, cylindrical, and thin.

Female paratype (MCZ:IZ:134472_1). Scute length 1.7, width at widest point 1.45. width at narrowest point 0.95. Only one female is known. Compared to all males it is slightly larger with less pigmentation (Fig. 6*B*, S3*C*). Pigmented scutal tubercles generally more ordered, and typically with more spines on the posterior segments. Pigmented area on coxae IV bearing a more obvious elongate tubercle directed dorsally. Tubercles at anterior margin of genital operculum smaller.

Distribution

Known only from south-western Western Australia.

Comments

Differences can be seen between the males from each locality, suggesting a potential for multiple species, as seen in other short-range endemics in the same region (e.g. Rix *et al*. 2015; Sato *et al*. 2018; Schwentner and Giribet 2018). Given the paucity of samples available we refrain from assessing this. However, we note some obvious morphological differences here: relative to males from Glenbourne Farm locality (MCZ: IZ:134472), males from the Crowea Road locality (MCZ: IZ:132893) are slightly larger, have heavier pigmentation on the body and legs, and have slightly longer legs (Fig. S4*A*, *D*).

Etymology

The specific epithet is a Latin noun used in apposition meaning ‘despoiler’, and as with the genus name, is in reference to the fictional character ‘Abaddon the Despoiler’ from the Warhammer 40,000 science fiction universe.

Family **BUEMARINOIDAE** Karaman, 2019, stat. nov.

ZooBank LSID: urn:lsid:zoobank.org:act:E8FDE896-2475-4CCA-9E24-50BB0F6D05CA

Included genera: *Buemarinoa* Roewer, 1956, *Flavonuncia* Lawrence, 1959, *Fumontana* Shear, 1977, *Turonychus* Derkarabetian, Prieto & Giribet, gen. nov.

Type genus: *Buemarinoa* Roewer, 1956.

Type species: *Buemarinoa patrizii* Roewer, 1956.

Diagnosis

Buemarinoids are diagnosed using male genitalia as for the tribe detailed in Karaman (2019). The penis has a ventral plate modified into two independent articulated and elongated lobes, each bearing two superior and three inferior setae (Fig. 7*B*) (Karaman 2019, fig. 9). As the only member of Triaenonychoidea in the Southern Hemisphere, *Flavonuncia* is easily differentiated from all other triaenonychids in Madagascar by a combination of its small body size, yellow integument colour, an ocularium without a spine, and 3-segmented tarsus on leg I (Lawrence 1959, fig. 3).

Genus ***Buemarinoa*** Roewer, 1956

(Fig. 8)

Type species: *Buemarinoa patrizii* Roewer, 1956

Material Examined

One female (ZUPV·ARACH#5872; used for SEM) from Italy: Sardinia: Urzulei, Su Eni E'istettai, N 40.14685 E 9.47145, 760 m, 7 August 2003, collected by P. Marcia.

Comments

This specimen was collected from a different cave on Sardinia ~18 km south-west of the type locality for *B. patrizii* (Grotta di

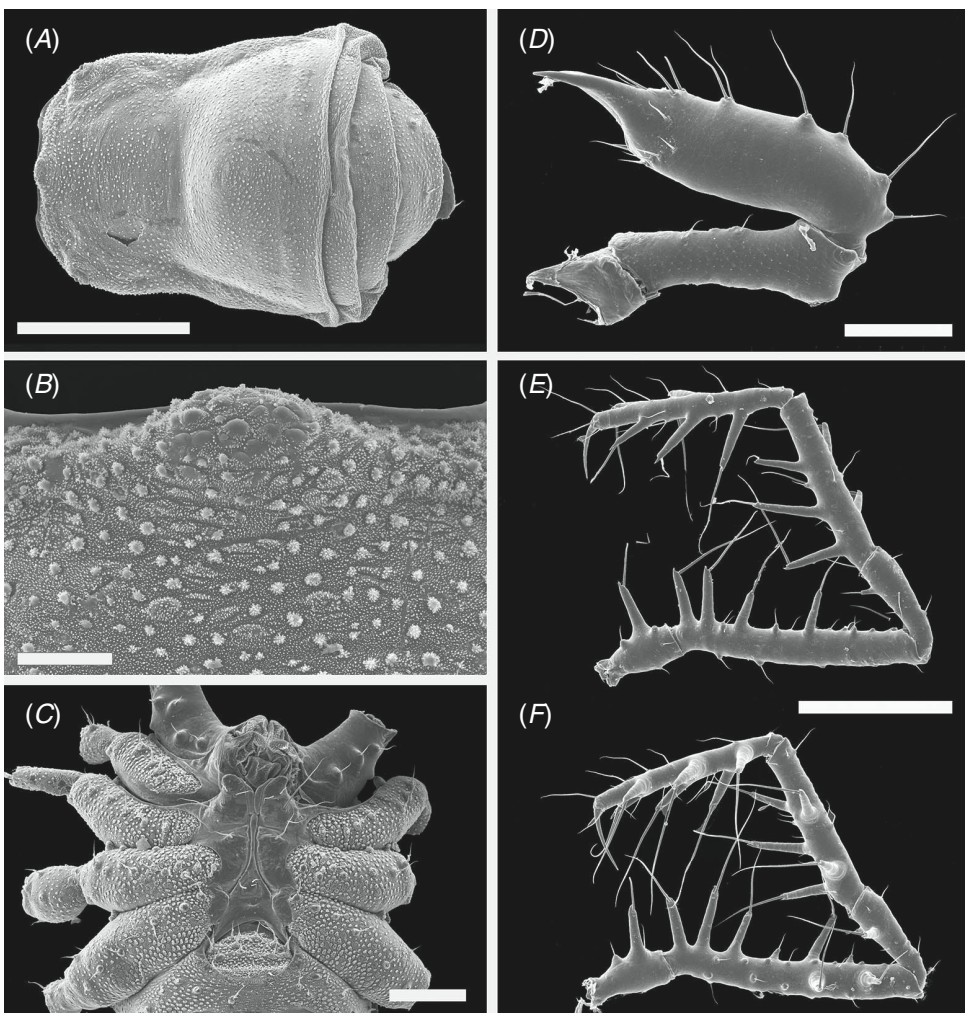

Fig. 8. *Buemarinoa* sp. Scanning electron micrographs of specimen from Su Eni E'istettai: (*A*) dorsum (scale bar: 500 µm); (*B*) detail of prosomal carapace and ocularium (scale bar: 50 µm); (*C*) sternal prosomal region (scale bar: 250 µm); (*D*) left chelicera, retrolateral view (scale bar: 200 µm); (*E*) left palp, retrolateral view (scale bar: 500 µm); (*F*) right palp, prolateral view (scale bar: 500 µm).

Bue Marino). The population clearly belongs to *Buemarinoa* based on the redescription provided by Karaman (2019), and we tentatively consider this specimen to be *B. patrizii*. However, this may potentially be a new species, and certainty either way will require more specimens and detailed analyses. Additionally, there are four other caves in this area from which specimens identified as *B. patrizii* have been recorded (De Waele and Spiga 1995; De Waele *et al*. 2001, 2002), but these have yet to be examined in detail.

Genus ***Turonychus*** Derkarabetian, Prieto and Giribet, gen. nov.

(Fig. 7*B*, 9, 10)

ZooBank LSID: urn:lsid:zoobank.org:act:A8BBEC1D-7252-4F82-ADF9-7A0816D28080

Type species: *Turonychus fadriquei* Derkarabetian, Prieto & Giribet, sp. nov., by monotypy.

Diagnosis

This genus can be distinguished from all other Buemarinoidae species based on the number of tarsal segments of leg I: *Turonychus* has 4+ segments whereas all others have three. Additionally, *Turonychus* can be distinguished from *Buemarinoa* by the number of spines on the retrolateral surface of the pedipalp tibia: *Turonychus* has two spines, whereas *Buemarinoa* has three (Fig. 9*B*). The type locality of *Turonychus* is in the Levantine region of Spain, ~300 km south of the Pyrenees Mountains, a region with a broad distribution of Travunioidea with many local cave-obligate species. *Turonychus* can be diagnosed from Travunioidea based on male genitalia, as noted for the family above (Fig. 7*B*).

Description

Troglomorphic species with unpigmented and uniformly granulated body (Fig. 9*A*). Eye mound highly reduced in size, smooth, rising from the anterior margin of the carapace (Fig. 9*A*, 10*A*, *B*), eyes and retinae completely lacking. Dorsal scutum outline Eta η of Kury and Medrano (2016) (Fig. 9*A*, 10*A*). Sternum thin and elongate (Fig. 10*C*). Genital operculum wide, bearing small tubercles (Fig. 10*C*). Pedipalps thin, elongate, lacking pigment, with elongate spines bearing setae (Fig. 9*B*, 10*E*, *F*). Legs extremely long, thin, lacking pigment. Tarsal formula: 4–5,13–15,4,4. Penis with ventral plate modified into two elongate articulated lobes each of which have two superior and three inferior spines (Fig. 7*B*).

Comments

We describe *Turonychus* as a new genus, as opposed to a second species of *Buemarinoa*, as it differs from the latter in multiple morphological characters noted above. Other differences may become more apparent with additional specimens of *Buemarinoa* (e.g. spine-bearing tubercles at lateral margins of scutal segments). Additionally, the divergence between these two genera is likely ancient, as Sardinia began separating from the mainland (now the north-eastern part of the Iberian Peninsula) beginning ~30 MA (Schettino and Turco 2006).

Etymology

The genus prefix is derived from the demonym for the province of Teruel ('turolense') where the type locality is found, and the suffix is derived from Latin *onyx* and Ancient Greek ὄνυξ (*ónux*) meaning 'claw', a common suffix applied to many travunioid and triaenonychoid genera. The prefix turol- may be more accurate; however we prefer tur- as it is more euphonious.

Turonychus fadriquei Derkarabetian, Prieto and Giribet, sp. nov.

(Fig. 7*B*, 9, 10)

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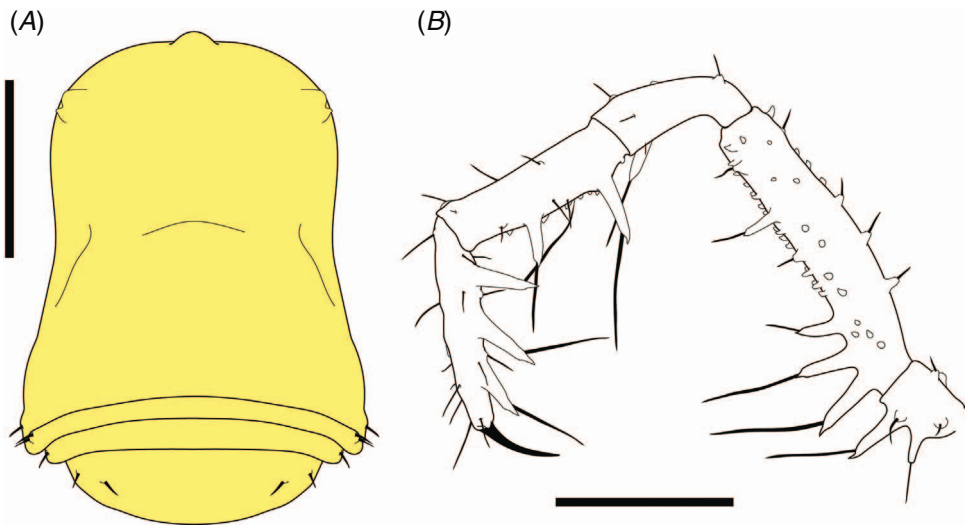

Fig. 9. General morphology of *Turonychus fadriquei*, gen. nov., sp. nov.: (*A*) dorsal habitus of female paratype (UPV/EHU Col. Arachnida #5122); (*B*) retrolateral view of pedipalp of female paratype (UPV/EHU Col. Arachnida #5122). Scale bars: 1 mm; figures at same scale.

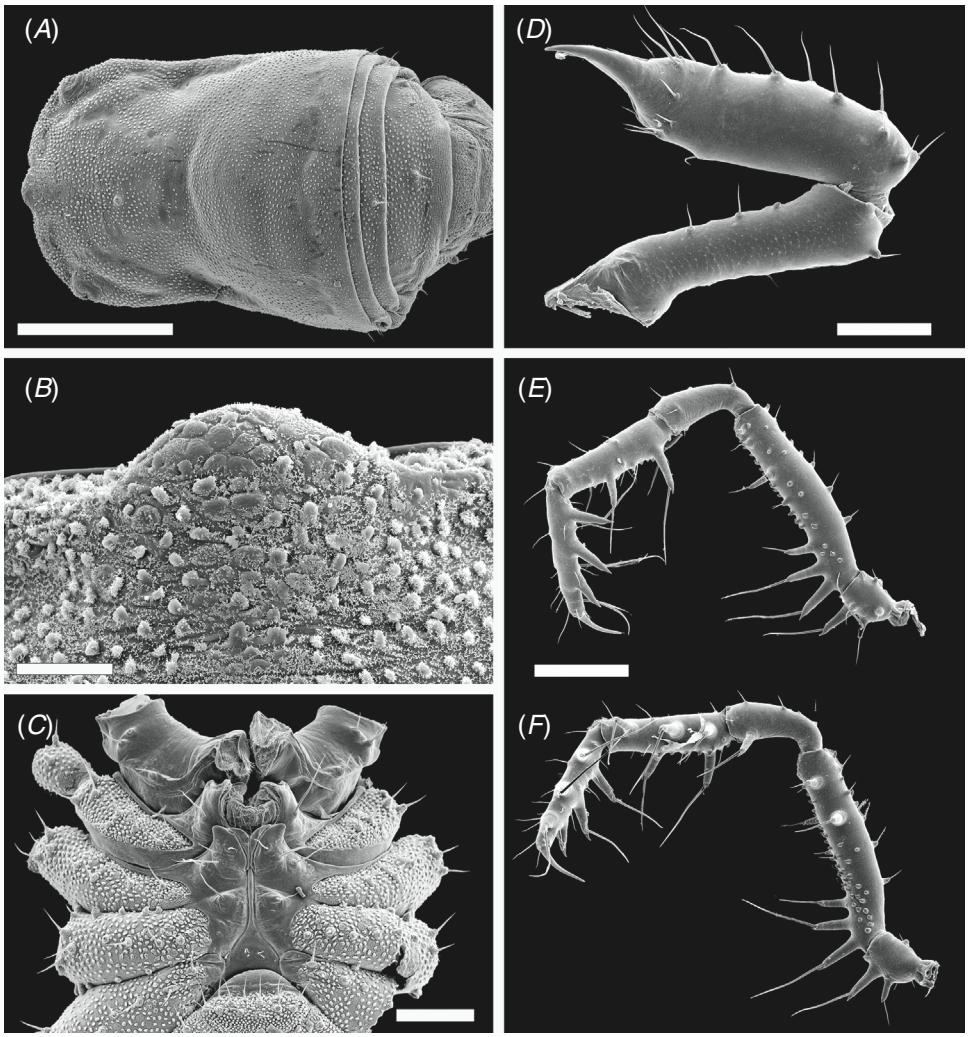

Fig. 10. *Turonychus fadriquei*, gen. nov., sp. nov. Scanning electron micrographs of paratype UPV/EHU Col. Arachnida #5122: (*A*) dorsum (scale bar: 500 µm); (*B*) detail of ocularium (scale bar: 50 µm); (*C*) sternal prosomal region (scale bar: 250 µm); (*D*) left chelicera, retrolateral view (scale bar: 200 µm); (*E*) left palp, retrolateral view (scale bar: 500 µm); (*F*) right palp, prolateral view (scale bar: 500 µm).

Type material

Holotype male (MNCN 20.02/19649, ex-ZUPV·ARACH#5155) from Spain: Aragón, Teruel, Fortanete, La Cija Cave (Sima de La Cija), 40.57933°N, 0.55978°W, elev. 1575 m, collected on 26 July 2014 by F. Fadrique and Carlos Prieto. All paratypes are from the same locality as the holotype. Two female paratypes (MNCN 20.02/19650, ex-ZUPV·ARACH#5156) with same collection information as holotype. Two female paratypes (MCZ:IZ:152706; ex-ZUPV·ARACH#5353) collected on 16 June 2015 by F. Fadrique (genetic voucher). Two female paratypes (ex-ZUPV·ARACH#5122; both used for SEM and optical microscopy) from same locality, collected on 18 April 2014 by F. Fadrique. One female and one juvenile paratype (ZUPV·ARACH#5734) collected on 17 August 2018 by F. Fadrique. Two female paratypes (ZUPV·ARACH#5999) collected on 27 December 2019 by F. Fadrique. One female paratype collected on 9 July 2014 by F. Fadrique (MCZ:IZ:152704, genetic voucher). Three female paratypes collected on 9 July 2014 by F. Fadrique and S. Pastor (deposited in MCZ; MNCN 20.02/19651, MCZ:IZ:152705, genetic voucher).

Diagnosis

As per genus.

Description

Male holotype (n = 1). Scutum length 1.21, width at widest point 1.1, width at narrowest point 0.8. Integument colour yellow, without any black pigmentation (Fig. 9*A*). Integument with microtuberculate-rivulose-microgranulate morphology of Murphree (1988) (Fig. 10*B*). Anterior margin of carapace smooth. Scutal segments 6–8 each with 1–2 small spine-bearing tubercles on the lateral margins (Fig. 9*A*, 10*A*). Pedipalp femur with a series of small spine-bearing

tubercles dorsally, four elongate spines ventrally (three basal, one distal), one elongate spine on the prolateral surface distally; patella with one spine on the prolateral surface distally; tibia with two spines on the retrolateral surface and three spines on the prolateral surface; tarsus with three spines on each side (Fig. 9*B*, 10*E*, *F*). Leg II length 9.25. Tarsal formula 5,15,4,4. Penis with two elongate articulated lobes; deeply bifurcate ventral plate with two superior (dorsal) and three inferior (ventral) spines on each half; stylus expanded apically, forming into two lobes (Fig. 7*B*).

Female. Very similar to male. Tarsal formula 4–5,13–14,4,4.

Distribution

Known only from the type locality.

Comments

The cave is structured in a joint stratification located at an anticline, which results in an almost complete vertical cave with a total depth of 117 m and length of 1343 m (Porcel and Gordillo 1997). It has an average temperature of 8.35°C and a relative humidity of 97.46% (Fadrique, pers. comm.). The biodiversity of this cave (Jordana *et al*. 2012; Ortuño *et al*. 2017; unpubl. data) is composed of oribatid and mesostigmate mites, collembolans including two troglobionts (*Pygmarrhopalites maestrazgoensis* Jordana, Fadrique & Baquero, 2012 and *Oncopodura fadriquei* Jordana & Baquero, 2012), and others such as *Megalothorax minimus* Willem, 1900, *Heteromurus nitidus* (Templeton, 1835), *Schaefferia decemoculata* (Stach, 1939) and *Pseudosinella encrusae* Gisin & da Gama, 1969, and four predators, including the campodeid *Campodea maestrazgoensis* Sendra & Escolà, 2004, the carabid *Paraphaenops fadriquei* Ortuño & Faille, 2017, the linyphid spider *Palliduphantes* sp. (J. Fernández, pers. comm.), in addition to the laniator *Turonychus fadriquei*, gen. et sp. nov. It is likely these predators feed on Diptera of different families (Sciaroidea, Platypezoidea, Lauxaniidae and Phoridae) that have also been recorded.

Etymology

The specific epithet is in honour of Floren Fadrique, who discovered this species and made the specimens available to us.

Discussion

Triaenonychoidea families and (no) subfamilies

Following our analyses, four well supported and deeply divergent families are now included within Triaenonychoidea: Synthetonychiidae, Lomanellidae, Buemarinoidae and Triaenonychidae. The monogeneric Synthetonychiidae (*Synthetonychia* with 14 species) is widespread throughout New Zealand but typically rare to collect and historical specimens are limited (e.g. Giribet *et al*. 2014) but would benefit from a species-level revision. *Synthetonychia* species are morphologically peculiar, made most obvious by their lack of eye mounds and elongate palps. The species of Lomanellidae are restricted to southern Australia and are the sister group to Synthetonychiidae, both of which are relict lineages broadly sympatric with triaenonychids. Lomanellidae and most triaenonychids are usually found in leaf litter or under woody debris and rocks, and *Synthetonychia* species are noted for also being associated with moss and leaf mould (Forster 1954). *Lomanella*, with 19 described species, would benefit from molecular systematic analyses and revisionary work. Eleven of the 19 species are found in Tasmania, with all but one of those being endemic to the state. The species *L. raniceps* is widely distributed across the island and largely sympatric with the other 10 Tasmanian species, which are mostly short-range or single-site endemics. It is likely that more intensive fieldwork in Western Australia may expand the known distribution for both *Lomanella* and *Abaddon*, gen. nov., and multiple species of *Abaddon* are likely.

The family Buemarinoidae is deeply diverged from Triaenonychidae and includes relictual taxa. Although not sequenced for molecular analyses, this clade also includes *Buemarinoa*, based on morphology (Karaman 2019). The European *Buemarinoa* and *Turonychus*, gen. nov. are all blind, highly troglomorphic cave-obligate taxa; *Turonychus* is found at high elevation in eastern Spain, whereas *Buemarinoa* is found only in Sardinia. Both *Fumontana* and *Flavonuncia* are small lightly pigmented surface-dwelling genera found in sympatry with other early-diverging laniatorean taxa: *Fumontana* in the southern Appalachians of North America is sympatric with Cladonychiidae (Travunioidea) and *Flavonuncia* in Madagascar is sympatric with Triaenonychidae (subclade D3). In contrast to previous hypotheses about relationships of *Fumontana* and Buemarinoini to certain triaenonychid taxa (Shear 1977; Karaman 2019), the genera *Monomontia*, *Austromontia*, *Ceratomontia* and *Hendea* were all found within ‘core Triaenonychidae’, and are therefore very distantly related to *Fumontana* and the Buemarinoidae. Our proposal of Buemarinoidae is sensible from a biogeographic perspective as they are largely a northern temperate lineage. This now emphasises that the remaining Triaenonychidae are a true Gondwanan lineage, originating and diversifying in the Southern Hemisphere solely in the landmasses (or portions thereof) most typically associated with temperate Gondwanan taxa. This separation from the Northern Hemisphere clade has been dated to the late Palaeozoic to early Mesozoic, and the initial diversification of the true Triaenonychidae was dated to the Triassic–Jurassic by Baker *et al*. (2020*b*).

The species of Triaenonychidae were historically divided into four subfamilies, mostly diagnosed according to sternum shape (Roewer 1915): Triaenonychinae Sørensen, 1886 having a thin sternum, Triaenobuninae Pocock, 1902 with an extremely wide sternum, and Adaeinae Pocock, 1902 with a pentagonal or subtriangular sternum. The members of Sorensenellinae Forster, 1954 are diagnosed by tarsal claw shape, where the lateral branches are longer than the median prong (almost all other taxa have lateral prongs shorter than the median). Some taxa show a ‘sorensenelline claw’ (e.g. *Tasmanonyx* Hickman, 1958 from Tasmania), but were not included in this subfamily. In our analyses, and those of Baker *et al*. (2020*b*), no subfamily is monophyletic, indicating the homoplastic nature and failure of the characters used to define and diagnose them. Similarly, Derkarabetian *et al*.

(2018) conducted a phylogenomic revision of the Travunioidea, another lineage that historically used subfamily ranks with diagnostic characters largely based on tarsal claw structure. That study, not surprisingly, found that all subfamilies were paraphyletic, and, in their revised classification, did not use or redefine subfamilies, and recommended against their use in Travunioidea in the future. Several early papers discussed the difficulty in morphological classification at a broad taxonomic scale within early-diverging Laniatores (e.g. Forster 1954; Shear 1977; Maury 1988; Hunt and Hickman 1993). These issues led several taxa to be described and assigned to Triaenonychidae, but left unplaced at the subfamily level. For example, Maury (1988) placed *Picunchenops* Maury, 1988 in Triaenonychidae based on genitalia but, given its mix of morphological characters relevant to diagnosing subfamilies at the time, left it unplaced at the subfamily level. The same was done with *Lomanella* by Hunt and Hickman (1993).

Given more detailed morphological examinations across all taxa, diagnostic characters may be identified for major clades A–E (or their subclades). The diversity of Triaenonychidae may necessitate naming groups below the family level, although not necessarily a formal subfamily rank. We do informally name clades within Triaenonychidae for easier discussion, but we refrain from formally creating a new subfamilial classification in this study as it would be difficult to identify diagnostic morphological characteristics for these lineages. Not all taxa have been examined for the most relevant characters. A thorough morphological survey of Triaenonychidae would require a monumental undertaking and is beyond the scope of this paper. It may even be the case, given the incredibly diverse morphology seen within Triaenonychidae, that subfamily ranks defined by exclusive synapomorphic morphological characters may be difficult to find for all lineages. This is largely due to the highly homoplastic nature of somatic morphology, few genitalic characters, and the suspected rapid diversification of this lineage (Baker *et al*. 2020*b*). However, ovipositor morphology has yet to be adequately assessed across Triaenonychoidea and may prove a reliable source in diagnosing natural lineages in Laniatores (Martens 1986; Townsend *et al*. 2015). Similarly, the characters traditionally used to define subfamilies may still be useful in defining lineages, but just at shallower or more regional levels (i.e. within clades defined here). Regardless, our highly supported phylogeny and clade names should provide sufficient context for future work.

Systematics of Triaenonychidae

Here we discuss each of the major lineages within Triaenonychidae, cover relevant taxonomic history and morphological characteristics, provide hypothesised placement of unsampled genera, and highlight potential for future revisionary work. Although there are differences in relationships among major clades across phylogenetic analyses, essentially all major clades and subclades are recovered, with the exception of a few individual taxa showing uncertain placement noted below. We present our discussion based on the IQ-TREE results, noting any uncertainty with the BEAST and SVDQuartets phylogenies in the relevant sections.

Clade A

Clade A is found in eastern Australia and New Zealand. Morphological phylogenetic studies placed *Pyenganella* as sister group to *Lomanella*, sharing several characters including some in the male genitalia (Hunt 1996; Mendes 2009). However, this was a hypothetical placement in Hunt (1996), and not the actual result of analysing his morphological dataset (see his fig. 1 and 2), and was obtained only with particular character weighting schemes in Mendes (2009), who also emphasised caution in this relationship. In the other analyses of Mendes (2009), *Pyenganella* was recovered as an early diverging core triaenonychid. In our analyses, *Pyenganella* is always found as sister group to the New Zealand endemic genera *Hendea* and *Hendeola* Forster, 1954. A potential synapomorphy for these three genera might be found in the male genitalia: on the ventral plate the single superior seta on each lobe is noted to be stronger and stouter than the 2–3 pairs of inferior setae, as noted by Forster (1954) for *Hendea* and *Hendeola*. Hickman (1958) noted that the superior setae of *Pyenganella* are longer than the inferior, but we add that they are also slightly stouter (S. Derkarabetian, pers. obs.)

This clade also includes what we call the '*Equitius* group' from eastern Australia, with a fairly complicated taxonomic history. The genus *Monoxyomma* Pocock, 1903 was a superficial group of taxa united by the number of tarsal segments on leg I. The type species was *M. spinatum* Pocock, 1903, and the genus later included two other species from Queensland, Australia: *M. manicatum* Roewer, 1920 and *M. rotundum* Forster, 1955. In a revision of *Equitius* Simon, 1880, Hunt (1985) synonymised the type species *M. spinatum* with *Equitius* (as *E. spinatus*), but stated that the other two species belong to a 'new genus together with some undescribed species ranging from northern Queensland to southern New South Wales'. It is unclear whether this undescribed genus has a continuous distribution along eastern Australia or a disjunct distribution; Hunt (1985) states that '*Equitius* is *replaced*' (emphasis added) in the north and south by species of this new genus, implying allopatry. Across studies, Hunt refers to multiple undescribed genera: the one mentioned above (discussed in Hunt 1985) and 'new genus C' and 'new genus D in Hunt (1996)'. Both of these new genera were included in the phylogenetic analyses of Hunt (1996) and recovered in a clade with *Equitius*. (Hunt never explicitly mentioned 'new genus A' and 'new genus B' implied by the previous statements.) It is likely that one of the new genera in Hunt (1996) is the undescribed genus mentioned in Hunt (1985), and equally likely that both of these genera are represented as sequenced specimens recovered in Clade A. Our sample of MCZ:IZ:23313 collected from southern Queensland may likely be a northern representative of this undescribed genus, whereas the two we have identified as '*Equitius*' cf. *Monoxyomma* (MCZ:IZ:152643 and NHMUC:Aus10b) may be the southern representatives. In the checklist of

Triaenonychidae, Kury *et al*. (2014) included *M. manicatum* and *M. rotundum* in *Equitius*. Given the comments of Hunt (1985), we consider these *incertae sedis* as the genus level and label them as '*Equitius*'. The '*Equitius* group' including the potential (and yet another) undescribed genus from the Otway Ranges of Victoria (MCZ:IZ:152660 and SDSU_TAC: OP2779) will require more detailed taxonomic attention.

Clade B

Clade B is exclusively found in South Africa, with the exception of *Ceratomontia argentina* from South America (MCZ:IZ152640, discussed below). Species in this clade are typically smaller in size relative to the other South African taxa (Clade D1). Kauri (1961) proposed two main groups, the '*Ceratomontia* group' and the '*Roewerania* group', divided according to the respective presence or absence of a longitudinal band of small granules ventrally on the pedipalp femur. Both groups are paraphyletic in our analyses. Kauri's '*Ceratomontia* group' mostly corresponds to Clade B, except that in our analyses *Paramontia* Lawrence, 1934 and *Planimontia* Kauri, 1961 are included, and *Micromontia* Lawrence, 1939 is excluded. Taxa from Kauri's '*Roewerania* group' are predominantly found in subclades D1 and D2, those subclades containing all the other South African taxa. More recently, Kury (2004) described the genus *Lizamontia* Kury, 2004 for the three South African species that were included in the otherwise entirely Madagascan genus *Acumontia* Loman, 1898, to which they are not closely related. These species were originally included as part of Kauri's '*Roewerania* group', but in our analyses the genus constituted an early-diverging lineage of Clade B, closely related to the '*Ceratomontia* group' taxa, a relationship perhaps reflected in its morphology. As detailed in Kury (2004), compared to the '*Ceratomontia* group' *sensu* Kauri, *Lizamontia* lacks the ventral longitudinal band of small granules, and, unlike most other South African taxa, *Lizamontia* lacks sexual dimorphism in the chelicerae and stout spines on the pedipalp femur. A potential synapomorphy for Clade B, found in the male genitalia, is fused parastyli that wrap around the stylus like a coat (e.g. Kauri 1961; Kury 2004), but all presumptive genera of this clade have not been examined. It is likely that a species-level revision of this lineage will find that some South African genera are paraphyletic; indeed, Baker *et al*. (2020*b*) recovered a polyphyletic *Biacumontia* Lawrence, 1931. Many taxa are differentiated by leg tarsus segmentation, and species assignment and identification can be ambiguous based on available descriptions, the majority of which were done by R.F. Lawrence in the 1930s before the standardised use of genitalic morphology in Opiliones systematics. The unsampled monotypic genus *Lispomontia* Lawrence, 1937 potentially falls in this clade. Lawrence (1937*b*) discusses its resemblance to *Ceratomontia* and *Biacumontia* based on tarsal formula, and its resemblance to '*Cryptobunus*' (now *Amatola* Lawrence, 1931) and *Biacumontia* based on cheliceral morphology.

As currently defined, *Ceratomontia* is one of two transcontinental triaenonychid genera, with four species in South America largely distributed east of the Andes in Argentina, Uruguay, and south-eastern Brazil, and 18 species found in South Africa. Each regional group is represented in our dataset by a single sample and our analyses support paraphyly, a result also found in the morphological analyses of Mendes and Kury (2008). In their study, the South African *Ceratomontia* species were more closely related to the South African genera *Monomontia* and *Austromontia*, having several apomorphic characters not shared with the South American *Ceratomontia*, such as a ventral plate with a narrower base relative to the apex. Our results thus concur with earlier work that *Ceratomontia* is not monophyletic, and therefore is not a trans-Atlantic genus. The South American *Ceratomontia* have a penis with an undivided ventral plate and five setae on each side of the stylus, whereas the South African group has a cleft ventral plate and four setae on each side. The type species of the genus is *C. capensis* Roewer, 1915 from South Africa, necessitating a new genus name for the South American *Ceratomontia* lineage. However, we refrain from doing so until more South American *Ceratomontia* can be included in molecular phylogenetic analyses.

Clade C

Clade C is entirely South American, with the exception of *Hedwiga* Roewer, 1931 from New Zealand. The monotypic *Picunchenops* is a single-site cave-obligate species from Argentina that shows extreme troglomorphy, including complete loss of eyes. When it was described, Maury (1988) placed it into Triaenonychidae based on male genitalia, but could not confidently assign it to any of the triaenonychid subfamilies. Later, Kury (2003) placed *Picunchenops* in the subfamily Triaenonychinae (tribe uncertain). Another lineage within Clade C comprises a set of closely related taxa including *Triaenonyx* Sørensen, 1886, all of which share a fairly similar male genitalic morphology, with an elongate and sometimes uniquely complex stylus (Maury 1987*a*, 1987*b*, 1988; Pérez-González and Werneck 2018) that is hypertrophied in the case of *Araucanobunus* Muñoz Cuevas, 1973 (Hunt and Maury 1993). Described as one of two South American genera in Triaenobuninae, the monotypic *Araucanobunus* was hypothesised to be closely related to *Ankaratrix*, the only Triaenobunine from Madagascar (Muñoz-Cuevas 1973). Although Muñoz-Cuevas (1973) noted many differences between *Araucanobunus* and *Americobunus* Muñoz Cuevas, 1972, comparisons with other South American taxa were lacking, largely because few South American triaenonychids were known at this time. The Triaenonychidae type genus *Triaenonyx* consists of six species, five of which were described before 1916. The inclusion of *Hedwiga* in this clade was unexpected and no morphological similarities are obvious.

Clade D

Subclade D1. This clade is found in South Africa, with the exception of the South American *Nuncia verrucosa* Maury, 1990 (MCZ:IZ:138122). The species *Nuncia verrucosa* is

representative of a lineage with similar somatic morphology that also includes *N. spinulosa* Maury, 1990, and potentially *N. rostrata* Maury, 1990. The type species of *Nuncia* is *N. obesa* (Simon, 1899), found in the diverse New Zealand *Nuncia* E2 subclade. As such, this South American lineage will need a new genus name. We refrain from naming this clade here as not all South American *Nuncia* were sampled, but their position among South African species was also found in the Sanger-based phylogeny of Baker *et al*. (2020*b*). *Speleomontia* Lawrence, 1931 was one of two South African genera included in the subfamily Sorensenellinae, and based on our results are completely unrelated to the Sorensenellinae from New Zealand: *Sorensenella* Pocock, 1902 and *Karamea* Forster, 1954. The South African '*Adaeum* group' includes several genera that share very similar somatic morphology to that of *Adaeum* Karsch, 1880, typically large-bodied with a highly denticulate dorsal scutum, often found dirt-encrusted. Based on this morphology, it is almost certain that the unsampled genera *Cryptadaeum* Lawrence, 1931, *Micradaeum* Lawrence, 1931, *Montadaeum* Lawrence, 1931, *Paradaeum* Lawrence, 1931, and *Heteradaeum* Lawrence, 1963 fall into the '*Adaeum* group' as well (Lawrence 1931, 1963). These taxa are largely differentiated by the structure of the sternum and tarsal claw segmentation. This lineage essentially corresponds to the subfamily Adaeinae as currently defined, excluding *Dingupa* Forster, 1952 from Australia. In the BEAST and SVDQuartets analyses D1 is sister group to Clade E, rendering Clade D paraphyletic. Similarly, both analyses placed *Mensamontia* in Clade C.

Subclade D2. This subclade includes the three South African genera *Roewerania* Lawrence, 1934, *Graemontia* Staręga, 1992, and *Micromontia*. The male genitalia of *Roewerania* and *Graemontia* both show a deeply cleft dorsal plate (Kauri 1961; Kury 2006). This lineage likely includes the unsampled genera *Austronuncia* Lawrence, 1931, the monotypic *Gunvoria* Kauri, 1961, and the monotypic *Yulella* Lawrence, 1939. *Gunvoria* also shows a deeply cleft dorsal plate (Kauri 1961). *Yulella natalensis* (Lawrence, 1937) was originally described as a species of *Roewerania*; Lawrence (1963) noted morphological similarities between *Austronuncia* and *Yulella*, and *A. spinipalpus* Lawrence, 1931 has extremely (and unusually) elongate pedipalps and chelicerae, much like *Roewerania lignicola* Lawrence, 1934 (Lawrence 1931, 1934). Although the BEAST analyses recover a paraphyletic D2 with respect to D3, the unsampled taxa would still be associated with D2 genera in a D2 + D3 clade.

Subclade D3. This clade includes all taxa from Madagascar, excluding *Flavonuncia* and *Ankaratrix*, most of which were described by Lawrence (1959) and have remained largely unstudied since then. Many of these genera show extremely similar somatic morphology (e.g. *Acumontia*): large bodied, most with large dorsal spines on the scutum, an elongate spine on the eye mound, and leg I with 4+ tarsal segments. The only genus not fitting this general pattern is *Hovanuncia* Lawrence, 1959, which lacks spines on the eye mound and scutum and only has three tarsal segments on leg I. In a checklist of Afrotropical Opiliones, Staręga (1992) states a synonymy for *Flavonuncia* and *Hovanuncia*; however, this synonymy only appeared in the abstract and was never followed, not even in the checklist included in the same paper. Obviously, these genera are distinct. The unsampled Madagascan genera *Ivohibea* Lawrence, 1959, *Millomontia* Lawrence, 1959, and *Millotonyx* Lawrence, 1959 will almost certainly fall in this clade: all three genera share the same general body plan as *Acumontia* and similar genitalic morphology. A sequenced specimen which could not be assigned to an existing genus based on morphology (MCZ:IZ:52828) potentially represents a new genus.

Subclade D4. This clade includes *Ankaratrix* from Madagascar as the sister group to three genera that are either endemic to Western Australia (*Breviacantha* Kauri, 1954 and *Dingupa*) or South Australia (*Yatala* Roewer, 1942). Recently, Porto and Pérez-González (2020) explored soil crypsis in *Ankaratrix* while also describing four new species. The unsampled genus *Perthacantha* Roewer, 1931 is also likely included in this clade, as Hunt (1996) stated '*Perthacantha* Roewer 1931 (=*Dingupa* Forster 1952)', though without any explanation or justification. We are keeping these two genera distinct until a more direct comparison can be made. Our examinations of *Dingupa* show that the male genitalia are similar to the drawings for *Breviacantha gisleni* Kauri, 1954 (Kauri 1954). In the SVDQuartets analysis, subclade D4 is not monophyletic with *Ankaratrix* grouped with subclade D2, although with weak support.

Subclade D5. This is a widespread Australian lineage that somewhat corresponds to a group recovered in Hunt's (1996) morphological phylogenetic analyses, though it does not include *Calliuncus* Roewer, 1931. This group had an apomorphy of a penis stylus completely enveloped by plates, a character shared with taxa in Clade E1 (where we find *Calliuncus* instead). The Tasmanian genera *Notonuncia* Hickman, 1958, *Bryonuncia* Hickman, 1958, and *Ankylonuncia* Hickman, 1958 were recovered as a closely related group. As shown in Hunt (1996) *Bryonuncia* and *Ankylonuncia* were not recovered in the above-mentioned group, and hence do not share this apomorphy. However, they were found to be each other's closest relatives united by a penis with a 'mid-dorsal large spiny lobe'. It is possible that re-examination and reinterpretation of genitalia may find that the 'large spiny lobes', which do surround the stylus (e.g. *Ankylonuncia barrowensis* Hickman, 1958), are homologous to the 'plates enveloping the stylus'. The monotypic genus *Tasmanonyx* is unique in this lineage in having hind claws with the lateral branches longer than median prong, a characteristic shared with the non-monophyletic Sorensenellinae. The unsampled genus *Leionuncia* Hickman, 1958 most likely falls in this clade, close to *Notonuncia*, as recovered in Hunt (1996).

The '*Nunciella* group' includes two deeply divergent clades. In our results, the genus *Nunciella* Roewer, 1929 is paraphyletic across three different lineages: (1) a clade including the *Nunciella* samples from Western Australia (MCZ:IZ:35908 and MCZ:IZ:132908) and *N. cheliplus* Roewer 1931 from Victoria; (2) *N. kangarooensis* Hunt, 1971, a species endemic to Kangaroo Island, South

Australia; and (3) *N. tasmaniensis* Hickman, 1958 from Tasmania. This non-monophyly is not surprising given the fact this genus is diagnosed by the number of tarsal segments of the first leg and Hunt's (1985) statement that *Nunciella* contains 'a miscellany of species of doubtful affinity'. The type species of *Nunciella* is *N. aspera* (Pocock, 1902), a species known from Western Australia, although Pocock's original description states the location for this species (then called *Triaenonyx aspera*) as just 'Australia'. Two new genus names will be needed for '*Nunciella*'. However, we do not name new genera here as detailed analyses of *Nunciella* are required. In this group, we also identify a new genus, called 'new genus B Australia NHMUC:Aus025b' (Fig. 1*J*), which differs from related taxa in both somatic and male genitalic morphology. The two specimens sequenced are both from the Otway Ranges, Victoria, but we refrain from describing this genus here until more specimens can be obtained for detailed anatomical study.

A species currently known as *Nuncia unifalculata* is recorded from the extremely isolated Crozet Islands, which have never had a continental connection. This species was first described as *Promecostethus unifalculatus* by Enderlein (1909) based on four specimens, three immatures and one adult. However, upon examination, Roewer (1923) concluded that all specimens were immature, and postulated that it may belong to the transcontinental genus *Nuncia*. Later, Hickman (1939) redescribed this species based on a large set of adult specimens and formally transferred it to *Nuncia*. Forster (1954), when describing the New Zealand *Nuncia* (i.e. true *Nuncia*) and considering Hickman's description, concluded that *N. unifalculata* does not belong in *Nuncia* and 'should in fact be placed in either *Nunciella* or *Neonuncia*'. The catalogue of Kury *et al*. (2014) lists this species as *Promecostethus unifalculatus*. We agree with Forster (1954): *N. unifalculata* does not belong to any lineage of *Nuncia*, and based on the description it is most similar to *Nunciella* and would therefore fall here in subclade D5. We further hypothesise, based on pedipalp spination, that this species is derived from the Western Australian *Nunciella*, related to *N. aspera*. This species must represent a long-distance dispersal event, but whether it differs at the genus level from *Nunciella* (or another potential source) is uncertain as no genitalia were ever drawn and specimens could not be obtained for this study. Despite previous synonymy, we follow Kury *et al*. (2014) and use the name *Promecostethus unifalculatus* for this species to signify its distinctiveness from *Nuncia*, while not adding a new name to potential future synonymy. Examination of genitalia and inclusion in a molecular phylogeny is needed to confirm its genus-level placement.

Clade E

Subclade E1. This subclade includes taxa from South America and Australia. The relationship among these taxa is not surprising as male genitalic morphology is very similar (Muñoz Cuevas 1971*a*, 1971*b*; Hunt 1972), with the stylus enclosed in a cup-like structure, a character shared with subclade D5. Although genitalia for *Callihamus* Roewer, 1931 and *Callihamina* Roewer, 1942 were not examined in initial descriptions, the sample of *Callihamina* included in our study (NHMUC:18A) is a male and our examination of the genitalia confirms this character. The Australian genera *Calliuncus*, *Callihamus* and *Callihamina* are all very similar morphologically and diagnosed solely based on the number of tarsal segments of leg II. *Calliuncus* is a widespread genus found in Western Australia, Victoria and Tasmania, and appears paraphyletic with respect to the other two genera. *Callihamus badius* Roewer, 1931 is known only from near Melbourne, Victoria, and *Callihamina adelaidia* Roewer, 1942 is known only from near Adelaide, South Australia (Roewer 1931, 1942). Whereas our sample of *Callihamus* (MCZ:IZ:152666) is from the Otway Ranges, fairly close to the type region of Melbourne, our sample of *Callihamina* (NHMUC:18A) is from New South Wales, extremely distant from the type locality of Adelaide. Despite this distance, the specimen keys to *Callihamina*, again distinguished from the other genera solely based on the number of tarsal segments. Given sampling of all *Calliuncus* species, synonymy of these three genera might be warranted. The unsampled genus *Parattahia* Roewer, 1915, only including *P. u-signatum* Roewer, 1915 from Tasmania most likely falls in this clade. *Parattahia* is generally similar in somatic morphology, possessing a characteristic hook on the eye mound like the other taxa. *Nuncia chilensis* was initially described as *Parattahia chilensis* by Soares (1968), placing it in this genus because of its similarity to *P. u-signatum*. Hunt (1996) noted that *Calliuncus* is actually a junior synonym of *Parattahia*, but formal changes should not be made until *P. u-signatum* can be included in analyses.

Subclade E2. This subclade represents the 'true *Nuncia*' from New Zealand, a large diversification with 58 named taxa (34 species with 34 subspecies), divided into three subgenera (*Nuncia*, *Corinuncia*, *Micronuncia*). Based on results from Baker *et al*. (2020*b*), who included 62 New Zealand *Nuncia* specimens covering much of the specific diversity of the genus, monophyly of these subgenera seems unlikely, and some species with multiple subspecies may be paraphyletic. This genus would greatly benefit from a taxonomic revision, and initial steps have been taken with the recent redescription of the type (sub)species *Nuncia obesa obesa* (Simon, 1889) (Porto and Pérez-González 2019) and the molecular work of Baker *et al*. (2020*b*). The unsampled genera *Neonuncia* Roewer, 1915 and *Psalenoba* Roewer, 1931 most likely fall into this lineage. *Neonuncia* was differentiated from *Nuncia* based only on tarsal segment count of leg I (Roewer 1914), but Forster (1954) found additional characters separating the two genera. *Neonuncia* are found either in mainland New Zealand or across multiple islands surrounding New Zealand. *Psalenoba* is a monotypic New Zealand endemic. Forster (1954) states that examination of this species will show it is placed within *Nuncia*, perhaps identical to a species described in his work, but the original description and figures are insufficient and the types were unavailable to him. The checklist of Kury *et al*. (2014) includes the genus *Metanuncia* Roewer, 1915 with two species, but both species were synonymised into *Nuncia* by Forster (1954).

Subclade E3. This lineage includes only a single species, *Americobunus ringueleti* Muñoz Cuevas, 1972. The

monotypic *Americobunus* is one of two triaenobunines from South America, the other being the distantly related *Araucanobunus*. Muñoz Cuevas (1972) stated that *Americobunus* shows similarities to the New Zealand genus *Pristobunus* Roewer, 1931 largely in somatic morphology (the armature of the body and legs, and tarsal segment count), but also in male genitalic morphology. In a broad sense, this hypothesis is correct as *Americobunus* is more closely related to *Pristobunus* (a member of subclade E5) than it is to any other South American taxa.

Subclade E4. This subclade includes a group of taxa from eastern Australia, ranging from Tasmania north to Queensland. The Australian genus *Triaenobunus* Sørensen, 1886 is paraphyletic. This genus is largely diagnosed by the structure of the eye mound, which is elongate and anteriorly directed with lateral spines. There is uncertainty in the placement of cf. *Triaenobunus* NHMUC:21B: in the IQ-TREE analysis it is recovered as sister group to subclade E5 with low support, the BEAST analyses placed it with *T. armstrongi* and *Heteronuncia*, and the SVDQuartets places it as sister group to *T. armstrongi* whereas *Heteronuncia* is placed as sister group to E3 + E4 + E5. The uncertainty with cf. *Triaenobunus* and *Heteronuncia* is likely because they are historical museum specimens with the associated DNA degradation (Derkarabetian *et al*. 2019). Our preferred hypothesis consists of two lineages (as reflected in the BEAST analysis). The first lineage includes *T. armstrongi* Forster, 1955 from New South Wales, cf. *Triaenobunus* from Victoria, and *Heteronuncia robusta* Roewer, 1920, a large species from northern Queensland. The second lineage corresponds to *T. asper* Hickman, 1958 and *T. pectinatus* Pocock, 1902, both of which are from Tasmania. *Triaenobunus* was also found to be non-monophyletic in Baker *et al*. (2020*b*), although nodal support for relevant nodes was low. It is possible that the samples we sequenced are representative of two groups of *Triaenobunus*: the lineage including *T. armstrongi* may represent a mainland Australian group of taxa largely described by Forster (1955) distributed from Victoria to Queensland, whereas *T. asper* and *T. pectinatus* represent the eight species from Tasmania. The unsampled genus *Dipristes* Roewer, 1931 with one species, *D. serripus* Roewer, 1931, is certainly related to *Triaenobunus*, and was originally separated based on the number of lateral spines on the eye mound and tarsal segment count. When originally described, these diagnostic characters were distinct between *Dipristes* and the *Triaenobunus* species known at the time. However, since the description of additional *Triaenobunus*, the diagnostic characters of *Dipristes* now fall within the variation seen in *Triaenobunus*, probably necessitating synonymy. We save formal synonymy until a more detailed analysis of *Triaenobunus* can be undertaken, but we hypothesise that it will be closely related to the mainland Australia clade. The type species of *T. bicarinatus* Sørensen, 1886 is likely associated with the mainland Australian group as well. Clearly, *Triaenobunus* needs revision.

This subclade also includes the Tasmanian genus *Nucina* Hickman, 1958, the genus *Cluniella* Forster, 1955, which has an extremely restricted distribution in southern Queensland, and the more widespread '*Hickmanoxyomma* complex'. The three species of *Cluniella*, each with very restricted but overlapping distributions, are particularly interesting because of their extreme hypertrophy of male genitalia (Hunt and Maury 1993). The '*Hickmanoxyomma* complex' is a group of closely related and rapidly diverged genera largely found in Tasmania and south-eastern mainland Australia, including the genera: *Hickmanoxyomma* Hunt, 1990, *Paranuncia* Roewer, 1915, *Odontonuncia* Hickman, 1958, *Holonuncia* Forster, 1955, and an indeterminate sample from the Otway Ranges in Victoria (cf. *Paranuncia* NHMUC:Aus025b). Hunt (1990) stated that *Hickmanoxyomma* is very similar to both *Odontonuncia* and an undescribed genus from Victoria (which may correspond to our 'cf. *Paranuncia* NHMUC:Aus025b'), and that these share similar genitalic morphology with *Paranuncia*, *Holonuncia* and *Equitius*. With the exception of *Equitius* (Clade A), our phylogeny agrees with Hunt's hypotheses. Notably, the genus *Hickmanoxyomma* is diphyletic. This genus is restricted to Tasmania and includes seven species, six of which are cave-obligate (Hunt 1990). Hunt (1990) split this genus into two species groups: the *cavaticum* and *tasmanicum* species groups. We recover *H. tasmanicum* (Roewer, 1915), the only surface species, as sister group to the two species of *Paranuncia* (Tasmania and Victoria), whereas *H. cavaticum* (Hickman, 1958) is sister species to the monotypic *Odontonuncia* (Tasmania). Complete species-level sampling will be needed to determine whether the species groups of Hunt (1990) are reciprocally monophyletic, or if the division corresponds to habitat (cave versus surface). The unsampled monotypic *Stylonuncia* Hickman, 1958 most likely falls within this lineage. *Stylonuncia spinosa* Hickman, 1958 was considered to be closely related to *Nucina* by Hickman (1958), differing in the eye mound and scutal spines. Hunt (1996) recovered *Stylonuncia* in a group with *Nucina* and the '*Hickmanoxyomma* complex' genera.

Subclade E5. This clade is found in Tasmania, New Zealand, and New Caledonia. Based on scutal patterns and genitalia, Forster (1954) stated that the New Zealand genus *Cenefia* Roewer, 1931 is related to *Pristobunus*, also from New Zealand, and *Triaenobunus* from Australia. Likewise, Forster (1954) compared *Pristobunus* to *Triaenobunus* and the unsampled genus *Dipristes*, largely because of similar eye mound structure. Given this, it is not surprising that *Cenefia* and *Pristobunus* are sister taxa, and they are early diverging in E5, as that eye mound may be plesiomorphic for clades E4 and E5. The unsampled monotypic *Muscicola* Forster, 1954, a green-pigmented arboreal species known only from Fiordland, New Zealand, was considered to be related to *Pristobunus* by Forster (1954) because it shares similar somatic and genitalic morphology. As such, it is likely related to *Pristobunus*. In the BEAST analysis the *Cenefia* + *Pristobunus* clade is sister group to E4, whereas the SVDQuartets analysis placed it within a Tasmanian group in subclade E5, although with very weak support. Ultimately, this has little effect on our discussion, including the plesiomorphic nature of the eye mound.

Clade E5 includes most of the endemic genus-level diversity of Tasmania, which constitute a well-supported subclade. This clade was largely recovered in the

morphological phylogenetic analyses of Hunt (1996), except that he included *Triaenobunus*, and was supported by two synapomorphies: sternum shape (essentially the Triaenobuninae type) and the ventral plate of the penis each with 2–3 superior setae. Similarly, internal relationships of this group largely agree with Hunt (1996) based on morphology. The group that includes *Mestonia* Hickman, 1958, *Allobunus* Hickman, 1958, *Chrestobunus* Roewer, 1915, and *Thelbunus* Hickman, 1958 shares a synapomorphy of three superior setae on each ventral plate. *Phoxobunus* Hickman, 1958 is recovered as sister group to a clade containing *Phanerobunus* Roewer, 1915, *Glyptobunus* Roewer, 1915, *Tasmanobunus* Hickman, 1958, *Miobunus* Roewer, 1915, and *Rhynchobunus* Hickman, 1958. This latter group has a synapomorphy of the penis stylus subdistally with a mediodistal spine. Several unsampled Tasmanian genera likely fall into this group. As recovered in Hunt (1996), the monotypic *Chilobunus* Hickman, 1958 is likely in the clade near *Mestonia* and *Thelbunus*, and the monotypic *Eubunus* Hickman, 1958 is likely in the clade with *Phanerobunus* and *Glyptobunus*. *Tasmanobunus* as a genus was synonymised with *Miobunus*, including the type species, *T. constans* Hickman, 1958, synonymised with the type species of *Miobunus*, *M. thoracicus* Roewer, 1915 by Hunt (1995). This synonymy is reflected in the catalogue of Kury *et al*. (2014). However, Hunt (1995) notes that *Tasmanobunus parvus* Hickman, 1958 'does not belong in *Miobunus*', and in our analyses it is not sister to *Miobunus thoracicus*. In the same study, Hunt also notes that *Miobunus levis* Hickman, 1958, unsampled in our study, does not belong in *Miobunus*. In our checklist we consider these *incertae sedis* and label them as '*Miobunus*' *parvus* and '*M*.' *levis* until more detailed work can be completed including all relevant taxa. Regardless of name, both species fall within this group, most likely allied with *Tasmanobunus*, *Miobunus* and *Rhynchobunus*. The unsampled genus *Tasmanonuncia* Hickman, 1958 is likely in the group with *Rhynchobunus* and *Tasmanobunus*; it was recovered as sister group to *Rhynchobunus* in Hunt (1996) and the genitalia drawn in Hunt and Maury (1993) is similar to those of *Tasmanobunus* (see Hickman 1958).

Finally, E5 includes a third subclade consisting of generally large-bodied taxa characterised by tuberculate or heavily spined bodies from New Zealand and New Caledonia. *Sorensenella* and *Karamea*, two taxa included in the subfamily Sorensenellinae, share very similar genitalia (Forster 1954), and have been treated in detail, including UCE work, elsewhere (Baker 2020). The unsampled monotypic genus *Prasmiola* Forster, 1954 is likely the sister group to *Prasma* Roewer, 1931, considered closely related by Forster (1954) but differing in tarsal segment counts. *Triregia* Forster, 1948, only recorded from the North Island of New Zealand, was found as the sister group to the New Caledonian genera *Diaenobunus* Roewer, 1915 and *Triconobunus* Roewer, 1915. These genera are very similar morphologically, being densely covered in spines, with the New Caledonian taxa differentiated only by the number of spines on the eye mound (Roewer 1914, 1915). More thorough sampling of *Triregia* may show this genus to be paraphyletic with respect to the New Caledonian genera and that the New Caledonian genera may in fact constitute two independent colonisations of the island, as suggested, albeit with low support, in Baker *et al*. (2020*b*), perhaps necessitating synonymy of some of these genera.

Taxa of uncertain affinity

Two unsampled genera cannot be placed with certainty. First, *Brasiloctis* Mello-Leitão, 1938 with a single species, *B. bucki* Mello-Leitão, 1938, is known from a single site in south-east Brazil. Based on the original description and the single drawing provided, this species has a *Triaenobunus*-like appearance, covered in spines with a forward-projecting eye mound with lateral spines. As such, it could be closely related to the South American *Americobunus* (subclade E3), another spiny–tuberculate-bodied species with forward-projecting eye-mound, which is the sister group to clade E4 + E5, where *Triaenobunus* is early diverging in E4. Conversely, based on biogeography, all South American taxa (except the cave-obligate *Picunchenops*) found east of the Andes (i.e. *Ceratomontia*) fall within Clade B.

Second, the monotypic genus *Lawrencella* Strand, 1932, which is the second of two Sorenesenellinae in South Africa (with *Speleomontia*), is also difficult to place. Lawrence (1931) states that *Lawrencella inermis* (Lawrence, 1931), then described as *Roeweria inermis*, resembles *Mensamontia* in tarsal segment count. Based on these similarities, and the results of the IQ-TREE analyses, we would hypothesise that *Lawrencella* is included in the *Speleomontia* + *Mensamontia* lineage (subclade D1), the three of which are restricted to the Western Cape Province of South Africa. However, the BEAST and SVDQuartets analyses do not recover *Speleomontia* + *Mensamontia*, instead placing *Mensamontia* in Clade C. As such, the placement of *Lawrencella*, and *Mensamontia*, remains uncertain.

Phylogenomic context for future work and concluding remarks

The context provided by our phylogenomic analyses offers great opportunity for future work from both an evolutionary and a systematics perspective. The family Triaenonychidae, as redefined here, constitutes an excellent system for integrative and comparative evolutionary studies. The family is now restricted to the terranes of former Gondwana, specifically circumscribed to the temperate zone, whereas the Northern Hemisphere species previously in Triaenonychidae now constitute a separate family. Triaenonychoidea is therefore divided into four families, three of which are exclusive to the Southern Hemisphere (Synthetonychiidae, Triaenonychidae and Lomanellidae, fam. nov.) and one including members in both hemispheres, Buemarinoidae, stat. nov. This framework will provide stability and a meaningful classification to a clade that diverged around the transition from the Palaeozoic to the Mesozoic (Baker *et al*. 2020*b*), long before most other Opiliones families were established. A study exploring the biogeographic history of Triaenonychidae using this dataset is currently underway.

Here we mention some morphological and behavioural patterns in the hopes it spurs future research in this group.

The variation in morphology across Triaenonychidae is most obvious (Fig. 1). Scutal ornamentation is particularly interesting, as some taxa are relatively smooth-bodied, whereas others can be covered in tubercles and spines, and sometimes are found dirt-encrusted like *Ankaratrix* from Madagascar (Porto and Pérez-González 2020), the '*Adaeum* group' of South Africa, and some *Triaenobunus*. The tuberculate–spiny body is a repeated pattern across essentially all continents and major clades. Some taxa are particularly appealing morphologically, like *Algidia viridata* Forster, 1954 and *Muscicola picta* Forster, 1954, both of which are associated with moss microhabitats and are pigmented green. Male dimorphism is well documented in the New Zealand taxa (Forster 1954), but also occurs in many other triaenonychid lineages, yet virtually no work has been done to further investigate behavioural and taxonomic implications. In describing the South African triaenonychids, Lawrence noted stridulatory organs on many taxa (e.g. Lawrence 1937*a*): an elongate row of tiny parallel ridges on the inner surface of the second cheliceral segments, found in both sexes. A phylogenetic pattern is unclear as several South African taxa with stridulatory organs were unsampled here – compared to all other regions, South Africa had the relatively smallest sampling effort in this study. Further exploration of these organs in Clade B and across Triaenonychidae may be worthwhile.

Several independent lineages of Triaenonychidae show varying levels of hypertrophy of the male genitalia: *Araucanobunus* (Clade C), multiple Tasmanian genera in Clade E5, and *Cluniella* (clade E4) where hypertrophy is most extreme (Hunt and Maury 1993). This hypertrophy may be associated with changes in the female ovipositor, like elongation of the vagina with spermathecae placed much more basally (Hunt and Maury 1993). These convergent changes in reproductive morphology across lineages would lead to interesting integrative and comparative studies exploring the process and possible explanations for this convergence. From a behavioural perspective, male egg guarding has been reported for the sister genera *Sorensenella* and *Karamea* (Machado 2007). Perhaps this behaviour is more widespread across Triaenonychidae, but behavioural and observational data are lacking.

Our well supported phylogeny can serve as the backbone for future revisionary work, making it easier to focus on smaller but well delimited clades. More focused molecular systematic work has begun on many lineages within Triaenonychidae (Baker 2020), and in some cases even basic taxonomic work has been needed to confirm identities of type specimens (Porto and Pérez-González 2019). The New Zealand taxa are currently undergoing more focused taxonomic revisions by several authors of this paper (e.g. Baker 2020). The South American taxa are becoming increasingly well studied including assessments of genital functional morphology (Pérez-González and Werneck 2018). The new genus from Chile (MCZ:IZ:138057) is currently being described and taxonomic revisions have begun for many other South American taxa as well (Pérez-González, pers. comm.). Lineages most in need of genus-level revisions largely include Australian taxa, specifically the '*Equitius* group' (Clade A), '*Hickmanoxyomma* group' (subclade E4), and '*Nunciella* group' (subclade D5) each of which include taxa representing new genera or lineages needing new generic names. Pending more detailed studies, several already described lineages will need new generic assignments because of non-monophyly, such as South American *Nuncia*, South American *Ceratomontia*, Tasmanian *Triaenobunus*, and two lineages of *Nunciella*. Efforts should also focus on including genera that were unsampled for this study (see Table S2), most of which are monotypic and morphologically similar to sampled taxa, allowing our hypothesised placements. These monotypic genera are typical of genus-level oversplitting by early taxonomists who relied on highly variable characters as diagnostic (i.e. the 'Roewerian system'), a problem plaguing many Opiliones groups. The South African taxa had the lowest proportional representation in our dataset with only 17 of 27 described genera sampled, and this should be a focus of future work.

There is extremely high potential for species discovery across all lineages and geographic areas, and descriptions of new species continue (Porto and Pérez-González 2020). The majority of species as currently defined can be considered short-range endemics (Harvey 2002). The biological and ecological characteristics of triaenonychoids (low dispersal and high microhabitat specificity) make it highly likely that species inhabit very small distributions, and there are many regions with suitable habitat that have yet to be explored for Opiliones. For example, the isolated mountains of south-western Victoria: recent fieldwork produced multiple species across three or four genera from these mountains, where, to our knowledge, no Trianeonychoidea had been reported previously. The fauna of Australia is in most need of revision, including more intense sampling. Initial work has begun with recent fieldwork and our description of *Abaddon*, gen. nov. endemic to Western Australia. Throughout the course of this work, one thing became increasingly clear: there is still an incredible amount of biodiversity left to describe in the large superfamily Triaenonychoidea.

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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