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Diversity and distribution of the New Zealand endemic mite harvestman genus *Aoraki* (Arachnida, Opiliones, Cyphophthalmi, Pettalidae), with the description of two new species

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ABSTRACT

New Zealand is home to 30 recognised endemic mite harvestman species and subspecies, 26 of which were described by Ray Forster in 1948 and 1952. These species comprise three genera: *Rakaia* Hirst, 1926, *Neopurcellia* Forster, 1948, and *Aoraki* Boyer & Giribet, 2007. Here, we focus on the diversity and distribution of *Aoraki*: we describe *A. grandis* Boyer, Tuffield & Dohr, sp. nov. and *A. meridialis* Boyer, Hahn & Ward, sp. nov. and we synonymise *A. granulosa* (Forster, 1952) with *A. tumidata* (Forster, 1948), bringing the total of named species and subspecies to twelve, and extending the southern range of the genus by over 100 km. Our phylogenetic analysis revealed three major lineages within the genus characterised by differing levels of granulation of the male fourth tarsus. We report striking variation in the range size and level of genetic structuring present within currently recognised species and subspecies of *Aoraki*, and propose future studies to address evolutionary, biogeographic and taxonomic questions in the group.
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Keywords: Arachnida, biogeography, Cyphophthalmi, endemism, New Zealand, Opiliones, systematics, taxonomy.

Introduction

Cyphophthalmi, also known as mite harvestmen, are tiny, slow-moving arachnids found in leaf litter and caves throughout temperate and tropical zones, and are known for poor dispersal abilities and small species ranges (Giribet and Sharma 2015). The cyphophthalmid family Pettalidae exhibits a classic Gondwanan distribution, with representatives in Chile, South Africa, Madagascar, Sri Lanka, Australia and New Zealand; a recent study based on transcriptomic data has demonstrated decisively that this distribution reflects a history of ancient vicariance rather than dispersal (Baker *et al.* 2020). Pettalids have also been the subject of historical biogeographic research at finer spatial scales, including studies that have described patterns of phylogenetic and phylogeographic structure within the three genera endemic to New Zealand: *Rakaia* Hirst, 1926, *Neopurcellia* Forster, 1948 and *Aoraki* Boyer & Giribet, 2007 (Boyer *et al.* 2007; Boyer and Giribet 2007, 2009; Fernández and Giribet 2014; Tardelli Canedo *et al.* 2021).

Hirst (1926) published the first description of a pettalid from New Zealand in 1926: *Rakaia antipodiana* Hirst, 1926, of which the type locality is in the South Island at Rakaia Gorge. Seemingly unaware of Hirst's (1926) work, Phillipps and Grimmett (1932) described *Purcellia dorothea* Phillipps & Grimmett, 1932 from Wellington and Rotorua in the North Island and the species was eventually transferred to *Rakaia* (Forster, 1948). Roewer added *Rakaia collaris* Roewer, 1942, based on a single female specimen from Akaroa, on Banks Peninsula. Subsequently, the prolific arachnologist Ray Forster described 26 species and subspecies in the genera *Rakaia* Hirst, 1926 and *Neopurcellia* Forster, 1948 (Forster 1948, 1952). Over half a century later, Boyer and Giribet (2007) undertook a phylogenetic analysis of the family Pettalidae based on DNA sequences from

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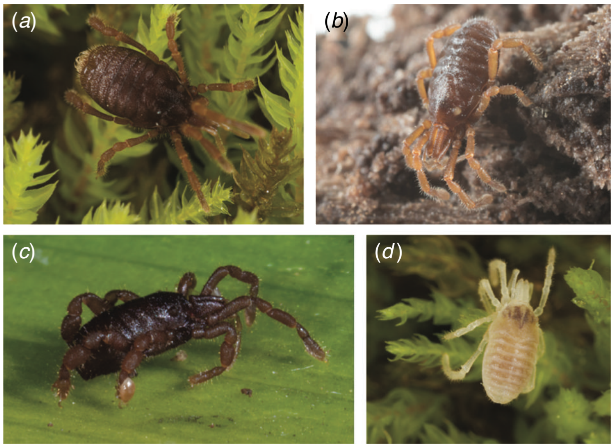

Fig. 1. Live habitus of *Aoraki*. Photographs (*a*, *b*) and (*d*) by Gonzalo Giribet; (*c*) by Caitlin Baker. (*a*) *A. longitarsa* male, MCZ IZ-29554. (*b*) *A. denticulata major* female, MCZ IZ-152035. (*c*) *A. tumidata* male, bearing a mite on leg III, MCZ-IZ152232. (*d*) *A. longitarsa* juvenile MCZ IZ-29554.

five loci. They erected the genus *Aoraki* (Fig. 1) to accommodate a group of species initially described in Forster's (1948, 1952) works as *Rakaia* but that was demonstrated to constitute a monophyletic lineage not closely related to the remaining members of that genus. The name *Aoraki* refers to the mountain, Aoraki (also known as Mount Cook), that marks the southern limit of the geographic range of the genus (type locality of *A. longitarsa* (Forster, 1952) in Fig. 2). The majority of Forster's subspecies were recently elevated to species status by Giribet (2021), resulting in a current total of eleven recognised species and subspecies of *Aoraki*.

Most species of Cyphophthalmi are morphologically distinct from one another but highly morphologically conserved across populations and these typically have very small ranges, not exceeding 50 km in any direction (e.g. Boyer *et al.* 2015; Jay *et al.* 2016). However, New Zealand is home to taxa that challenge this paradigm. *Neopurcellia salmoni* Forster, 1948 that occurs in the South Island west of the Southern Alps throughout a 400-km transect, was recently demonstrated to constitute a monophyletic group that includes some well supported deep genetic divergences but no diagnostic morphological characters corresponding to phylogeographic lineages (Tardelli Canedo *et al.* 2021). Two studies have addressed the problematic taxon *Aoraki denticulata denticulata* (Forster, 1948) that occurs throughout the northern third of the South Island (Boyer *et al.* 2007; Fernández and Giribet 2014) (Fig. 2). In both cases, researchers found high genetic divergences within and among populations of *A. denticulata denticulata*, probable paraphyly of *A. denticulata* with respect to *A. longitarsa* and probable paraphyly of *A. denticulata denticulata* with respect to *A. denticulata major*. Finally, *Aoraki granulosa* (Forster, 1952) has a widespread distribution across the North Island; in the original description, Forster (1952) identified the type locality as Te Kauwhata and also reported this from Ohingaiti and Vinegar Hill, over 300 km to the south.

While multiple studies of the New Zealand cyphophthalmid fauna have focused on biogeography and relationships among genera, there has been little taxonomic revision at the species level. In this study, we describe two new species of *Aoraki* and synonymise one of Forster's (1952) species, based on examination of morphology and analysis of mitochondrial DNA sequence data. We provide commentary on some of the unusual aspects of the diversity and distribution of this genus and the potential of this system to illuminate historical biogeographic processes in New Zealand.

Methods

Specimen collection

New specimens were collected on the South Island of New Zealand in January 2019 by leaf-litter sifting *in situ* and sorting by hand. Specimens were preserved in 95% ethanol immediately after collection. Locality data were recorded by GPS. We borrowed additional specimens, requested locality records, or both from the Museum of Comparative Zoology (MCZ), the Field Museum of Natural History (FMHD), the American Museum of Natural History (AMNH), the Otago Museum (OM), the New Zealand Arthropod Collection (NZAC), the Museum of New Zealand Te Papa Tongarewa (MONZ), the Auckland War Memorial Museum (AMNZ), the Natural History Museum of Denmark (ZMUC) and the Canterbury Museum (CMNZ); institutional acronyms will appear as such throughout the remainder of this manuscript. Locality and species information for 190 collections was used to map the distribution of *Aoraki*. For 19 collections, exact coordinates were not available and were estimated based on locality descriptions.

Scanning electron microscopy (SEM)

Specimens were initially sorted under an Olympus SZX10 light microscope; measurements of holotype specimens were also taken using this equipment. Many collections were also imaged with SEM, with a focus on male individuals as only males bear characteristics diagnostic at the species level. Typically, one male from each species was dissected. One set of appendages (tarsi I–IV, palp, chelicera) was mounted on one stub and the body on another stub. In widespread species, males from multiple localities were examined. For some collections, females were also examined. Stubs were coated with a gold–palladium alloy in a Denton Vacuum Desk III sputter coater of 50 mTorr at 40% rotation and 40% sputter for 2–3 min. Images and measurements of paratypes were taken with a JEOL JSM-6610LV SEM. Images were taken using scanning electron imaging (SEI) of 1–5 kV, a working distance (WD) of 10–15 mm and a spot size (SS) of 40–50. Stubs were numbered 1–12 in numbered boxes (e.g.

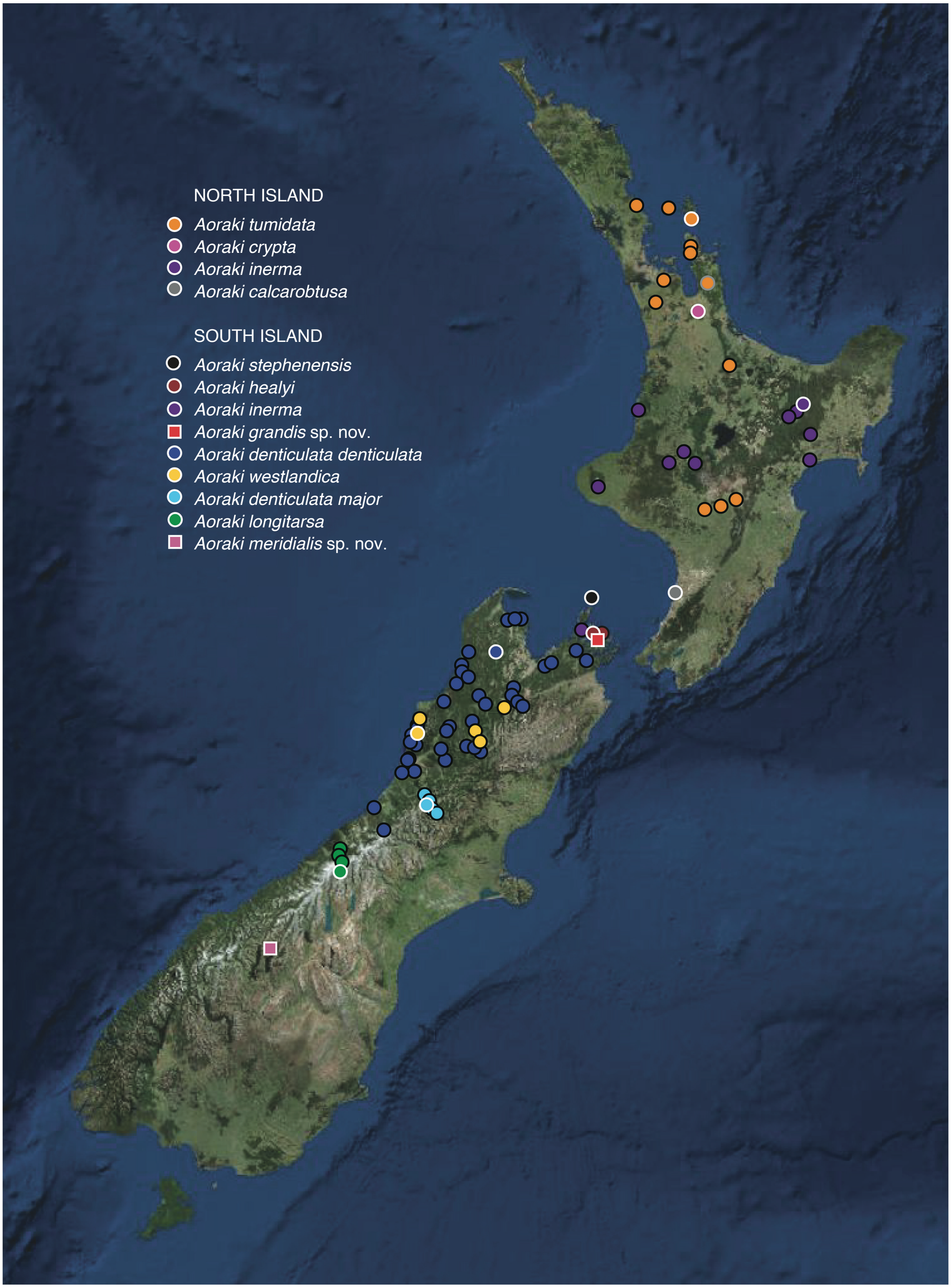

Fig. 2. Map of all currently known *Aoraki* localities. Point interior colour indicates species or subspecies. Point border indicates type status: black, non-type; white, holotype; grey, holotype locality of species synonymised in this paper. Squares represent new species described in our study.

10–1 is stub 1 in box 10); stub numbers without an M prefix hold specimens mounted at the MCZ 2001–2006, whereas stubs with the M prefix hold specimens mounted at Macalester College after 2007. Species diagnoses focused on morphology of the ventral posterior region of the body and the fourth tarsus of males, body regions that have previously been shown to bear characters of taxonomic utility in pettalids (Boyer and Giribet 2007).

DNA extraction and sequencing

DNA was extracted from a single leg or a whole body using QIAGEN's DNEasy Blood and Tissue Kit following the modifications described by Boyer *et al.* (2005).

We sequenced two fast-evolving mitochondrial loci: cytochrome *c* oxidase subunit I (*COI* hereafter) and *16S* rRNA. For *16S* rRNA, a ~400-bp region was amplified using the primers 16Sa and 16Sb, or 16S_PET3 and 16Sb (Xiong and Kocher 1991; Fernández and Giribet 2014). For *COI*, an ~750-bp region was amplified using the primers LCO1490 and either HCO2198 or HCOoutout (Folmer *et al.* 1994; Schwendinger and Giribet 2005). PCR reactions were carried out using an Applied Biosystems 2720 thermal cycler and involved an initial denaturation step (5 min at 95°C) following by 35 cycles of denaturation at 95°C for 30 s, annealing (43–47°C) for 30 s, and extension at 72°C for 1 min 30 s, with a final extension step at 72°C for 6 min.

Amplified DNA fragments were visualised using gel electrophoresis (1% agarose). Successful PCR reactions were purified using QIAGEN's QIAquick PCR Purification Kit. Sequencing was performed by Functional Biosciences, Inc. (Madison, WI, US). Chromatograms were viewed, edited, and assembled into contigs with Geneious Prime (ver. 2019.0.4, see www.geneious.com, Kearse *et al.* 2012).

Phylogenetic analysis

We generated new DNA sequences from 16 individuals of *Aoraki,* deposited in GenBank under numbers MW990401–MW990408, MZ108213–MZ108222 and MZ020607. We combined these new data with previously published data for *Aoraki*, plus the outgroups *Neopurcellia* and *Karripurcellia* Giribet, 2003 that together represent the sister group of *Aoraki* (Baker *et al.* 2020). GenBank, voucher and collection information are available in Supplementary Table S1.

Sequences were aligned using the MAFFT algorithm in Geneious Prime (ver. 2019.0.4, see www.geneious.com, Kearse *et al.* 2012). Areas of ambiguity were eliminated from the *16S* rRNA dataset using Gblocks (ver. 0.91b, see http://molevol.cmima.csic.es/castresana/Gblocks.html; Castresana 2000). Phylogenetic analyses were performed in IQ-TREE (Trifinopoulos *et al.* 2016) under a maximum likelihood criterion. Best-fit models were determined in IQ-TREE using the Bayesian information criterion; the model chosen for *COI* was GTR + F + I + G4 and the model chosen for *16S* rRNA was TPM3u + F + G4. We analysed *COI* data alone, assigning different models of substitution to the third codon position vs first and second positions. We analysed *16S* rRNA data alone, both the full alignment and the alignment that had been treated with Gblocks. We performed two analyses of the combined dataset: one that included all available data and one that included only individuals for which data from both loci were available. Resulting phylogenies were visualised using FigTree (ver. 1.4.4, see http://tree.bio.ed.ac.uk/software/figtree/).

Taxonomy

All material examined is from New Zealand.

Aoraki granulosa (Forster, 1952) is considered a junior synonym of *Aoraki tumidata* (Forster, 1948) **new synonymy**. In both of Forster's holotype specimens, we examined photographs of the body of the holotype male and the slide-mounted fourth tarsus of the male.

Aoraki tumidata (Forster, 1948)

Type material

Holotype. Male, Cuvier Island, Hauraki Gulf, North Island, coll. R. R. Forster, (MONZ AH.000080 [MONZ vial DM 2/50] and slide 4/11).

Paratype. Male (AH.001102 [MONZ vial DM 2/521]) from same locality as holotype; 'Allotype': female (AH.001162 [DM 2/52]) from same locality.

Aoraki granulosa (Forster, 1952)

Type material

Holotype. Male, Taniwha Stream, east of Te Kauwhata, Waikato, North Island, (MONZ AH.000026 [vial DM 2/114] and slide 4/48).

Paratypes. 5 individuals (males and females) (CMNZ A.39) Vinegar Hill Domain, Hunterville, Manawatu-Whanganui, Rimutakas, North Island, coll. R. R. Forster, 12.xii.1948, SEM stubs 12–8 and 12–9, slide CMNZ 2005.135.501; 'Allotype': female (MONZ AH.001131 [DM 2/115]) from same locality.

Additional material examined. 1 male, South-west slopes of Cuvier Island, coll. P. F. Jenkins xi–xii.1971, SEM stub M42–6, AMNZ 61129; 4 males, 4 females, Mount Ngongotaha Scenic Reserve, North Island, −38.1184333333, 177.2006, 717 m, coll. C. M. Baker & B. Snawder, 26.i.2019, field number CMB-NZ-0041, photos P1260967–0984, SEM stubs M41–10 through M42–3, MCZ IZ-152232; 1 female, 2 juveniles, Vinegar Hill Campground, Rimutakas, North Island, −39.93478096, 175.6404610164, 160 m, coll. S. L. Boyer & G. Giribet, 27.vi.2004, MCZ IZ-134675; 1 male, Kepa Bush Reserve, Auckland, North Island, −36.86274, 174.8308, 40 m, coll. A. Schomann & A. J. Pedersen, 08.i.2011, ZMUC; 1 male, Hunua Ranges Regional Park, Workman Track, North Island, −37.1245833333, 175.2214583333, 140 m, coll. A. Schomann & J. Pedersen, 1.iii.2011, MCZ IZ-133838; 3 males, 1 female, 1 juvenile, Waiau Kauri Grove, Coromandel Peninsula, North Island, −36.8369166667, 175.5503888889, 160 m, coll. A. Schomann & J. Pedersen 03.iv.2011, MCZ IZ-134684; 1 male, Rakitu Island, Coll. L. Roberts 7.i.1981, SEM stubs 9–11 and 9–12, NZAC; 1 male, 1 female, 4 juveniles, South of Warkworth, North Island, coll. Dept Scientific and Industrial Research, xii.1978, SEM stubs 10–1 and 10–2, MONZ AH.001011

Forster (1948) described *Aoraki tumidata* as a species of *Rakaia*, along with nine other new species and subspecies of *Rakaia* and three species of *Neopurcellia,* and developed a key to New Zealand's Cyphophthalmi. Forster (1952) subsequently described *A. granulosa* (as *Rakaia granulosa* Forster, 1952), along with an additional eleven new species and subspecies; many species of *Rakaia* were transferred to *Aoraki* by Boyer and Giribet (2007) when the genus was erected. Forster's (1952) prolific taxonomic output may have come at the expense of some attention to detail; in the key to New Zealand's Cyphophthalmi, *Rakaia solitaria* Forster, 1948 appears twice and *Aoraki tumidata* does not appear. Although Forster (1952) did not directly compare the two species, the fourth tarsus of *A. granulosa* was considered granulose ('All segments including the tarsi granulate, but tarsi only sparsely so as compared with the remaining segments') and *A. tumidata* was described as follows: 'All segments except tarsi uniformly and strongly granulate.' Scanning electron microscopy was not available in Forster's day, but now allows us to refine our understanding of the morphology of these animals. Examination of male fourth tarsi across populations previously identified as *A. tumidata* and *A. granulosa,* including one of Forster's (1952) paratypes of *A. granulosa* and a specimen from the type locality of *A. tumidata*, revealed similar levels of granulation across all individuals (e.g. Fig. 3*c*, *f*). In previous works, SLB and others have relied on the granulation of the male fourth tarsus to distinguish *A. granulosa* from *A. tumidata*; however, this character is very difficult to observe with light microscopy (e.g. compare Fig. 3*b*, *e* with Fig. 3*c*, *f*). Phylogenetic analysis of molecular data has previously called into question the species status of *A. granulosa* and *A. tumidata*; *A. tumidata* appears as paraphyletic grade sister to *A. granulosa* in one analysis and *A. granulosa* appears as a paraphyletic grade sister to *A. tumidata* in another analysis by Giribet *et al.* (2016). Our most recent phylogenetic analysis, presented later in this paper, supports the proposed synonymy.

Aoraki grandis Boyer, Tuffield & Dohr, sp. nov.

(Fig. 4–7)

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Material examined

Holotype. Male, Mount Stokes, Marlborough Sounds, South Island, −41.0867469851, 174.1381059587, 539 m, coll. G. Giribet and S. Vélez 9.ii.2009, MONZ AH.001160 (ex. MCZ IZ-129610).

Paratype. Male and female from same collection as holotype, SEM stubs M40–8 (male leg IV) and M46–5 (female body), MCZ IZ-129610.

Additional material. 1 juvenile, Mount Stokes, Marlborough Sounds, South Island, −41.0870789923, 174.1370820254, 630 m, coll. S. L. Boyer, C. D'Haese, G. Giribet 28.i.2003, MCZ IZ-134652; 1 male, 2 females, Mount Stokes, Marlborough Sounds, South Island, −41.090833, 174.101667, coll. S. Boyer and J. M. Baker, 19.i.2006, SEM stubs 15–12, 16–1, MCZ IZ-134657.

Diagnosis

Males can be distinguished from congeners by the combination of a very smooth male fourth tarsus and a lack of scopula on the anal plate.

Description of holotype male

Body dark brown with legs somewhat lighter (Fig. 4). Cuticle mostly covered by microstructure of large tubercles and much

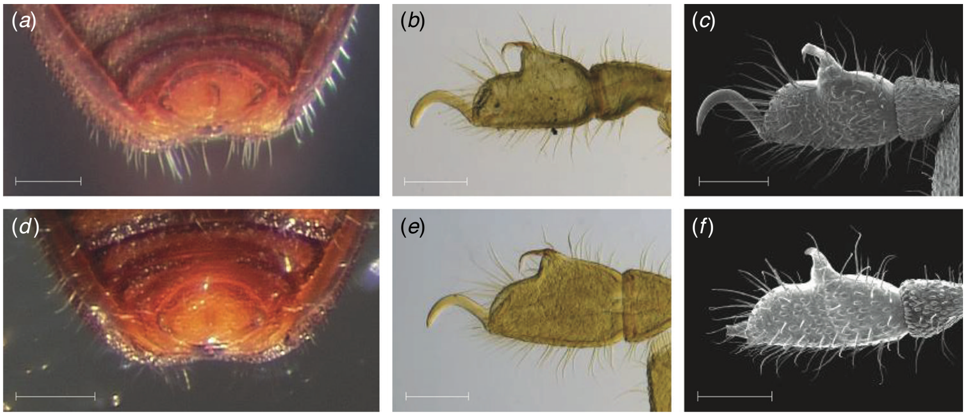

Fig. 3. Comparison of *Aoraki tumidata* and *A. granulosa* type material. Scale bar in every image: 200 μm. Photographs (*b*) and (e) by Phil Sirvid and Jean-Claude Stahl. (*a*) *A. tumidata* holotype, ventral posterior view, MONZ AH.000080 (DM 2/50). (*b*) *A. tumidata* holotype, male fourth tarsus, MONZ AH.000080 (slide 4/11). (*c*) *A. tumidata* from type locality, AMNZ 61129, SEM stub M42–3. (*d*) *A. granulosa* holotype, ventral posterior view, MONZ AH.000080 (DM 2/114). (e) *A. granulosa* holotype, male fourth tarsus, MONZ AH.000080 (slide 4/48). (*f*) *A. granulosa* paratype, male fourth tarsus, CMNZ A.39, SEM stub 12–9.

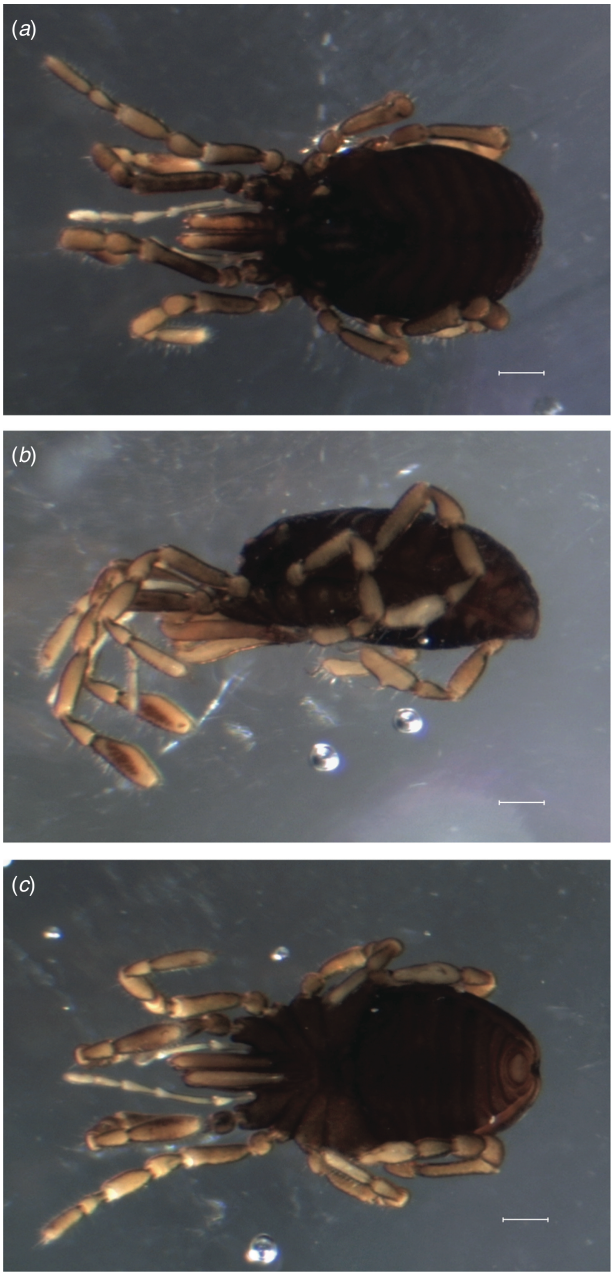

Fig. 4. *Aoraki grandis*, sp. nov. holotype male, MONZ AH.001160 (ex. MCZ IZ-129610). Scale bar: 0.5 mm. (*a*) Dorsal view. (*b*) Lateral view. (*c*) Ventral view.

smaller granules, with tubercles convex and smooth on the upper surface (as described for Cyphophthalmi by Murphree 1988) (Fig. 4; see also paratypes in Fig. 5). Dorsal scutum curves moderately towards the ventral in posterior region (Fig. 4*b*). Ozophores in 45° position (Fig. 4*a, b*), with 0.9 mm separation; eye visible as white mass below cuticle and incorporated into base of ozophore without lens. Ventral transverse sulci present and prominent (Fig. 4*c*, see also paratype in Fig. 5*b, d*). Dorsal sulci visible due to lack of granulation, and undulating (Fig. 4*a*; see also paratypes in Fig. 5*b, d*). Spiracles C-shaped (*sensu* Giribet and Boyer 2002). Gonostome subtriangular with height:width ratio 0.6; sternal opisthosomal region without modifications or glandular pores (Fig. 4; see also paratype in Fig. 5*b*). Anal region with sternites 8 and 9 and tergite IX free, not forming a corona analis (Fig. 4; see also paratype in Fig. 5*b*). Area of contact of tergite IX and sternite 9 of 'pettalid' type (Giribet and Boyer 2002) in which tergite IX laterally covers sternite 9 and clearly meets sternite 8. Anal plate sparsely granulose and lacking scopular hairs, with height:width ratio 0.7 (Fig. 4*c*; see detail in image of paratype, Fig. 5*b*). Length of body 2.9 mm and width 1.9 mm.

Palp lacking process on the trochanter, as in other *Aoraki* (as in image of paratype, Fig. 6*a*). Chelicerae very gracile relative to other Pettalidae (as in image of paratype, Fig. 6*b*). Chelicera with a small ornamented dorsal process and a very prominent ornamented granulose ventral process, and without a distinct apodeme on the second article (as in image of paratype, Fig. 6*b*). Measurements of cheliceral articles of male paratype (mm): proximal article 1.1, second article 1.3, mobile digit 0.4 (as in image of paratype, Fig. 6*b*). Measurements of palpal articles of male paratype from proximal to distal (mm): 0.3, 0.5, 0.3, 0.5, 0.4.

Metatarsi I and II mostly smooth, with ornamentation only very close to proximal edge (F as in image of paratype, Fig. 7*a, b*). Metatarsi III and IV with full ornamentation (as in image of paratype, Fig. 7*c–f*). Distinct solea on tarsus I (as in image of paratype, Fig. 7*a*). Tarsus IV of male elongate and ovular and entirely smooth, bearing a short curved adenostyle with a prominent protuberance at the base and a single seta emerging at the junction of the protuberance and the adenostyle (as in image of paratype, Fig. 7*d, e*).

Additional description of paratype male and female

Length of male paratype (Fig. 5*a, b*) 2.92 mm and width at widest point 1.94 mm. Gonostome 0.21 mm wide and 0.12 mm high, anal plate 0.39 wide and 0.27 wide (Fig. 5*b*). Measurements of cheliceral articles: proximal article 1.11 mm, second article 1.32 mm, mobile digit 0.38 mm (Fig. 6*b*). Measurements of palpal articles of male paratype from proximal to distal (mm): 0.34, 0.54, 0.32, 0.48, 0.42. Length measurements of male paratype of leg articles from proximal to distal (mm): leg I [trochanter absent, femur damaged], 0.44, 0.69, 0.32, 077; leg II 0.25, 0.77, 0.31, 0.47, 0.28, 0.60; leg III 0.28, 0.60, 0.30, 0.45, 0.27, 0.50; leg IV 0.40, 0.78, 0.42, 0.52, 0.29, 0.64.

Length of female paratype (Fig. 5*c, d*) 3.13 mm and width at widest point 1.81 mm. Anal plate of female uniformly granulose (Fig. 5*d*). Tarsus IV of female smooth (Fig. 7*f*).

Etymology

The specific epithet, *grandis*, refers to the size of this species that is the largest in the genus.

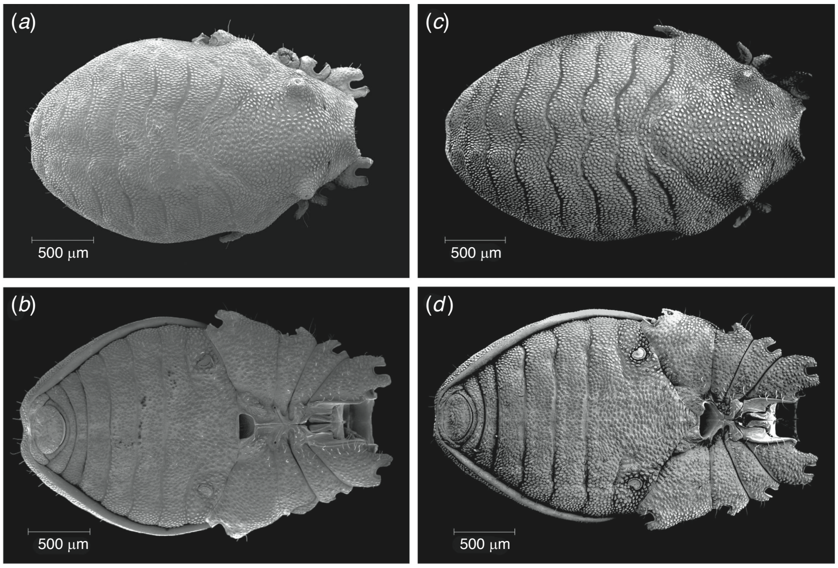

Fig. 5. *Aoraki grandis*, sp. nov. paratypes. (*a*) Male in dorsal view, MCZ IZ-134657, SEM stub 16–1. (*b*) Male in ventral view, MCZ IZ-134657, SEM stub 16–1. (*c*) Female in dorsal view, MCZ IZ-129610, SEM stub M46–5. (*d*) Female in ventral view, MCZ IZ-129610, SEM stub M46–5.

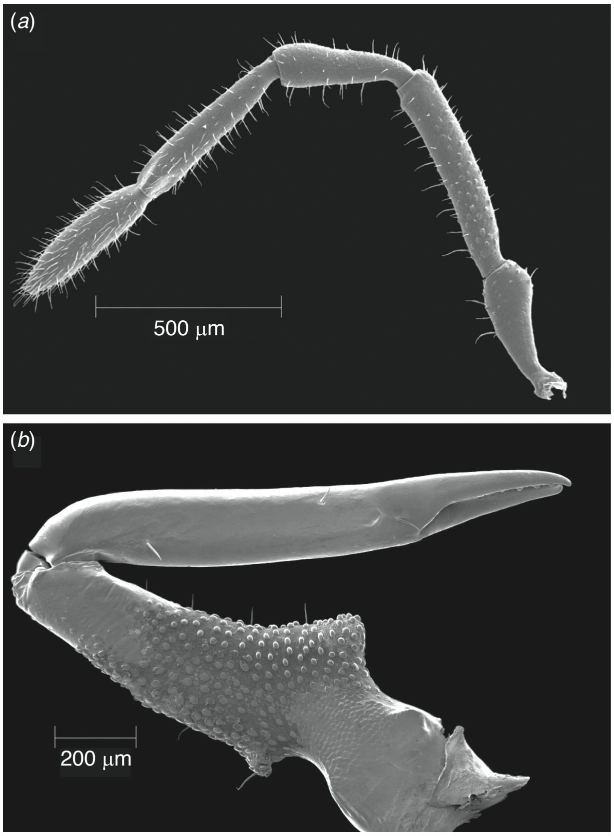

Fig. 6. *Aoraki grandis*, sp. nov. male paratype, MCZ IZ-134657, SEM stub 15–12. (*a*) Palp. (*b*) Chelicera.

Notes

This species is known only from Mount Stokes in the Marlborough Sounds, co-occurring with *Aoraki healyi*, another species with a severely restricted geographical range. Females lack characteristics diagnostic at the species level, however, size serves to distinguish *A. grandis* from *A. healyi* (Forster, 1948), with which this species co-occurs. *A. grandis* is larger than any other species of *Aoraki* (male 2.9 mm long, female 3.1 mm long), whereas males of *A. healyi* are 2.2 mm long and females 2.7 mm long.

Aoraki meridialis Boyer, Hahn & Ward, sp. nov.

(Fig. 8–11)

urn:lsid:zoobank.org:act:945C0129-E0B1–4226-B85F-4ECD4A06E070

Material examined

Holotype. Male, Kidds Bush Reserve, Otago Lakes, South Island, −44.4402666667, 169.2644, 474 m, coll. C. M. Baker, S. L. Boyer, R. Morisawa, E. J. Pessereau and P. Tardelli Canedo, 15.i.2019. MONZ AH.001161 (ex. MCZ IZ-152142).

Paratypes. 23 males, 14 females, 4 juveniles from same collection as holotype. SEM stubs M35–6, M35–7, M37–10, M38–5, M46–1, MCZ IZ-152142.

Diagnosis

Males can be distinguished from congeners by a lightly granulose male fourth tarsus in combination with lack of a scopula on the anal plate.

Description of male holotype

Body colouration dark brown, with lighter appendages (Fig. 8). Dorsum flat, with overall body shape rectangular in lateral view (Fig. 8*b*). Ozophores angled ~45° relative to body, with 0.7 mm separation between these and eye visible as white mass below the cuticle, without lens (Fig. 8). Body mostly covered by microstructure of large tubercles and much smaller granules, with tubercles convex and smooth on the upper surface (as described for Cyphophthalmi by

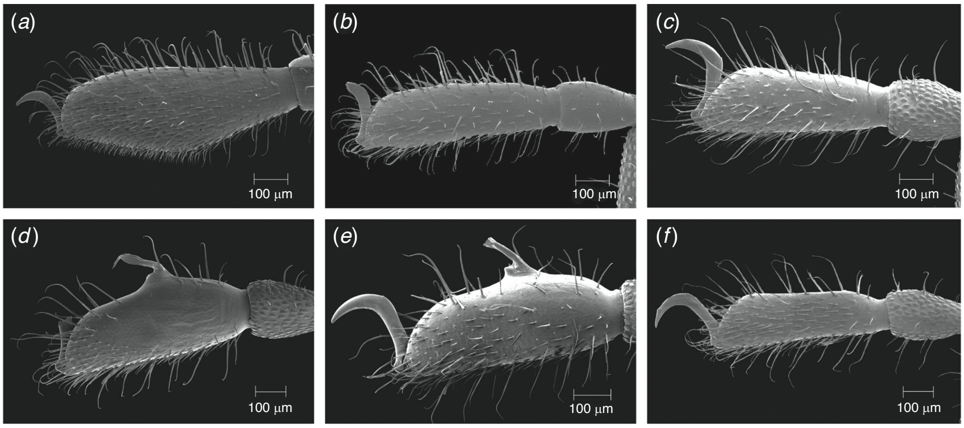

Fig. 7. *Aoraki grandis*, sp. nov. male paratype. (*a*) Male tarsus I, MCZ IZ-134657, SEM stub 15–12. (*b*) Male tarsus II, MCZ IZ-134657, SEM stub 15–12. (*c*) Male tarsus III, MCZ IZ-134657, SEM stub 15–12. (*d*) Male tarsus IV, medial view, MCZ IZ-134657, SEM stub M40–8. (*e*) Male tarsus IV, lateral view, MCZ IZ-134657, SEM 15–2. (*f*) Female tarsus IV, FMHD 85–455, SEM stub 10–3.

Murphree [1988]) (Fig. 8; see also images of paratypes in Fig. 9). Dorsal sulci essentially linear (non-undulating) and granulose (Fig. 8*a*, and as in images of paratype: Fig. 9*a, c*). Ventral transverse sulci present and prominent (Fig. 8*c*, and as in images of paratype: Fig. 9*b, d*). Spiracles of the open circle type (as in Fig. 9*b*). Gonostome subtriangular (as in Fig. 9*b*), with height:width ratio 0.6. Anal plate of male sparsely granulose anteriorly, smooth posteriorly and lacking scopular hairs (as in Fig. 9*b*), with height:width ratio 0.6. Total length of male holotype 1.9 mm, width 1.1 mm.

Palp lacking process on the trochanter (as in Fig. 10*a*). Measurements of palpal articles (mm): 0.2, 0.4, 0.2, 0.3, 0.3. Second article of chelicera without apodeme (as in Fig. 10*b*). Mobile digit with unevenly sized dentition, as is typical in pettalids (as in Fig. 10*b*). Chelicera with a small ornamented dorsal process and a very prominent ornamented granulose ventral process, and without a distinct apodeme on the second article. Measurements of cheliceral articles (mm): proximal article 0.4 mm, second article 0.8 mm, mobile digit 0.2 mm (Fig. 10*b*).

Metatarsi I and II partially ornamented on proximal half, with distal half largely smooth (as in Fig. 11*a, b*). Metatarsi III and IV with full ornamentation (as in Fig. 11*c–f*). Distinct solea on tarsus I (as in Fig. 11*a*). Tarsus IV of male subrectangular and very sparsely granulose, bearing a short curved adenostyle with a prominent protuberance at the base and a single seta emerging at the junction of the protuberance and the adenostyle (as in Fig. 11*d, e*).

Length measurements from male paratype of leg articles from proximal to distal (mm, measured on specimens mounted on stubs M35–7 and M37–10): leg I 0.3, 0.6, 0.3, 0.4, 0.2, 0.5; leg II 0.1, 0.4, 0.2, 0.3, 0.2, 0.4; 15 leg III 0.1, 0.4, 0.2, 0.3, 0.2, 0.3; leg IV 0.3, 0.5, 0.2, 0.3, 0.2, 0.4.

Additional description of paratypes

Length of male paratype (Fig. 9*a, b*) 1.9 mm and width at widest point 1.1 mm. Length of female paratype (Fig. 9*c, d*) 2.26 mm and width at widest point 1.12 mm. Gonostome 0.12 mm wide, 0.74 mm high. Anal plate 0.27 wide and 0.16 high. Measurements of palpal articles of male paratype from proximal to distal (mm): 0.22, 0.36, 0.24, 0.29, 0.32 (Fig. 10*a*). Measurements of cheliceral articles of male paratype: proximal article 0.41 mm, second article 0.78 mm, mobile digit 0.26 mm (Fig. 10*b*). Length measurements from male paratype of leg articles from proximal to distal (mm, measured on specimens mounted on stubs M35–7 and M37–10): leg I [trochanter damaged], 0.56, 0.26, 0.42, 0.20, 0.45; leg II 0.15, 0.43, 0.20, 0.33, 0.19, 0.36; 15 leg III 0.15, 0.37, 0.20, 0.30, 0.16, 0.32; leg IV 0.29, 0.46, 0.22, 0.36, 0.15, 0.37.

Anal plate of female uniformly granulose (Fig. 9*d*); tarsus IV of female with extremely sparse granulation (Fig. 11*f*).

Etymology

The specific epithet, *meridialis*, an adjective, refers to the only known locality for this species that has replaced Aoraki as the southernmost documented population of *Aoraki*, hence the 'southern *Aoraki*'.

Notes

Aoraki meridialis is only 1.9 mm long, making this the smallest known member of the genus; all other species and subspecies are longer than 2 mm. Although females do not have any characteristics that permit diagnosis at the species level, *A. meridialis* is the only species of Cyphophthalmi known to occur at Kidds Bush. The discovery of this species extends the southern range of the genus by over 100 km.

Emended diagnosis of *Aoraki*

Ozophores in dorsal 45° position. Eyes present, incorporated into ozophores, without lenses. No projections surrounding gonostome. Absence of a ventral process on the palp trochanter. Chelicera with prominent ornamented ventral process and without a distinct apodeme on the second article. Solea present in tarsus I. Male tarsus IV entire.

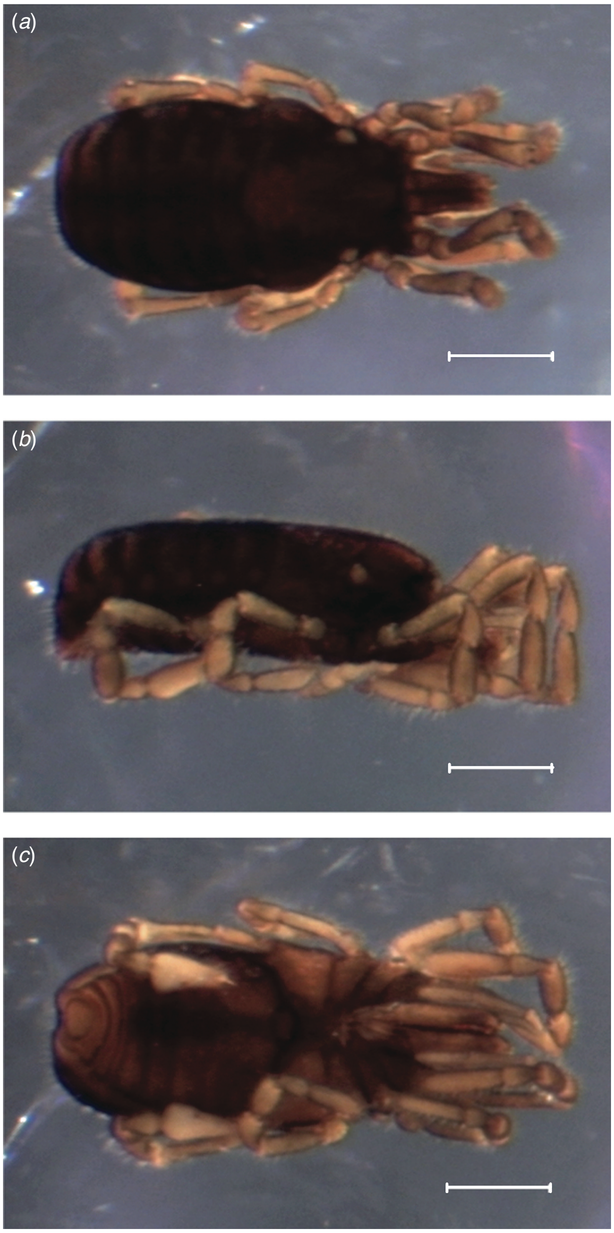

Fig. 8. *Aoraki meridialis*, sp. nov. holotype male, MONZ AH.001161 (ex. MCZ IZ-152142). Scale bar: 0.5 mm. (*a*) Dorsal view. (*b*) Lateral view. (*c*) Ventral view.

Phylogenetics

The individuals identified as *Aoraki grandis* sp. nov. form a monophyletic group with 100% bootstrap support in analyses of all datasets (*COI* alone, *16S* alone and combined *COI* + *16S* dataset), as do all individuals identified as *Aoraki meridialis* sp. nov. Given the morphological uniformity and the small number of collections (three and one respectively) these results were not surprising. In analyses of all datasets (*COI* alone, *16S* alone and combined *COI* + *16S* dataset), specimens of *A. granulosa* previously and newly sequenced for this study formed a paraphyletic group, as did specimens of *A. tumidata* previously sequenced; together, specimens previously identified as *A. granulosa* + *A. tumidata* form a well-supported group (Fig. 12).

In our analysis of the *16S* dataset and the combined *COI* + *16S* dataset, we find three groups of species within *Aoraki*, each with a distinct level of granulation on the male fourth tarsus. Sister group to all of the rest of *Aoraki* is a moderately supported lineage consisting of four species with smooth male fourth tarsus: *A. crypta* (Forster, 1948), *A. inerma* (Forster, 1948), *A. healyi* and *A. grandis* sp. nov. (Fig. 13*a–d*). The remaining *Aoraki* consist of two well supported lineages, one consisting of a pair of species with heavily granulose male fourth tarsus (*A. tumidata* + *A. westlandica* (Forster, 1952)), clearly demarcated and each in a different island (Fig. 13*f–g*); and the other lineage characterised by lightly granulose male fourth tarsus (Fig. 13*i–l*): *A. denticulata denticulata, A. denticulata major* (Forster, 1948), *A. longitarsa* and *A. meridialis* sp. nov. Relationships among *A. denticulata denticulata* lineages are poorly supported and the subspecies appears as a paraphyletic grade, with the other species and subspecies nested inside (Fig. 12). When *COI* is analysed alone, the species with smooth fourth tarsus form a paraphyletic grade at the base of the genus, and species with heavily granulose fourth tarsus form a paraphyletic grade with respect to the lightly granulosa clade; support for the branch that contradicts the monophyly of *A. tumidata* + *A. granulosa* is 86%, whereas support for branches that contradict the monophyly of the smooth fourth tarsus clade is 79–90%.

Discussion

Systematics

We have subtracted one species from *Aoraki* and added two, increasing the number of named species and subspecies in the genus to twelve. The new species described here are the smallest and largest known species of *Aoraki* and the discovery of *A. meridialis* sp. nov. extends the southern range of the genus by over 100 km (Fig. 2). Results of our phylogenetic analyses indicate monophyly of each of our new species and support the synonymisation of *Aoraki granulosa* with *Aoraki tumidata* (Fig. 12).

The relationships recovered among species are concordant with results from previous studies (Boyer *et al.* 2007; Boyer and Giribet 2007, 2009; Giribet *et al.* 2012, 2016; Fernández and Giribet 2014; Baker *et al.* 2020). As in all previous phylogenetic analyses of this group, we find a well-supported sister group relationship between the two species with heavily granulose fourth male tarsi and anal plates that lack scopulae but bear a distinctive central cuticular protuberance (*A. tumidata* and *A. westlandica*) (Fig. 13*f*, *g*, 14*f*, *g*) (though, this relationship is contradicted by our analysis of *COI* data alone, with moderate support). We find a second strongly supported group, consisting of species with lightly

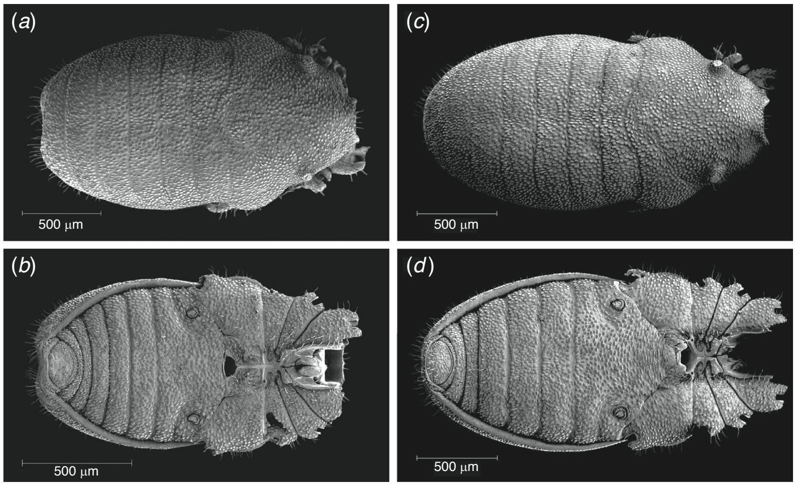

Fig. 9. *Aoraki meridialis*, sp. nov. paratypes. (*a*) Male in dorsal view, MCZ IZ-152142, SEM stub M35–6. (*b*) Male in ventral view, MCZ IZ-152142, SEM stub M35–6. (*c*) Female in dorsal view, MCZ IZ-152142, SEM stub M36–1. (*d*) Female in ventral view, MCZ IZ-152142, SEM stub M36–1.

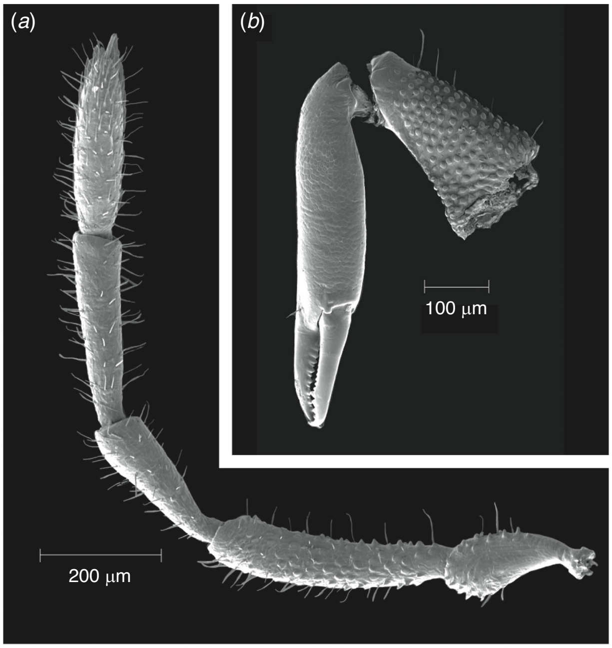

Fig. 10. *Aoraki meridialis*, sp. nov. male paratype, MCZ IZ-152142, SEM stub M37–10. (*a*) Palp. (*b*) Chelicera.

granulose fourth tarsi bearing a protuberance at the base of the adenostyle (*A. denticulata denticulata, A. denticulata major*, *A. longitarsa* and *A. meridialis* sp. nov.) (Fig. 13*i–l*), consistent with previous findings. The two lineages with granulose male fourth tarsi are each other's sister taxa and were collectively termed '*Aoraki* clade a' by Boyer and Giribet (2009). Finally, in all but our analysis of *COI* alone, we retrieve a moderately supported monophyletic group consisting of *A. crypta* + *A. inerma* + *A. healyi* + *A. grandis* sp. nov. that has been found in some (but not all) previous phylogenetic analyses. This group was termed '*Aoraki* clade b' by Boyer and Giribet (2009) and is characterised by an entirely smooth male fourth tarsus bearing a long thin adenostyle (Fig. 13*a–d*) and undulating transverse dorsal sulci in both males and females (Fig. 5*a, c*). Other *Aoraki* have essentially straight linear transverse dorsal sulci (e.g. Fig. 1, 9*a, c*); Forster did not depict dorsal anatomy in his species descriptions, but this region of the body may prove to be a rich source of informative characters across New Zealand's Cyphophthalmi.

A lack of fresh material prevented us from generating DNA sequence data from two other species. *Aoraki stephenensis* (Forster, 1952), known only from Stephens Island, was considered by Forster to be a subspecies of *Aoraki inerma. Aoraki stephenensis* has a smooth fourth tarsus (Fig. 13*e*), indicating a probable close relationship with *A. inerma* + *A. crypta* + *A. healyi* + *A. grandis* sp. nov. *Aoraki calcarobtusa* (Forster, 1952), known only from the male holotype specimen, is found at Levin, near Wellington. Forster (1952) considered *A. westlandica* to be a subspecies of *A. calcarobtusa;* he described both as having ungranulated fourth tarsi. We have no *A. calcarobtusa* material for SEM, hence assessing the level of granulation on the fourth tarsus (Fig. 13*h*) is difficult. However, we have demonstrated that *A. westlandica* has a granulose fourth tarsus (Fig. 13*g*) and expect that *A. calcarobtusa* displays a similar morphology. In any case, the lack of scopulae and the presence of a central protuberance in the anal plate of *A. calcarobtusa* suggests a close relationship to *A. tumidata* and *A. westlandica* (Fig. 14*f–h*), two species with heavily granulose fourth tarsi (Fig. 13*f, g*).

Relationships within the *A. denticulata* complex (*A. denticulata* + *A. longitarsa* + *A. meridialis* sp. nov.) remain poorly resolved, illustrating the limits of analyses based on mtDNA alone. We find likely paraphyly of the widespread subspecies *Aoraki denticulata denticulata*; *A. denticulata major*, *A. meridialis* sp. nov. and *A. longitarsa* were found nested within the subspecies (Fig. 12). This is not surprising, as *A. denticulata denticulata* has been recovered as paraphyletic in past studies, with *A. denticulata major* and *A. longitarsa* nested within (Boyer *et al.* 2007; Boyer and Giribet 2009; Giribet *et al.* 2016). At this time, we refrain from revising either of the *A. denticulata* subspecies.

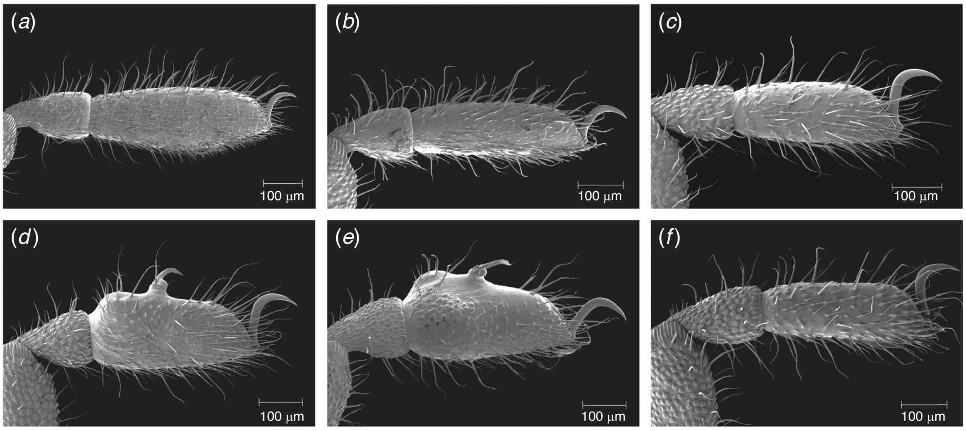

Fig. 11. *Aoraki meridialis*, sp. nov. male and female paratypes. (*a*) Male tarsus I, MCZ IZ-152142, SEM stub M37–10. (*b*) Male tarsus II, MCZ IZ-152142, SEM stub M35–7. (*c*) Male tarsus III, MCZ IZ-152142, SEM stub M37–10. (*d*) Male tarsus IV, medial view, MCZ IZ-152142, M37–10. (*e*) Male tarsus IV, lateral view, MCZ IZ-152142, SEM stub M35–7. (*f*) Female tarsus IV, MCZ IZ-152142, SEM stub M38–5.

Biogeographic patterns

The three lineages recovered in our phylogenetic analyses display distinct and intriguing biogeographic patterns, including surprising variation in species range size (Fig. 2, 12).

Aoraki westlandica is known from a handful of localities in Buller, in the South Island of New Zealand. The sister taxon, on the other hand, is dramatically widespread across the North Island: the range of *A. tumidata* spans ~400 km, from Rangitikei up to Auckland. Most mite harvestmen are known from only a handful of localities with species ranges typically not exceeding 50 km in any direction. We initially suspected that *A. tumidata* consisted of multiple species, based on previous work on Cyphophthalmi (Boyer *et al.* 2007, 2015; Clouse *et al.* 2016). We were therefore surprised to find that the *A. tumidata* specimens we sequenced were all extremely genetically similar to one another, with no apparent correspondence between geography and population structure (Fig. 12). These genetically similar individuals are united by a relatively long branch (Fig. 12), a pattern suggestive of a history of recent population expansion.

The North Island is home to another notably widespread cyphophthalmid, *Aoraki inerma* (Fig. 2). Unfortunately, despite employing a variety of primer pairs and PCR optimisation approaches, we were only able to generate a single short, low-quality *COI* sequence for *A. inerma* and no *16S* rRNA sequences at all. This reflects past experiences of SLB and others over these years; previous studies that have included multiple *A. inerma* individuals have only presented data from the nuclear loci *18S* rRNA, *28S* rRNA and histone *H3* (e.g. Boyer and Giribet 2009). Although genetic data for *A. inerma* are currently sparse, this does seem to represent a second widespread North Island species (Fig. 2). Notably, there is a single collection from the South Island (FMHD 85–455) that also seems to be *A. inerma,* making this the only species in the genus that is found on both islands. Although initially seeming unlikely that such dispersal-limited animals could achieve a distribution spanning Cook Strait, the North and South Islands were connected during the Last Glacial Maximum. One other species of Cyphophthalmi, *Rakaia minutissima* (Forster, 1948), is also found in both the North Island and northern South Island, and in this case, molecular data have confirmed the species status (Boyer and Giribet 2009).

There is yet another cyphophthalmid, *Rakaia media* Forster, 1948 that is co-distributed at many of the same localities as *A. inerma* and *A. tumidata;* Forster (1948) noted the co-occurrence with *A. inerma* in the original description. Although the Wellington area at the southern tip of the North Island harbours at least 12 morphologically distinct short-range endemics in the genus *Rakaia* (see Morisawa 2020), most of the North Island is possibly characterised by widespread, genetically uniform species as a result of recent expansion of suitable habitat.

Within the North Island, a biogeographic break between areas to the north and south of ~38° is recognised in many animal lineages (Ellis *et al.* 2015); this latitude is also the southern limit of kauri trees (*Agathis australis*) in New Zealand and is therefore known as the Kauri Line. The Northland peninsula harbours a high level of endemism in both plants (McGlone 1985) and insects (Buckley *et al.* 2015), and in taxa that span the Kauri Line, genetic diversity is higher north of the break than in the rest of the North Island (Ellis *et al.* 2015). Geological history provides a possible explanation for this pattern of low diversity across most of the North Island. During the Pliocene, strike-slip movement in the central North Island led to flooding and establishment of a seaway that covered much of the south and central areas of the island. This submergence persisted until the Pleistocene, when waters retreated progressively

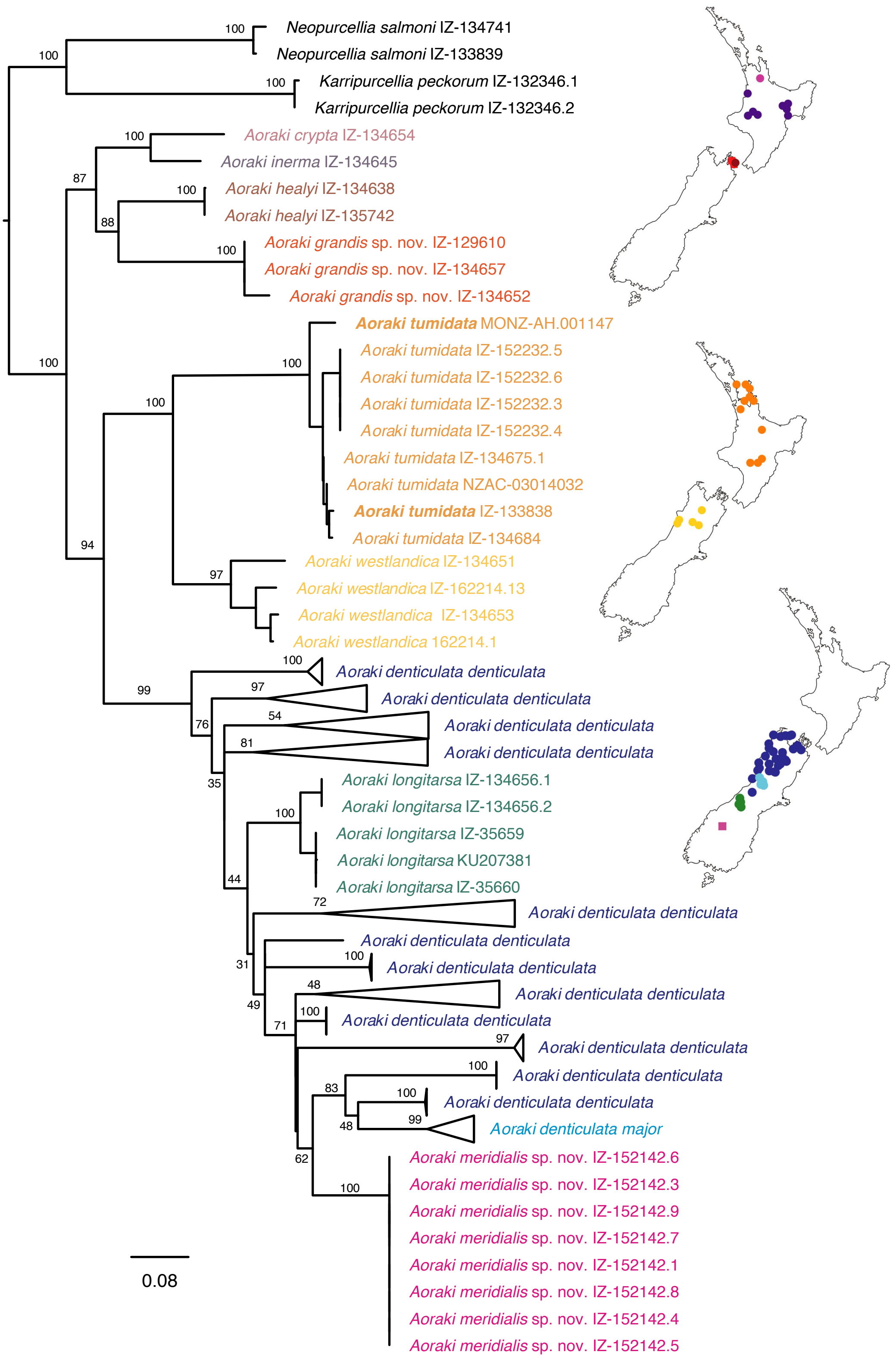

Fig. 12. Phylogeny of *Aoraki,* resulting from analysis in IQ-TREE of combined *16S* and *COI* data partitioned by locus and codon position. Numbers on branches represent bootstrap support. *Aoraki tumidata* indicated in bold were previously identified as such; *Aoraki tumidata* specimens, of which the name appears and are not in bold were previously identified as *Aoraki granulosa.* Maps appear beside corresponding lineages, from top to bottom: the smooth-tarsus clade, the heavily granulose tarsus clade and the lightly granulose tarsus clade. Colours on the maps correspond to colours on the phylogeny.

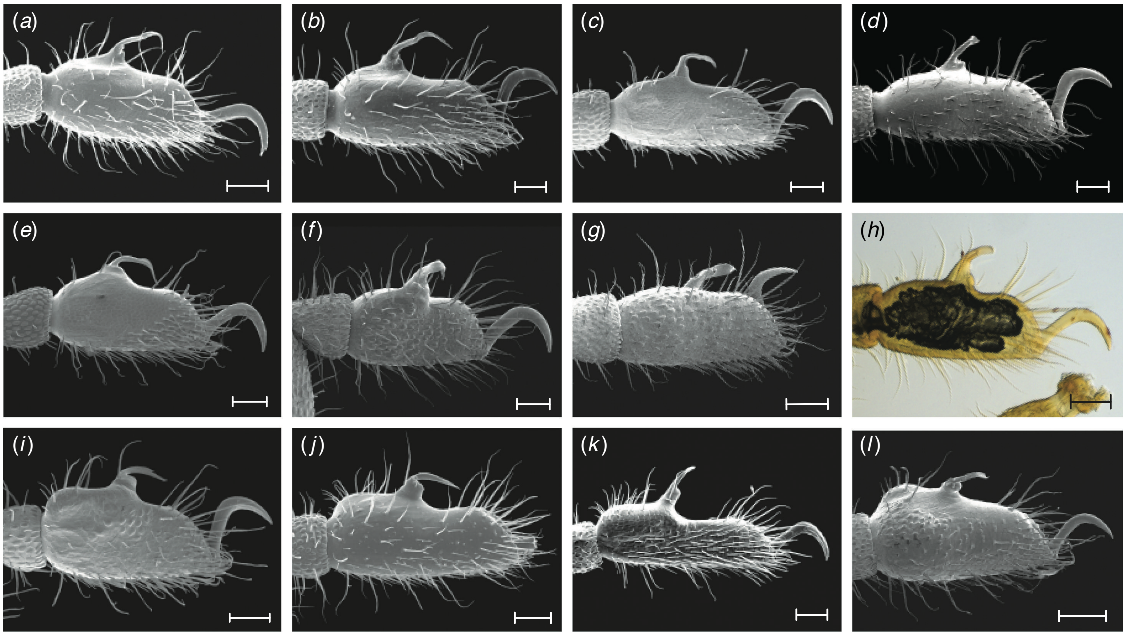

Fig. 13. Male fourth tarsus of all species and subspecies of *Aoraki*, scale bar in every image: 100 μm. Photograph H by Phil Sirvid and Jean-Claude Stahl. (*a*) *A. crypta*, MCZ IZ-134654, SEM stub 13–10. (*b*) *A. inerma*, MONZ DOC E. Horopito pitfall trap, SEM stub 1–11. (*c*) *A. healyi,* MCZ IZ-134638, SEM stub 4–7. (*d*) *A. grandis,* sp. nov., MCZ IZ-129610, SEM stub M40–8. (*e*) *A. stephenensis*, OM, collected 1.xii.1953 by B. A. Holloway, SEM stub 11–11. (*f*) *A. tumidata*, AMNZ 61129, SEM stub M42–3. (*g*) *A. westlandica,* MCZ IZ-162214, SEM stub 16–11. (*h*) *A. calcarobtusa,* holotype specimen, MONZ AH.000011 (DM 2/119). (*i*) *A. denticulata denticulata,* MCZ IZ-134640, SEM stub 4–12. (*j*) *A. denticulata major,* MCZ IZ-134644, SEM stub M42–7. (k) *A. longitarsa,* MCZ IZ-134656, SEM stub 15–4. (*l*) *A. meridialis,* sp. nov., MCZ IZ-152142, SEM stub M35–7.

southward, permitting population expansion in taxa that had been restricted to land north of the seaway (Lewis *et al.* 1994; Ellis *et al.* 2015). Baker (2020) has argued that this geological history has been a driver of the evolution of parthenogenesis – a most extreme form of genetic uniformity – in another North Island opilionid, *Sorensenella rotara*. Post-Pleistocene expansion may explain *Aoraki tumidata*'s low genetic divergence that is truly striking, given that the range is similar in geographic scale to that of the South Island's *A. denticulata* complex (*A. denticulata* + *A. longitarsa* + *A. meridialis* sp. nov.) (Fig. 2, 12).

Future directions

Although our understanding of the diversity of *Aoraki* has been furthered by the analyses presented here, mitochondrial DNA sequence data alone clearly cannot fully resolve relationships within the *A. denticulata* complex (Fig. 12). *Aoraki denticulata major*, *A. longitarsa* and *A. meridialis* sp. nov. are each well supported by genetic data and anatomical features, but resolving relationships among lineages currently classified as *A. denticulata denticulata* will require novel approaches. The use of target capture of ultraconserved elements (UCEs) (Starrett *et al.* 2017) has allowed arachnologists to generate next-generation sequence data from hundreds of loci in recent years, resolving relationships within the Opiliones groups Travuniodea Absolon & Kratochvil, 1932 and Triaenonychidae Sørensen, 1886 (e.g. Derkarabetian *et al.* 2018, 2021*a*, 2021*b*; Baker 2020; Frigyik 2021). Preliminary data generated using this approach suggest that this will resolve relationships within New Zealand Cyphophthalmi generally and the *A. denticulata* complex in particular (Morisawa 2020; Dohr *et al.* 2021).

Next-generation sequencing data may also allow us to describe relationships within *Aoraki inerma* that may exhibit phylogeographic patterns similar to those of *A. tumidata. A. crypta*, known only from the type locality at Mount Te Aroha (Fig. 2), is notably morphologically very similar to the widespread *A. inerma* (Fig. 13*a*, *b*, 14*a*, *b*), distinguished only by the degree of ventral curvature of the body, a character that may be affected by artefacts of collection and preservation. The single *A. crypta* and single *A. inerma* we have sequenced for mitochondrial loci are recovered as sister taxa in our analyses (Fig. 12) and discovering that the two are not reciprocally monophyletic would not be surprising; preliminary next-generation data from one individual of each species indicate that these species are very closely related (Dohr *et al.* 2021).

Aoraki has great potential as a system for testing hypotheses related to mechanisms by which New Zealand's eventful geological history has shaped the evolution of the endemic terrestrial fauna. While we have made progress towards

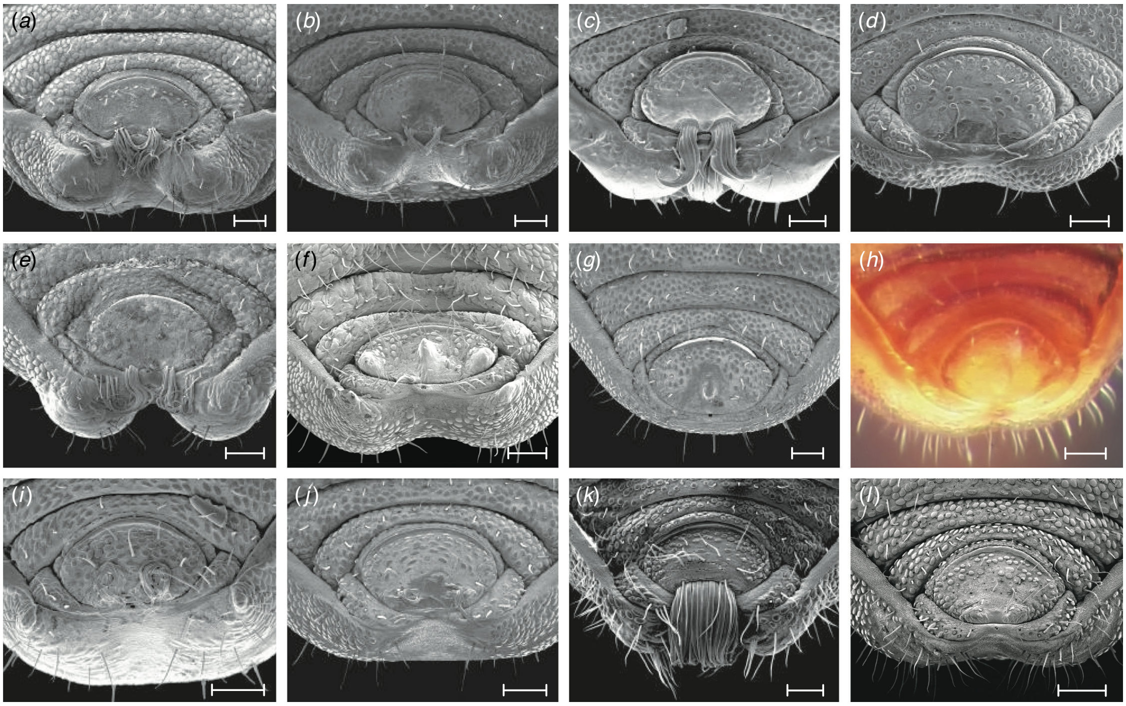

Fig. 14. Posterior ventral region of males of all species and subspecies of *Aoraki*. Scale bar in every image: 100 μm. (*a*) *A. crypta,* MCZ IZ-134654, SEM stub 13–11. (*b*) *A. inerma,* MCZ IZ-134969, SEM stub 4–2. (*c*) *A. healyi,* MCZ IZ-134638, SEM stub 4–8. (*d*) *A. grandis,* sp. nov., MCZ IZ-134657, SEM stub 16–1. (e) *A. stephenensis*, OM, collected 1.xii.1953 by B. A. Holloway, SEM stub 11–11. (*f*) *A. tumidata,* MCZ IZ-134684, SEM stub M39–1. (*g*) *A. westlandica,* MCZ IZ-162214, SEM stub 7–1. (*h*) *A. calcarobtusa,* holotype specimen, MONZ AH.000011 (DM 2/119). (*i*) *A. denticulata denticulata,* MCZ IZ-134640, SEM stub 4–12. (*j*) *A. denticulata major,* MCZ IZ-134570, SEM stub 7–7. (*k*) *A. longitarsa,* MCZ IZ-134656, SEM stub 15–1. (*l*) *A. meridialis,* sp. nov., MCZ IZ-152142, SEM stub M35–6.

understanding the diversity and distribution of the genus, clearly many questions remain to be answered.

Supplementary material

Supplementary material is available online.

References

Absolon K, Kratochvíl J (1932) Peltaeonychidae, nova čeled slepych opilionidu z jeskyn jiihoillyrské oblasti. *Príoda* **25**, 153–156.

Baker CM (2020) Phylogenetics and biogeography of soil invertebrates across Gondwana. PhD thesis, Harvard University, Cambridge, MA, USA.

Baker CM, Boyer SL, Giribet G (2020) A well-resolved transcriptomic phylogeny of the mite harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) reveals signatures of Gondwanan vicariance. *Journal of Biogeography* **47**, 1345–1361. doi:10.1111/jbi.13828

Boyer SL, Giribet G (2007) A new model Gondwanan taxon: systematics and biogeography of the harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand. *Cladistics* **23**, 337–361. doi:10.1111/j.1096-0031.2007.00149.x

Boyer SL, Giribet G (2009) Welcome back, New Zealand: regional biogeography and Gondwanan origin of three genera of mite harvestmen. *Journal of Biogeography* **36**, 1084–1099. doi:10.1111/j.1365-2699.2009.02092.x

Boyer SL, Karaman I, Giribet G (2005) The genus *Cyphophthalmus* (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. *Molecular Phylogenetics and Evolution* **36**, 554–567. doi:10.1016/j.ympev.2005.04.004

Boyer SL, Baker JM, Giribet G (2007) Deep genetic divergences in *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi): a widespread 'mite harvestman' defies DNA taxonomy. *Molecular Ecology* **16**, 4999–5016. doi:10.1111/j.1365-294X.2007.03555.x

Boyer SL, Baker CM, Popkin-Hall ZR, Laukó DI, Wiesner HA, Quay RH (2015) Phylogeny and biogeography of the mite harvestmen (Arachnida: Opiliones: Cyphophthalmi) of Queensland, Australia, with a description of six new species from the rainforests of the Wet Tropics. *Invertebrate Systematics* **29**, 37–70. doi:10.1071/IS14025

Buckley TR, Krosch M, Leschen RAB (2015) Evolution of New Zealand insects: summary and prospectus for future research. *Austral Entomology* **54**, 1–27. doi:10.1111/aen.12116

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**, 541–552. doi:10.1093/oxfordjournals.molbev.a026334

Clouse RM, Sharma PP, Stuart JC, Davis LR, Giribet G, Boyer SL, Wheeler WC (2016) Phylogeography of the harvestman genus *Metasiro* (Arthropoda, Arachnida, Opiliones) reveals a potential solution to the Pangean paradox. *Organisms, Diversity & Evolution* **16**, 167–184. doi:10.1007/s13127-015-0233-7

Derkarabetian S, Starrett J, Tsurusaki N, Ubick D, Castillo S, Hedin M (2018) A stable phylogenomic classification of Travunioidea (Arachnida, Opiliones, Laniatores) based on sequence capture of ultraconserved elements. *ZooKeys* **760**, 1–36. doi:10.3897/zookeys.760.24937

Derkarabetian S, Baker CM, Giribet G (2021*a*) Complex patterns of Gondwanan biogeography revealed in a dispersal limited arachnid (Opiliones: Triaenonychidae). *Journal of Biogeography* **48**(6), 1336–1352. doi:10.1111/jbi.14080

Derkarabetian S, Baker CM, Prieto C, Hedin M, Giribet G (2021*b*) Phylogenomic reevaluation of Triaenonychoidea (Opiliones, Laniatores), and systematics of Triaenonychidae, including new families, genera, and species. *Invertebrate Systematics* **35**, 133–157.

Dohr SR, Tuffield MS, Hahn KM, Ward RS, Moore CD, Shu Y, Morisawa R, Derkarabetian S, Boyer SL (2021) Phylogenetic placement of two new species of New Zealand mite harvestmen based on target-capture of ultra-conserved elements (UCEs). *Integrative and Comparative Biology* **61**(Supplement_1), e1101. doi:10.1093/icb/icab002

Ellis EA, Marshall DC, Hill KBR, Owen CL, Kamp PJJ, Simon C (2015) Phylogeography of six codistributed New Zealand cicadas and their relationship to multiple biogeographical boundaries suggest a re-evaluation of the Taupo Line. *Journal of Biogeography* **42**, 1761–1775. doi:10.1111/jbi.12532

Fernández R, Giribet G (2014) Phylogeography and species delimitation in the New Zealand endemic, genetically hypervariable harvestman species, Aoraki denticulata (Arachnida, Opiliones, Cyphophthalmi). *Invertebrate Systematics* **28**, 401–414. doi:10.1071/IS14009

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Forster RR (1948) The sub-order Cyphophthalmi Simon in New Zealand. *Dominion Museum Records in Entomology* **1**, 79–119.

Forster RR (1952) Supplement to the sub-order Cyphophthalmi. *Dominion Museum Records in Entomology* **1**, 179–211.

Frigyik E (2021) Phylogeographic investigation into the New Zealand harvestman genus *Algidia* (Arachnida: Opiliones: Triaenonychidae). BA(Hons) thesis, Harvard University, Cambridge, MA, USA.

Giribet G (2021) An updated catalogue of the suborder Cyphophthalmi (Arachnida: Opiliones). *Revista Iberica de Aracnologia* **37**, 61–100.

Giribet G, Boyer SL (2002) A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). *The Journal of Arachnology* **30**, 110–128. doi:10.1636/0161-8202(2002)030[0110:ACAOTC]2.0.CO;2

Giribet G, Sharma PP (2015) Evolutionary biology of harvestmen (Arachnida, Opiliones). *Annual Review of Entomology* **60**, 157–175. doi:10.1146/annurev-ento-010814-021028

Giribet G, Sharma PP, Benavides LR, Boyer SL, Clouse RM, de Bivort BL, Dimitrov D, Kawauchi GY, Murienne J, Schwendinger PJ (2012) Evolutionary and biogeographical history of an ancient and global group of arachnids (Arachida: Opiliones: Cyphophthalmi) with a new taxonomic arrangement). *Biological Journal of the Linnean Society. Linnean Society of London* **105**, 92–130. doi:10.1111/j.1095-8312.2011.01774.x

Giribet G, Boyer SL, Baker CM, Fernández R, Sharma PP, de Bivort BL, Daniels SR, Harvey MS, Griswold CE (2016) A molecular phylogeny of the temperate Gondwanan family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) and the limits of taxonomic sampling. *Zoological Journal of the Linnean Society* **178**, 523–545. doi:10.1111/zoj.12419

Hirst S (1926) On some new genera and species of Arachnida. *Proceedings of the Zoological Society of London* **1925**, 1271–1280.

Jay KR, Popkin-Hall ZR, Coblens MJ, Oberski JT, Sharma PP, Boyer SL (2016) New species of *Austropurcellia*, cryptic short-range endemic mite harvestmen (Arachnida, Opiliones, Cyphophthalmi) from Australia's Wet Tropics biodiversity hotspot. *ZooKeys* **586**, 37–93. doi:10.3897/zookeys.586.6774

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**, 1647–1649. doi:10.1093/bioinformatics/bts199

Lewis KB, Carter L, Davey FJ (1994) The opening of Cook Strait – interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Marine Geology* **116**, 293–312. doi:10.1016/0025-3227(94)90047-7

McGlone MS (1985) Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany* **23**, 723–749. doi:10.1080/0028825X.1985.10434240

Morisawa R (2020) Sequencing Ultraconserved Elements in the New Zealand Mite Harvestman Genus Rakaia. BA(Hons) thesis, Macalester College, Saint Paul, MN, USA.

Murphree CS (1988) Morphology of the dorsal integument of ten opilionid species (Arachnida, Opiliones). *The Journal of Arachnology* **16**, 237–252.

Phillipps WJ, Grimmett RER (1932) Some new opiliones from New Zealand. *Proceedings of the Zoological Society of London* **102**, 731–740. doi:10.1111/j.1096-3642.1932.tb01094.x

Roewer CF (1942) Einige neue Arachniden I. *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen* **3**, 277–280.

Schwendinger PJ, Giribet G (2005) The systematics of the south-east Asian genus Fangensis Rambla (Opiliones: Cyphophthalmi: Stylocellidae). Invertebrate Systematics. **19**, 297–323. doi:10.1071/IS05023

Sørensen WE (1886) Opiliones. In 'Die Arachniden Australiens nach der Natur beschrieben und abgebildet'. (Eds L Koch, E von Keyserling) Vol. 2, pp. 53–86. (Bauer & Raspe: Nürnberg, German Empire)

Starrett J, Derkarabetian S, Hedin M, Bryson RW Jr, McCormack JE, Faircloth B (2017) High phylogenetic utility of an ultraconserved element probe set designed for Arachnida. *Molecular Ecology Resources* **17**, 812–823. doi:10.1111/1755-0998.12621

Tardelli Canedo P, Baker CM, Morisawa R, Pessereau EJ, Boyer SL (2021) Phylogeography of *Neopurcellia salmoni*, a widespread mite harvestman from the South Island of New Zealand, with the first report of male polymorphism in the suborder Cyphophthalmi (Arachnida, Opiliones). *The Journal of Arachnology* **49**, 205–216.

Trifinopoulos J, Nguyen L-T, von Haeseler A, Minh BQ (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* **44**, W232–W235. doi:10.1093/nar/gkw256

Xiong B, Kocher TD (1991) Comparison of mitochondrial-DNA sequences of 7 morphospecies of black flies (Diptera, Simuliidae). *Genome* **34**, 306–311. doi:10.1139/g91-050

Data availability. All genetic data are publicly available on GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Collecting information, SEM images and life habitus pictures are available through the Harvard Museum of Comparative Zoology's MCZbase (https://mczbase.mcz.harvard.edu/SpecimenSearch.cfm).

Conflicts of interest. The authors declare that they have no conflicts of interest.

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