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Original Article

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Cockroach species from alpine and forest habitats are not monophyletic within the *Celatoblatta* radiation of Aotearoa New Zealand

Mary Morgan-Richards*, and Steven A. Trewick

Ecology, SFTNS, Massey University Manawatū, Palmerston North, 4410, New Zealand

*Corresponding author. Ecology, SFTNS, Massey University Manawatū, Palmerston North, New Zealand. E-mail: m.morgan-richards@massey.ac.nz

Abstract

Among the Aotearoa New Zealand radiation of 14 flightless *Celatoblatta* cockroaches, some species are confined to forest habitat and some to alpine habitat. We examine the phylogenetic relationships of the New Zealand cockroaches, including endemic and invasive taxa in subfamily Polyzosteriinae, using DNA sequences from the entire mitochondrial genome, and nuclear ribosomal DNA and histones. The New Zealand *Celatoblatta* radiation is monophyletic within our sampling and sister to representatives of genera endemic to New Caledonia. Our phylogenetic analyses suggest that habitat use is not constrained within a monophyletic group in this genus. We estimated that the most recent common ancestor of the New Zealand *Celatoblatta* was alive during the early or mid-Miocene. If the radiation of New Zealand *Celatoblatta* had begun before the development of alpine landscape in New Zealand (~8–5 Mya), then it is more likely that adaptations to alpine environments have evolved multiple times rather than being the ancestral state of this lineage. We describe two additional New Zealand cockroach species: *Celatoblatta johnsi* sp. nov. from North Island forests and *Celatoblatta pata* sp. nov. from southern South Island snow tussock habitat.

Keywords biodiversity, Blattidae, cockroach evolution, mitochondrial DNA, *Platyzosteria* radiation, systematics

Introduction

Given that we live and work in an interglacial phase of a Milankovitch cycle it is easy to assume that adaptations to cold and alpine habitats are derived from ancestral warm-adapted species because these are the most common and abundant ecotype today. However, only 20000 years ago much of Aotearoa New Zealand was too cold and dry for forests and their fauna (Newnham *et al.* 2013, Williams *et al.* 2015). Indeed, for the majority of the Pleistocene, cool, dry 'glacial' conditions prevailed (Carmelet-Rescan *et al.* 2021). Rather than considering alpine specialists as recent derivatives, it is equally likely that they are ecologically more similar to a common ancestor than their lowland forest relatives. Lineage extinction means that inferring ancestral states can be problematic because tip traits might represent lineage evolution and not shared ancestral conditions (Crisp *et al.* 2011, Grandcolas *et al.* 2014).

Fossil-calibrated molecular phylogenetic analysis of Pacific cockroaches estimated that the most recent common ancestors (MRCAs) of the New Zealand species, *Celatoblatta vulgaris* Johns, 1966 and *Celatoblatta sedilloti* (Bolivar, 1882), lived in the Eocene (~40 Mya; Malem *et al.* 2023). In contrast, a species radiation of New Zealand *Celatoblatta* cockroaches concurrent with the origin of Pliocene (5.33–2.58 Mya) alpine habitats in New Zealand was inferred using the universal insect mitochondrial substitution rate of 2%–2.4% divergence/Myr (Chinn and Gemmell 2004). Similar short mitochondrial DNA (mtDNA) sequence data suggested that within the genus *Celatoblatta* alpine species are not monophyletic (Morgan-Richards *et al.* 2023). Could the cockroaches of New Zealand have diversified and occupied alpine habitats as they became available? Convergence of the Pacific and Australian tectonic plates has driven land uplift in New Zealand since the early Miocene, but the formation of the major mountain range in South Island is estimated to be no earlier than 8 Mya (Jiao *et al.* 2017). Most of this orogenesis began in the Pliocene (~5 Mya; Batt *et al.* 2000, Trewick and Bland 2012, Jiao *et al.* 2017). The resulting increased landscape elevation provided the opportunity for a true alpine zone to establish in New Zealand for the first time. Some models indicate

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that specialist alpine flora developed even later, during the Pleistocene, because persistent and widespread alpine habitat might not have been available until 2 Mya (Heenan and McGlone 2013).

If the New Zealand radiation of *Celatoblatta* began before alpine habitat was available, then it is possible that shifts into high-elevation open environments occurred multiple times in parallel as a result of local selection on different ancestral populations (Dennis *et al.* 2015). Within the New Zealand *Celatoblatta* radiation, six species are recorded from both above and below the local treeline, six are recorded only in low-elevation habitat, and five species are restricted to subalpine and alpine habitat above the local treeline (Supplementary Table S1). One of these, *Celatoblatta quinquemaculata* Johns, 1966, is restricted to open habitat above 1100 m a.s.l. in Otago and has been the subject of numerous studies of freeze-tolerance physiology (e.g. Block *et al.* 1998, Sinclair 2001, Wharton *et al.* 2009). Little is known of the physiology and ecology of the other alpine-restricted taxa or the forest inhabitants (Johns 1966, Chinn and Gemmell 2004).

We infer phylogenetic relationships among New Zealand cockroaches to test whether forest and alpine species form reciprocally monophyletic groups and estimate the age of their MRCA. Whole mitochondrial DNA genome sequences were used from taxa restricted to lowland forest habitat, taxa restricted to alpine/subalpine habitat, and more cosmopolitan species recorded both above and below the local treeline (Supplementary Table S2). In addition to the cockroach mtDNA genomes already available (Bourguignon *et al.* 2018), we generated new outgroup data for New Zealand *Platyzosteria novaeseelandiae* (Brunner von Wattenwyl, 1865) [previously *Maoriblatta novaeseelandiae* (Morgan-Richards and Trewick 2025a)], Australian *Austrostylopyga immunda* (Shelford, 1911) [previously *Celatoblatta immunda* (Princis 1971, Rentz 2014, Djernæs and Murienne 2022)], and two representatives of the New Caledonian fauna putatively sister to the New Zealand *Celatoblatta* (*Rothisilpha* sp. and *Angustonicus* sp.; Malem *et al.* 2023). Three invasive cockroach species collected in New Zealand represent Australian Polyzosteriinae, allowing us to infer their evolutionary relationships within Polyzosteriinae. Our sampling of New Zealand *Celatoblatta* identified two morphologically and genetically distinct species, which we describe here. Using 13 species, we tested whether the New Zealand *Celatoblatta* species (=tribe Celatoblattini) are monophyletic with respect to other available Polyzosteriinae sampling and sought evidence for monophyly of alpine-restricted and/or forest lineages.

Materials and methods

Taxa and sampling

The genus *Celatoblatta* was established by Johns (1966) for 14 cockroach species from New Zealand. Additional undescribed species of *Celatoblatta* are known from New Zealand (Johns 1966, 1970, Bolton 1976, Chinn and Gemmell 2004, Goldberg and Trewick 2011, Morgan-Richards and Trewick 2025b). We sampled 10 of the described *Celatoblatta* species from New Zealand and 3 undescribed species (Fig. 1; Table 1; Supplementary Table S2). Here, we describe a widespread and commonly encountered North Island species with large

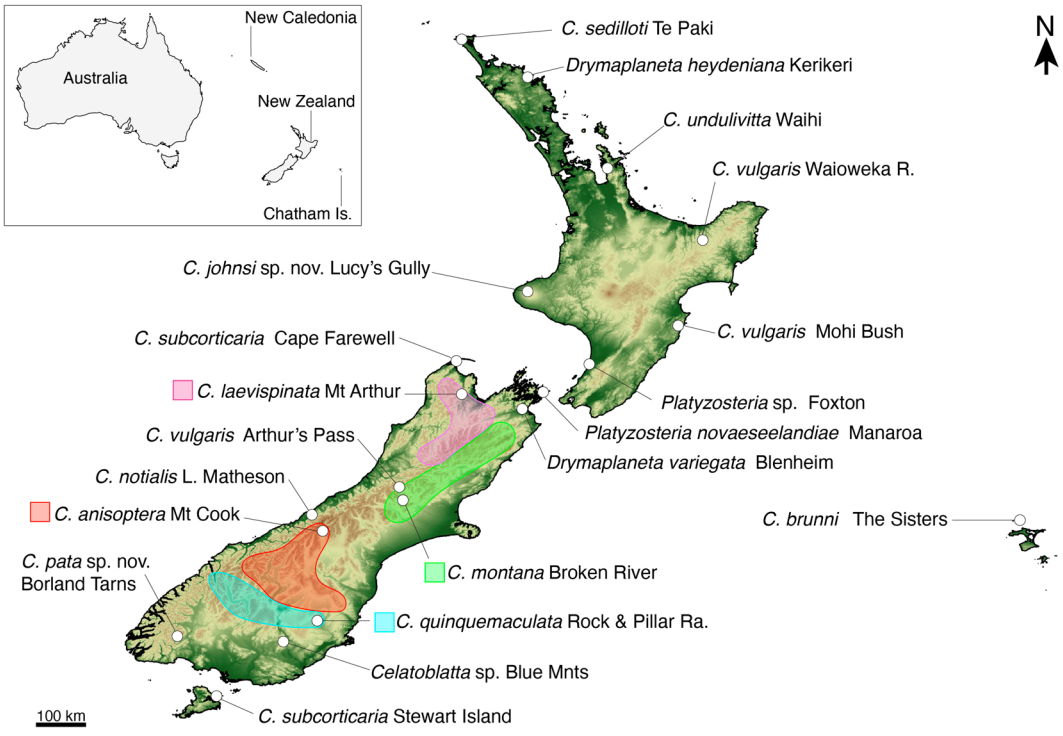

Figure 1 Sampling locations of *Celatoblatta* cockroaches and other Polyzosteriinae in New Zealand for phylogenetic analysis. Inset shows the position of New Zealand relative to Australia and New Caledonia, from where outgroup taxa derive. The approximate ranges of four described species included in the present analysis that are widespread in South Island alpine habitat are indicated.

Table 1 Sampling of New Zealand cockroaches for DNA sequencing of mitochondrial genomes (MtDNA), 45S cassettes and histones (*H3* and *H4*) for phylogenetic analysis, and the outgroup taxa included in this study.

Subfamily	MPN Code	Species	Collecting location	Country	Records in relationship to local treeline	GenBank accessions			Dating	Reference
						MtDNA	rRNA: 18S, 28S	*H3* and *H4*		
Polyzosteriinae	CK129	*Celatoblatta anisoptera*	Canterbury	NZ	Above/below; Alpine-restricted	PZ486386	PZ441572, PZ441593	PZ459875, PZ459896	Yes	This study
Polyzosteriinae	CK99.2	*Celatoblatta brunni*	Chatham Islands	NZ	Below; Forest-restricted	PZ486387	PZ441571, PZ441592	PZ459874, PZ459895	Yes	This study
Polyzosteriinae	CK390.1	***Celatoblatta johnsi***	Taranaki	NZ	Below; Forest-restricted	PZ486381	PZ441580, PZ441601	PZ459883, PZ459904	Yes	This study
Polyzosteriinae	CK358	*Celatoblatta laevispinata*	Northwest Nelson	NZ	Above; Alpine-restricted	submitted	PZ441576, PZ441597	PZ459879, PZ459900	Yes	This study
Polyzosteriinae	CK364	*Celatoblatta montana*	Canterbury	NZ	Above; Alpine-restricted	PZ481754	PZ441577, PZ441598	PZ459880, PZ459901	Yes	This study
Polyzosteriinae	CK15	*Celatoblatta notialis*	Westcoast	NZ	Above/below	PZ486380	PZ441569, PZ441590	PZ459872, PZ459893	Yes	This study
Polyzosteriinae	CK403	***Celatoblatta pata***	Fiordland	NZ	Above; Alpine-restricted	PZ481743	PZ441584, PZ441605	PZ459887, PZ459908	Yes	This study
Polyzosteriinae	CK344	*Celatoblatta quinquemaculata*	Otago	NZ	Above; Alpine-restricted	PZ481751	PZ441575, PZ441596	PZ459878, PZ459899	Yes	This study
Polyzosteriinae	CK67.1	*Celatoblatta sedilloti*	Far North	NZ	Below; Forest-restricted	PZ481752	PZ441570, PZ441591	PZ459873, PZ459894	Yes	This study
Polyzosteriinae	CK420	*Celatoblatta* sp.	Southland	NZ	Above; Alpine-restricted	PZ459940	PZ441585, PZ441606	PZ459888, PZ459909	Yes	This study
Polyzosteriinae	CK391.2	*Celatoblatta subcorticaria*	Northwest Nelson	NZ	Below; Forest-restricted	PZ481749	PZ441581, PZ441602	PZ459884, PZ459905	Yes	This study
Polyzosteriinae	CK396	*Celatoblatta subcorticaria*	Stewart Island	NZ	Below; Forest-restricted	PZ481744	PZ441583, PZ441604	PZ459886, PZ459907	Yes	This study
Polyzosteriinae	CK566	*Celatoblatta undulivitta*	Coromandel	NZ	Below; Forest-restricted	PZ481750	PZ441589, PZ441610	PZ459892, PZ459913	Yes	This study
Polyzosteriinae	CK225b	*Celatoblatta vulgaris*	Urewera	NZ	Above/below	PZ481746	PZ441573, PZ441594	PZ459876, PZ459897	Yes	This study
Polyzosteriinae	CK237	*Celatoblatta vulgaris*	Canterbury	NZ	Above/below	PZ481745	PZ441574, PZ441595	PZ459877, PZ459898	Yes	This study
Polyzosteriinae	CK394.1	*Celatoblatta vulgaris*	Hawkes Bay	NZ	Above/below	PZ481747	PZ441582, PZ441603	PZ459885, PZ459906	Yes	This study
Polyzosteriinae	CK386	*Drymaplaneta heydeniana*	Northland	NZ*	Below	PZ486384	PZ441578, PZ441599	PZ459881, PZ459902	N/A	This study

(Continued)

Table 1 Continued.

Subfamily	MPN Code	Species	Collecting location	Country	Records in relationship to local treeline	GenBank accessions			Dating	Reference
						MtDNA	rRNA: 18S, 28S	*H3* and *H4*		
Polyzosteriinae	CK388	*Drymaplaneta variegata*	Blenheim	NZ*	Below	PZ486385	PZ441579, PZ441600	PZ459882, PZ459903	N/A	This study
Polyzosteriinae	CK431	*Platyzosteria (Melanaria)*	Manawatu	NZ*	Below	PZ486383			N/A	This study
Polyzosteriinae	CK438	*Platyzosteria novaeseelandiae*	Marlborough	NZ	Below	PZ481753	PZ441586, PZ441607	PZ459889, PZ459910	N/A	This study
Polyzosteriinae	CK422	*Austrostylopyga immunda*	Queensland	Aus	Below	PZ481748			N/A	This study
Polyzosteriinae	CK518	*Angustonicus* sp.	Godu	NC	Below	PZ486382	PZ441588, PZ441609	PZ459891, PZ459912	Yes	This study
Polyzosteriinae	CK517	*Rothisilpha* sp.	Godu	NC	Below	PZ481755	PZ441587, PZ441608	PZ459890, PZ459911	Yes	This study
Polyzosteriinae		*Melanozosteria* sp.	Cairns, QLD, Australia		Below	MG882223	N/A	N/A	N/A	Bourguignon *et al.*(2018)
Polyzosteriinae		*Melanozosteria nitida*	NC, Taiwan, Australia, Melanesia		Below	MG882204	N/A	N/A	N/A	Bourguignon *et al.* (2018)
Polyzosteriinae		*Polyzostera viridissima*	NSW, Australia		Below	MG882209	N/A	N/A	N/A	Bourguignon *et al.* (2018)
Polyzosteriinae		*Cosmozosteria* sp. B117	Cape Upstart, QLD, Australia		Below	MG882203	N/A	N/A	N/A	Bourguignon *et al.* (2018)
Polyzosteriinae		*Methana* sp. AUS1	North Manly, NSW, Australia		Below	MG882130	N/A	N/A	N/A	Bourguignon *et al.* (2018)
Polyzosteriinae		*Platyzosteria* sp. AUS3	Olney Forest, NSW, Australia		Below	MG882132	N/A	N/A	N/A	Bourguignon *et al.* 2018
Blattinae		*Periplaneta brunnea*	Unclear, now global		Below	MG010455	N/A	N/A	N/A	Gong *et al.* (2018)
Blattinae		*Deropeltis paulinoi*	Southern Africa		Below	MG882175	N/A	N/A	N/A	Bourguignon *et al.* (2018)
Eurycotiinae		*Eurycotis opaca*	Cuba, Central America		Below	MG882178	N/A	N/A	Yes	Bourguignon *et al.* (2018)
Eurycotiinae		*Eurycotis floridana*	Southeast USA		Below	MG882177	N/A	N/A	Yes	Bourguignon *et al.* (2018)
Eurycotiinae		*Eurycotis decipiens*	Trinidad and Tobago, South America		Below	MG882176	N/A	N/A	Yes	Bourguignon *et al.* (2018)

The MPN Code provides the sample identification. Full collecting details for new material are provided in Supplementary Table S2 (Aus = Australia, NC = New Caledonia, NZ = New Zealand, NZ* = invasive Australian species sampled in New Zealand); known range is given for species from previous studies. The subset of taxa used for molecular clock analysis are indicated 'Yes' under Dating, N/A = not applicable.

tegmina [mistakenly called *Celatoblatta undulivitta* (Walker 1868) by Johns 1966, Morgan-Richards and Trewick 2025a], and a species from South Island open snow tussock habitat >850 m a.s.l., Borland Tarns, Southland. A third taxon recorded only from open habitat above the treeline of the Blue Mountains, Otago is included in our study, but given that we have no male specimens it is not named.

We used records from the Canterbury Museum of New Zealand to identify the elevational range of all *Celatoblatta* species (Supplementary Table S1). These records represent material examined by Peter M. Johns, who described the genus *Celatoblatta* (Johns 1966). New Zealand treeline varies with latitude, averaging 1500 m a.s.l. in North Island and ranging from ~1400 to 900 m a.s.l. in South Island (Cieraad and McGlone 2014). We categorized species according to their recorded elevation with respect to the local treeline. Thus, New Zealand species known only from above the treeline are referred to as 'alpine-restricted' and species recorded only below the local treeline are referred to as 'forest-restricted'. From the genus *Celatoblatta*, we sampled five forest-restricted species, five alpine-restricted species, and three species recorded from both above and below the local treeline (Table 1). Although *Celatoblatta anisoptera* Johns, 1966 has been recorded at elevations ranging from 290 to 1830 m a.s.l., it is always found in open habitat dominated by low-growing exotic or native alpine vegetation. The low-elevation sites where *C. anisoptera* is recorded are in the intermontane basin of central Otago, South Island, where the cold, dry climate limits forest growth (McGlone 2001), although the prehuman extent of natural woodland in this area is uncertain (Walker *et al.* 2003). Evidence that this habitat is equivalent to 'alpine' comes from the freeze-tolerant insect *Hemideina maori* (Pictet & Saussure, 1891), which has central Otago populations at 450 m a.s.l. that survive freezing (Sinclair *et al.* 1999). Despite some populations living at relatively low elevations, *C. anisoptera* is not found in forest habitat, and we therefore group it with 'alpine-restricted' *Celatoblatta* species.

Cockroach Species File (https://cockroach.speciesfile.org/; accessed 5 May 2026) lists 22 species of *Celatoblatta* (15 from New Zealand, 4 from Australia, 2 from New Caledonia, and 1 from Papua New Guinea; Beccaloni 2014); however, genetic data suggest that this treatment makes the genus polyphyletic (Malem *et al.* 2023). The New Zealand *Celatoblatta sensu* Johns, 1966 formed a coherent phylogenetic group within Polyzosteriinae and was given tribe status Celatoblattini (Djernæs and Muriene 2022). Putative *Celatoblatta* from outside of New Zealand are each sister to other genera from the same country: New Caledonian *Celatoblatta punctipennis* (Chopard, 1924) is sister to New Caledonian *Polyzosteria*; Australian *Celatoblatta marksae* (Mackerras, 1968) is sister to Australian *Methana*; and *Celatoblatta papuae* (Shaw, 1925) is nested within the *Neostylopyga* diversity of Papua New Guinea (Malem *et al.* 2023). Together, this evidence supports *Celatoblatta* Johns, 1966 as an endemic New Zealand genus, as originally described. Analysis of short DNA sequences inferred two New Caledonian genera (*Rothisilpha* and *Angustonicus*) as phylogenetically sister to the New Zealand *Celatoblatta* radiation (Malem *et al.* 2023), hence we included representatives of these two genera in our analysis (Table 1; Fig. 1). New data were generated for additional representatives of subfamily Polyzosteriinae from Australia and New Zealand: *Platyzosteria novaeseelandiae*, *Austrostylopyga immunda* (previously *Celatoblatta*), *Drymaplaneta variegata* (Shelford, 1909), and *Drymaplaneta heydeniana* (Saussure, 1864). We supplemented these data with available complete mitochondrial genome sequences for representative Blattoidea (Table 1).

Individual specimens were identify using a combination of traits: tegmina size and shape, pits/glands in abdominal tergite I of males, spines on femora, spines and pulvilli on tarsal segments, and body coloration with reference to Johns (1966), Mackerras (1968), and Rentz (2014). Specimens were stored in 98% ethanol before DNA extraction.

DNA sequencing

Each eukaryotic cell has multiple mitochondria, hence it is possible to assemble the entire mtDNA genome using short, anonymous DNA sequences generated from high-throughput approaches. Likewise, highly replicated markers, such as the nuclear 45S ribosomal (rRNA) cassette and histones, can also be assembled from the same skim sequencing data (Richard *et al.* 2008, Vaux *et al.* 2017, Koot *et al.* 2020). Despite biparental inheritance, the 45S ribosomal cassette tends to be homogenized via concerted evolution and thus can provide phylogenetic signal (Nei and Rooney 2005). The rDNA regions of the cassette are highly conserved, although subject to indels and thus show a slow rate of nucleotide substitution that has been used to study deep phylogenetic relationships (Raué *et al.* 1988, Song *et al.* 2015, Koot *et al.* 2020). A second nuclear gene family assembled here codes histone proteins H3 and H4, which we found to be adjacent to one another in the genomes of these cockroaches.

Insect DNA was extracted using a high-salt method (Sunnucks and Hales 1996, Trewick and Morgan-Richards 2005) and quantified using Qubit fluorometry (Life Technologies, Thermo Fisher Scientific Inc.). Genomic DNA samples were paired-end sequenced with high-throughput sequencing on an Illumina HiSeq 2500 following fragmentation and indexing using the Illumina TruSeq Nano DNA kit. The resulting 150 bp paired-end reads were sorted and edited to remove sample barcodes and were paired and assembled in Geneious Prime (Kearse *et al.* 2012). A 3 Gb sequencing scale per sample was found to be sufficient.

Mitochondrial genomes were obtained from each specimen using an iterative reference mapping approach. The first genome assemblies used an annotated mtDNA genome (GU947663) of *Periplaneta americana* (Linnaeus, 1758) (Xiao *et al.* 2012) for initial mapping. Paired reads were iteratively mapped to the reference sequence in Geneious Prime, generating novel consensus sequences, which were then used as a reference to remap the raw sequence reads. This process was repeated until all alignment gaps were filled by extension with the new sequence data and ambiguities resolved. Once reads were assembled to the putative mitochondrial genome, they were extracted and subject to *de novo* assembly in Geneious Prime to ensure naive unambiguous synteny. Subsequent assemblies began with the more similar

reference templates from our first New Zealand cockroach mtDNA genomes. This approach has proved fast and efficient for invertebrates (Koot *et al.* 2020, Trewick *et al.* 2024). Sequences were uploaded as raw FASTA files to Mitos2 (Donath *et al.* 2019) via the Galaxy Australia platform (The Galaxy Community 2024), for initial identification of protein-coding regions, rDNAs, and transfer RNAs. Annotations were assigned manually and cross-checked individually by comparison of open reading frame (ORF), amino acid translation, and RNA structure, and comparison with published genomes in the NCBI RefSeq database.

A similar approach was taken to assemble, align and edit 45S ribosomal cassettes and histone (*H3* and *H4*) sequences. Initial mapping of the 45S cassette used a published sequence (AF321248) from *Periplaneta americana* (Mukha *et al.* 2002) spanning 18S–28S, with the conserved 5.8S region provided the optimal starting point. Likewise, a published sequence of histone *H3* from *Drymaplaneta* cf. *semivitta* (Walker, 1868) (Inward *et al.* 2007) provided a starting point for mapping short reads. Putative *H4* was identified adjacent to *H3* on the complementary strand and identified by BLAST search and ORF comparison with genome assembly of *Zootermopsis nevadensis* (Hagen, 1874) (Blattoidea): NW_019061573, LOC110840705. Subsequently, templates derived from our ingroup data were used iteratively for further mapping.

Phylogenetic analysis

Phylogenetic relationships were inferred using maximum likelihood (ML) implemented in IQ-TREE v.2.2 through IQ-TREE tools (Trifinopoulos *et al.* 2016, Minh *et al.* 2020) using model selection (Kalyaanamoorthy *et al.* 2017) and ultrafast bootstrapping (Hoang *et al.* 2018). Partition models were applied in ML analyses. Initially, gene and codon partitions were identified, and subsequently, these were optimized in IQ-TREE using the partition model test and merge functions to reduce overparameterization. Final trees used the optimal model scheme identified and 10000 bootstrap replicates.

We used tree constraints to test support for alternative topologies and making statistical comparisons of the fit of the data to the resulting ML topologies using the bootstrap proportion RELL approximation (Kishino *et al.* 1990), Kishino–Hasegawa test (Kishino and Hasegawa 1989), Shimodaira–Hasegawa test (Shimodaira and Hasegawa 1999), expected likelihood weights (Strimmer and Rambaut 2002), and approximately unbiased test (Shimodaira 2002). Specifically, we compared the unconstrained topology with a topology that grouped the four known alpine-restricted lineages (*Celatoblatta montana* Johns, 1966, *C. anisoptera*, *C. quinquemaculata*, and *Celatoblatta laevispinata* Johns, 1966). We used an alignment of 13 mtDNA and two histone coding DNA sequences (11715 bp) with 13 New Zealand *Celatoblatta* and two New Caledonian taxa as an outgroup (Supplementary Fig. S1).

Time calibration

To estimate the time of the MRCA of the New Zealand *Celatoblatta* species, we used evidence from published fossil-calibrated molecular clock analyses of cockroaches (Bourguignon *et al.* 2018, Li 2022, Deng *et al.* 2023, Malem *et al.* 2023) to calculate a substitution rate. Fossil-calibrated analyses of cockroaches have used whole mitochondrial sequences with either RNA gene sequences excluded (Li 2022) or third position of protein-coding genes excluded (Deng *et al.* 2023), hence they are appropriate for incorporation into this study. We created a DNA alignment of the mtDNA protein-coding genes with 19 *Celatoblatta*, 2 New Caledonian taxa, and 3 *Eurycotis* taxa (Table 1). To test whether the DNA substitution rate remains constant over time for this dataset (homogeneity), we performed tests of symmetry (Naser-Khdour *et al.* 2019) in IQ-TREE to determine whether a strict or relaxed clock model was appropriate for our data. To infer the approximate time of the MRCA, we implemented a molecular clock analysis in BEAST v.10.5 (Bouckaert *et al.* 2014), using a 10992 bp alignment of mtDNA sequence. The 19 *Celatoblatta* taxa were constrained to be monophyletic, and a GTR + G + I substitution model was used with base frequency estimated. We reran the analysis with codon positions as separate partitions by implementing the SRD06 model (Shapiro *et al.* 2006). We implemented a strict clock model with Yule process speciation tree prior.

We calculated a DNA substitution rate from larger-scale studies that incorporated multiple fossils, which estimated the MRCA of *Eurycotis* sp. and other Blattidae from 150–100 Mya (Malem *et al.* 2023) to 120–62 Mya (Bourguignon *et al.* 2018). Here, we use the estimate of 77.3 Mya for the MRCA of *Eurycotis* sp. and other Blattidae from an analysis with eight fossil calibration points (Deng *et al.* 2023) to infer a DNA substitution rate of 0.0056326 substitutions per site/Myr within our dataset (node height inferred from ML analysis). For one set of analyses, we placed a uniform distribution on the clock rate, setting the upper bound based on Bourguignon *et al.* (2018) (0.00707) and lower bound based on Malem *et al.* (2023) (0.00290) as priors in our clock analysis. We also specified a normal distribution on the substitution rate, as recommended by Ho and Phillips (2009), with 95% prior intervals to match the confidence interval reported by Deng *et al.* (2023) for the MRCA of *Eurycotis* sp. and other Blattidae from 64.7–90.4 Mya. Unless stated otherwise, default parameters were used. Markov chain Monte Carlo simulations had chain lengths of 100 million, sampling every 1000 generations. For each analysis, the log output files of two independent BEAST runs were combined using LogCombiner v.10.5, as recommended (Bouckaert *et al.* 2014). We assessed convergence through visual inspection of posterior statistics in Tracer v.1.7 (Rambaut and Drummond 2007).

Results

Data

Approximately 12–15 million paired-end reads of DNA sequence were generated for each sample. For mtDNA genomes this resulted in a mean coverage of >150 reads. Complete mtDNA genome sequences were assembled for 25 individuals, representing 20 cockroach species (Table 1). All mitochondrial genomes comprised the expected arrangement of 13 protein-coding genes, 22 transfer RNAs, two rDNAs,

and a repeat region (D-loop). For phylogenetic analysis, we used DNA sequence alignments of ~11256 bp of concatenated mtDNA sequence from the 13 protein-coding genes.

The 45S rRNA cassettes and two histone genes, *H3* and *H4*, were assembled for 22 specimens. The resulting alignment showed high sequence conservation at 28S, 18S, 5.8S, *H3*, and *H4*, contrasting with higher sequence variation at ITS1, ITS2, and the intergenic spacer between *H3* and *H4* including many indels. Most of the 3598 bp of rRNA data were invariant (95.3%), and indels were numerous. The two histone genes (730 bp) were more variable, mostly at third codon positions, with 79% identical sites across the alignment of 22 taxa.

For analysis of the phylogenetic signal from nuclear markers, nine representative *Celatoblatta*, one each of *P. novaeseelandiae*, *Rothisilpha* sp., and *Angustonicus* sp., and two *Drymaplaneta* species were selected. The three rRNAs from 45S (18S, 1791 bp; 5.8S, 141 bp; and 28S, 1679 bp) were concatenated with the two histone gene sequences, and a partition file was used to define the rRNA and coding DNA segments and the codon position for the histones.

Phylogeny

Phylogenetic analyses performed using ML methods implemented in IQ-TREE yielded consistent tree topologies. In all analyses, we found strong support for the monophyly of the New Zealand *Celatoblatta* species and a sister relationship with *Rothisilpha* and *Angustonicus* from New Caledonia (Fig. 2). Within the New Zealand *Celatoblatta* radiation, the species identified as alpine-restricted were not monophyletic. In the tree from mtDNA, we have good support for the sister relationship between alpine *C. montana* and *C. laevispinata*, but this pair are sister to a clade with three northern lowland species [*Celatoblatta sedilloti* (Bolivar, 1882), *C. undulivitta*, and *Celatoblatta johnsi*] and the widespread forest species *Celatoblatta subcorticaria* Johns, 1966. The alpine-restricted *C. quinquemaculata* and *C. anisoptera* form a clade with the lowland Chatham Island species *Celatoblatta brunni* (Alfken, 1901). Within the New Zealand *Celatoblatta* sampled here, *Celatoblatta pata* and an undescribed taxon from high elevation are sister to the rest of the *Celatoblatta* diversity, based on mtDNA sequences. Constraining the topology such that four species that do not occur in forest formed a group (consistent with a shared origin of alpine-restricted species) resulted in significantly worse ML scores in all statistics (Table 2).

Time calibration

We estimated the age of the MRCA of the mtDNA lineage associated with the New Zealand *Celatoblatta* using a rate of molecular evolution derived from taxonomically broader studies that incorporated multiple cockroach fossils. Our mtDNA alignment did not deviate from constant substitution rates over time (homogeneity test; first and second position, $P = .27$; third position, $P = .62$) and was therefore appropriate for the strict clock model. Our estimate suggests the sampled *Celatoblatta*

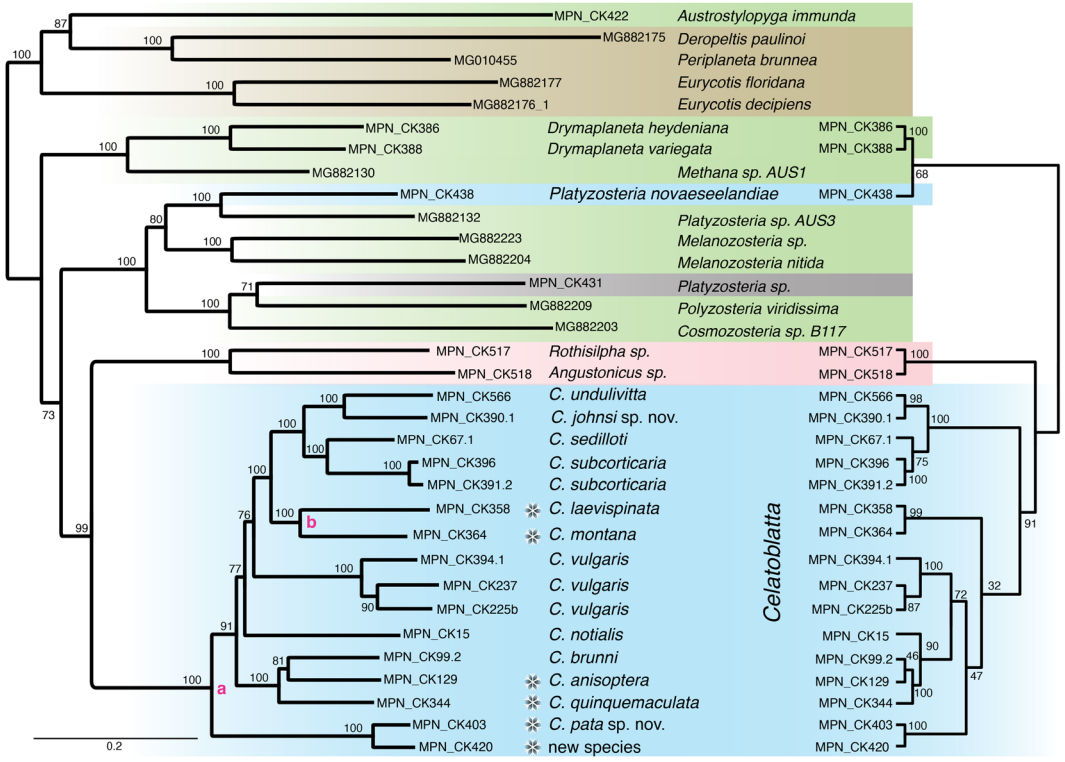

Figure 2 Phylogeny of cockroaches (Polyzosteriinae) from Australia (green), New Caledonia (red), and New Zealand (blue) inferred from alignment of 13 concatenated mitochondrial protein-coding genes (left), and nuclear ribosomal RNA and histone (right) DNA sequences. Values at nodes are bootstrap support resulting from 10000 replicates. Alpine/open habitat taxa are indicated by a snowflake symbol. Node labels indicate the common ancestor of the New Zealand radiation (a) and the MRCA of two alpine taxa (b).

Table 2 Support for monophyly of known alpine-restricted *Celatoblatta* cockroaches was examined by comparing the maximum likelihood tree (unconstrained Tree 1) with trees that grouped four alpine-restricted taxa together (including some lowland taxa; Tree 2) or constrained four alpine-restricted taxa to be monophyletic (Tree 3) and used topology constraints tests to compare these hypotheses.

Tree	logL	deltaL	bp-RELL	p-KH	p-SH	c-ELW	p-AU
1	−46470.389	0	1 +	1 +	1 +	1 +	1 +
2	−46711.151	240.76	0	0	0	-4.89×10^{-67}	-9.06×10^{-50}
3	−46737.176	266.79	0	0	0	-7.53×10^{-72}	-2.72×10^{-58}

Abbreviations: bp-RELL, bootstrap proportion using RELL method (Kishino *et al.* 1990); c-ELW, expected likelihood weight (Strimmer and Rambaut 2002); deltaL, logL difference from the maximal logL in the set; p-AU, *P*-value of approximately unbiased (AU) test (Shimodaira 2002); p-KH, *P*-value of one sided Kishino–Hasegawa test (1989); p-SH, *P*-value of Shimodaira–Hasegawa test (2000).

share a common ancestor that was alive during the early or mid-Miocene [~21.4 Mya with 95% highest posterior density (HPD) interval 19.2–24.0 Mya using uniform distribution prior and ~16.6 Mya with 95% HPD interval 14.3–19.1 Mya using a normal distribution prior]. Within the radiation, two alpine species (*C. montana* and *C. laevispinata*) share a common ancestor ~6–11 Mya (Fig. 2). We note, however, that application of codon position partitioning to the model made estimates of the age of the *Celatoblatta* MRCA ~10 Myr older (24.8 Mya with 95% HPD interval 22.4–27.8 Mya using uniform distribution prior and ~26.1 Mya with 95% HPD interval 22.2–30.3 Mya using a normal distribution prior).

Taxonomy

The relatively common and widespread North Island New Zealand forest cockroach with large tegmina has previously been ascribed to *Celatoblatta undulivitta* (Walker, 1868) (Johns 1966, Morgan-Richards and Trewick 2025b). Re-examination of type material and modern specimens show that a morphologically similar species with a more limited northern distribution that is concordant with the natural range of kauri forest in New Zealand is, in fact, *C. undulivitta* (Walker, 1868). *Celatoblatta undulivitta* (=*Periplaneta undulivitta* Walker, 1868) has distinctive black stripes on its face, as described by Walker (1868): 'Head not extending beyond the prothorax; two black stripes, which are dilated towards the vertex'. Although Walker had five specimens in his collection, Karl Princis designated in 1956 a lectotype from the specimens housed in the Natural History Museum London. Photographs of this lectotype show an adult female with two black stripes on her face, BMNH(E) #877976 (https://www.gbif.org/occurrence/1265654073). We note that paired face stripes are not present in other North Island *Celatoblatta* species. Thus, *Celatoblatta kauri* Morgan-Richards & Trewick, 2025 is a junior synonym of *C. undulivitta*. The more frequently encountered and widespread North Island large-tegmina *Celatoblatta* species therefore requires formal description.

Celatoblatta johnsi sp. nov.

ZooBank registration

LSIDurn:lsid:zoobank.org:act:19B59826-2B71-425E-BF1F-9CAAF7D06F35

Material examined

Holotype

♂ adult: NEW ZEALAND: Turitea, Manawatū, North Island (Lat/Long: −40.41477, 175.66380), 9 January 2026, M. Morgan-Richards. *MPN_CK651*, *MNZ_AI.089856*. https://inaturalist.nz/observations/335527557.

Paratype

♀ adult, NEW ZEALAND: Turitea, Manawatū, North Island (Lat/Long: −40.41477, 175.66380), 9 January 2026, M. Morgan-Richards. MPN_CK652, MNZ_AI.089857. https://inaturalist.nz/observations/335527555.

Other material examined

17♂ adults, 18♀ adults, and 4 juveniles (see Supplementary Table S3).

Diagnosis

Flightless gold/brown/black cockroach of native forest in North Island, New Zealand. Adults (14–18 mm long) have large, square tegmina (Fig. 3a, g, and l), meeting each other at the dorsal midline of the thorax and extending to and partly or completely covering the first abdominal tergite. Morphologically similar to *C. undulivitta*, but brown colour marks on a pale face form spots or bar below base of antennae (socket) above clypeus (Fig. 3c). More numerous articulated spines on ventral surface of fore femora and spinules on hind tarsal segments distinguish this species.

Etymology

Named for Peter Malcolm Johns, who established the genus *Celatoblatta* and has described 15 New Zealand cockroach species.

Description (Fig. 3; Morgan-Richards and Trewick 2025b: fig. 2J)

Adults 14–18 mm long and 7–8.5 mm wide (Fig. 3a and g). Pale face with brown/black band of colour on vertex between black eyes (Fig. 3c). Diffuse brown spots below antennae socket, sometimes joined to create horizontal band or block of colour. Distal segment (and sometime one surface of penultimate segment) of maxillary palps darker than preceding segments (Fig. 3c).

Tegmina/elytra square (Fig. 3l), meeting each other at the dorsal midline of the thorax, covering meso- and meta-nota

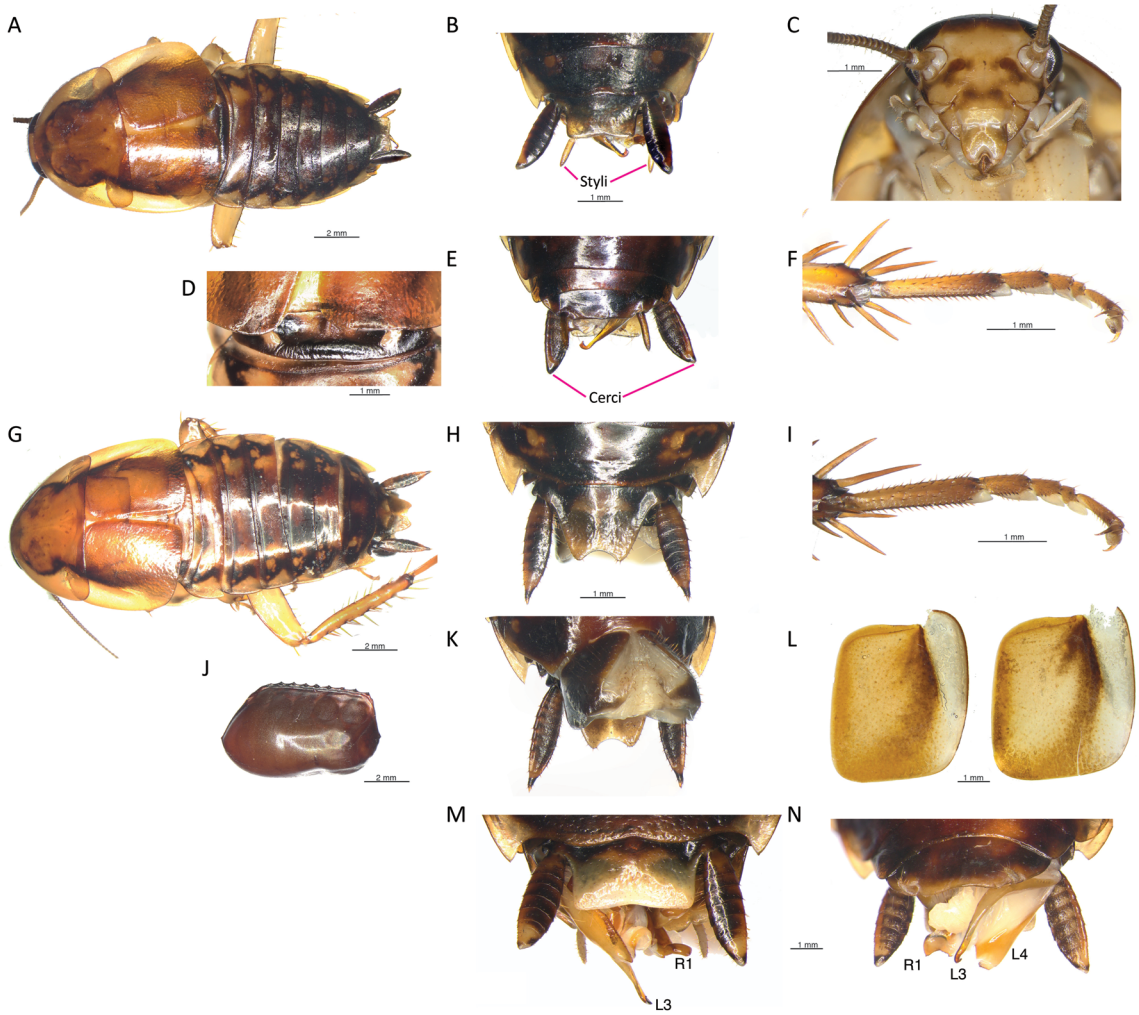

Figure 3 ***Celatoblatta johnsi***. A–F, male holotype *MPN_CK651*, *MNZ_AI.089856*. A, adult male dorsal view. B, male terminalia (dorsal view). C, face of adult male. D, posterior margin of male tegmina and pit in abdominal tergite-1. E, male terminalia (ventral view). F, tarsi segments of hind leg of adult male. G–k, female paratype MPN_CK652, MNZ_AI.089856. G, adult female dorsal view. H, female terminalia (dorsal view). I, tarsal segments of hind leg of adult female. J, lateral view of ootheca (egg case). K, female terminalia (ventral view). L, tegmina MPN_CK553, male (left) MPN_CK552 female (right). M and N, (dorsal; M) and (ventral; N) exposed male terminalia MPN_CK553. Sclerotized elements (phallomeres) are labelled following Deng *et al.* (2023), but homology is not assumed. Abbreviations: L3, left sclerite-3; L4, left sclerite-4; R1, right sclerite-1.

and reaching and partly or completely covering the first abdominal tergite (Fig. 3a and g). Wings thin, short, fused to metanotum but distinctly outlined. *Male*: first abdominal tergite with double pit (pocket-like tergal gland covered by posterior edge of tegmina), central ridge with long hairs (Fig. 3d).

Legs typical blattid form. Femoral articulated ventral spines: fore, usually 11 (range observed 9–13) prolateral spines and 4 (range 2–5) retrolateral spines; mid, 8 (sometimes 7) prolateral and 6 retrolateral; and hind, 8 (range 5–7) prolateral and 4–7 retrolateral. Metatarsi of hind leg are the same length or slightly longer than the following tarsal segments combined (Fig. 3f and i). Metatarsi with small pulvilli and two ventral rows of spinules. Second tarsi large pulvilli and two ventral rows of about five spinules, other tarsal segments with at least one spinule on each side of pulvillus (Fig. 3f and i). There are normally five tarsal segments, but it is not uncommon to have hind leg with four tarsal segments, in which case the second tarsi may not have a distinct pair of ventral rows of three to five spinules.

Terminalia

Male: suranal plate rectangular (Fig. 3b and m) sparse, short setae on top and posterior edge, pigmented at anterior/proximal edge with pale posterior margin; brown cerci short with rounded tips, smooth dorsally, many hairs on ventral surface, pigmented on ventral and dorsal surface (Fig. 3b and m); subgenital plate simple, posterior edge smooth, few setae (Fig. 3e and n). Styles pale, straight. Genitalia asymmetrical as for Blattinae (Fig. 3m and n; see Morgan-Richards and Trewick 2025b: fig. 4).

Female: suranal plate (Fig. 3h and k) truncate, the hind edge emarginate, partly pigmented, usually with pale central triangle; cerci sharply pointed, tips black. Brown ootheca with serrated keel approximately one-third the length of female (Fig. 3j).

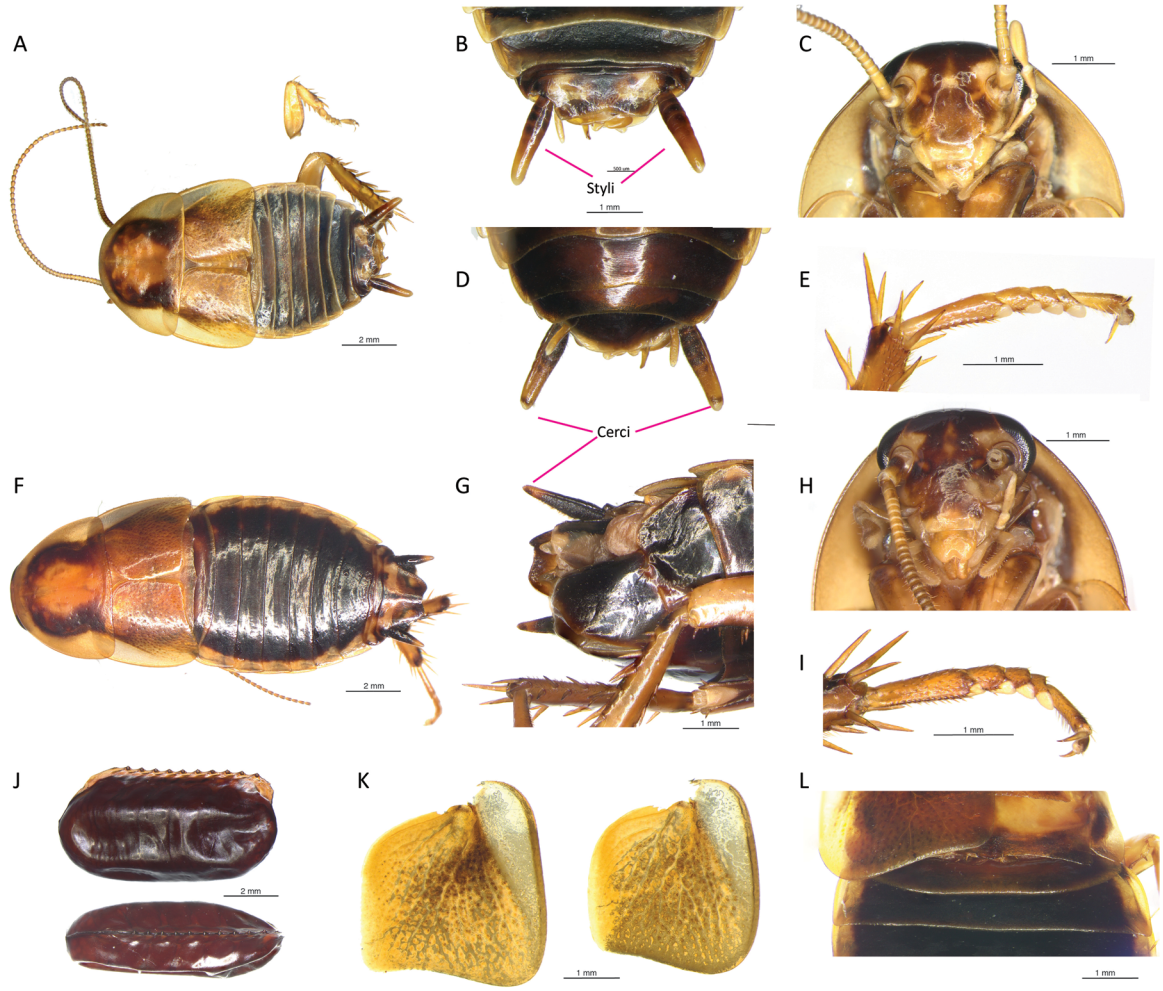

Figure 4 ***Celatoblatta pata***. A–E, male holotype *MPN_CK25.4*, *MNZ_AI089858*. A, adult male dorsal view. B, male terminalia (dorsal view). C, face of adult male. D, male terminalia (ventral view). E, tarsi segments of hind leg of adult male. F–I, paratype MPN_CK25.6, MNZ_AI089859. F, adult female dorsal view. G, female terminalia lateral view. H, face of adult female. I, tarsi segments of hind leg of adult female. J, MPN_CK25.2: top, lateral view of ootheca (egg case); bottom, dorsal view of egg case. K, MPN_CK25.1: right tegmina from adult female (left), MPN_CK25.2 tegmina from adult male (right). L, MPN_CK25.2: posterior margin of male tegmina and pit in abdominal tergite-1.

Distribution

Widespread in forests of North Island New Zealand. Sympatric with other forest *Celatoblatta* species, including the large tegmina *C. undulivitta* in northern North Island (Johns 1966, Morgan-Richards and Trewick 2025b).

Celatoblatta pata sp. nov.

ZooBank registration

LSIDurn:lsid:zoobank.org:act:6A30C80C-EAE0-4374-979F-861FBE9E5F39

Material examined

Holotype

♂ adult: NEW ZEALAND: Borland Tarns, Southland, South Island (Lat/Long: −45.750838, 167.386249), 8 January 2000, S. A. Trewick. *MPN_CK25.4*, *MNZ_AI.089858*.

Paratype

♀ adult: NEW ZEALAND: Borland Tarns, Southland, South Island (Lat/Long: −45.750838, 167.386249), 8 January 2000, S. A. Trewick. MPN_CK25.6, MNZ_AI.089859.

Other material examined

2♂ adults, 11♀ adults, and 4 juveniles (see Supplementary Table S3).

Diagnosis

Flightless black/brown cockroach of tussock grasslands in Fiordland New Zealand. Adults (11–14 mm long) have large brown tegmina (Fig. 4) meeting each other at the dorsal midline of the thorax with concave posterior margin only partly covering the metanotum. Dorsal surface of abdomen black with brown margins.

Etymology

'Pata', from Te Reo Māori, means a drop of water (noun) or to drip (verb). Males of this cockroach are small in comparison to other *Celatoblatta* species, and females have a distinct rain-droplet shape. They are found at high elevation in an area with high rainfall (~1.5 m of rain per year).

Description (Fig. 4)

Adult males (~11 mm long and 5–6 mm wide) smaller than adult females (13–14.5 mm long and 6–6.5 mm wide) (Fig. 4a and f). Head and face brown/black, pale area restricted to

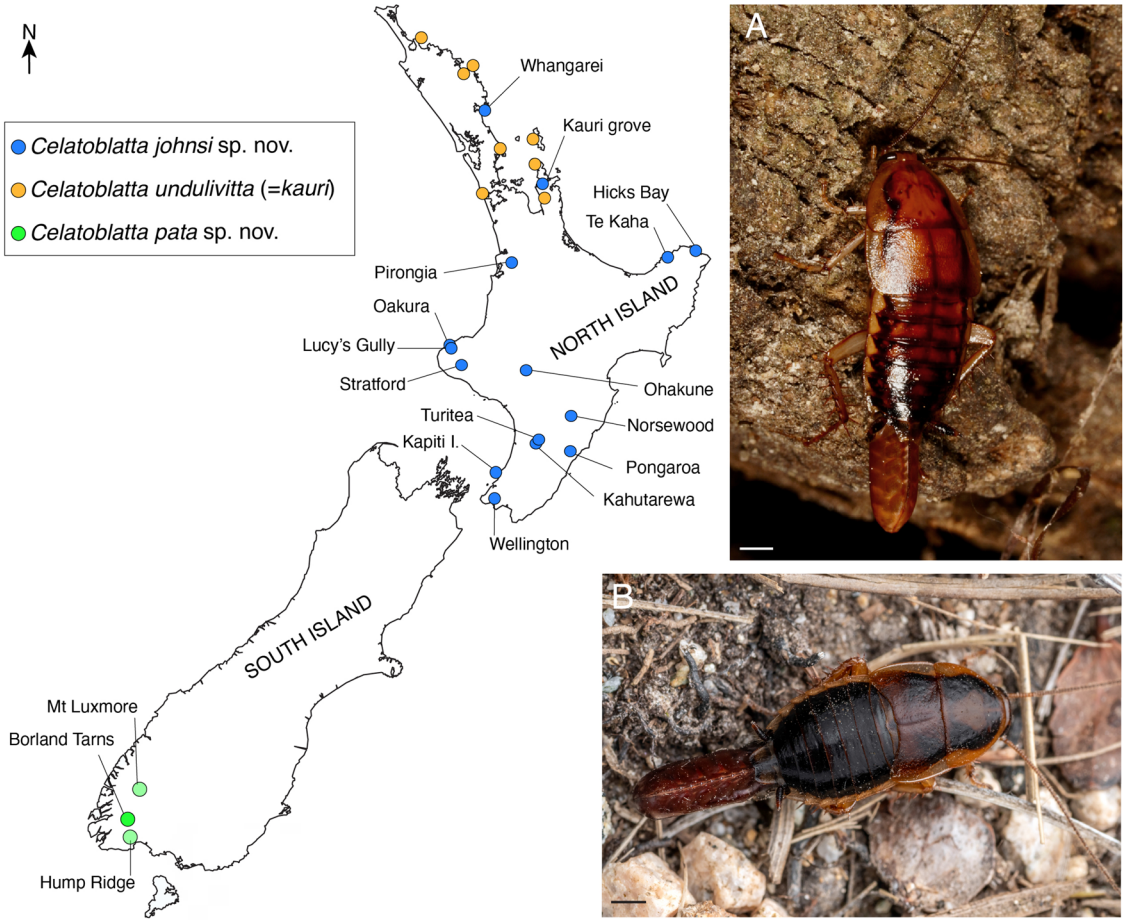

Figure 5 Locations of three endemic *Celatablatta* cockroaches in New Zealand based on morphological and DNA evidence. A, ***Celatoblatta johnsi***: adult female with ootheca, https://inaturalist.nz/observations/311788964 at Turitea, Manawatū, S. A. Trewick. B, ***Celatoblatta pata***: adult female with ootheca, https://inaturalist.nz/observations/106846996 at Borland Tarns, Southland, D. Hegg. Hump Ridge and Mount Luxmore records from Bolton (1976) are probable populations of this species; see also https://inaturalist.nz/observations/146677233.

above antennae socket (Fig. 4c and h). All five segments of maxillary palps with some pigmentation (Fig. 4c and h).

Tegmina/elytra meet each other at the dorsal midline of the thorax, covering meso-nota and partly covering meta-nota (Fig. 4a, f, k and l). Convex posterior edge reveals the midline of the meta-nota. Tegmina surface textured and pigmented to give appearance of venation. Wings thin, short, fused to metanotum on one edge. Dorsal surface of abdomen black with pale lateral margins of each tergite.

Legs typical blattid form. Femoral articulated ventral spines: fore, usually 8 (range observed 6–10) prolateral spines and 1 or 2 retrolateral spines; mid, 3–4 prolateral and 3–4 retrolateral; and hind, 3–4 prolateral and 3–4 retrolateral. Metatarsi of hind leg approximately the same length or shorter than the following tarsal segments combined, pulvilli small, two ventral rows of spinules (Fig. 4e and i). Second tarsi pulvilli with one row of three spinules, other tarsal segments with at least one spinule on each side of pulvillus. There are normally five tarsal segments (Fig. 4e and i), but it is not uncommon to have four tarsal segments.

Terminalia

Male: suranal plate broad and short (Fig. 4b) with a few short setae, pigmented in centre line and anterior/proximal edge but pale lateral margins; cerci long, relatively narrow, cylindrical with blunt tips, smooth dorsally (Fig. 4b), some setae on ventral surface, pigmented on ventral and dorsal surface with pale tip; subgenital plate simple, posterior edge irregular, few setae. Styles short, pale, straight (Fig. 4d). Genitalia asymmetrical as for Blattinae.

Female: suranal plate (Fig. 4g) truncate, the hind edge emarginate, rounded corners, partly pigmented, usually with darker posterior margin and central triangle; cerci weakly pointed, pale tips (Fig. 4g). Dark brown ootheca with serrated keel approximately half the length of female (Fig. 4j).

Distribution

Known from one location, where road access between Monowai and Lake Manapouri has made observations of insects in high-elevation habitat near Mt Burns and Borland tarns relatively easy (Fig. 5). For example, see https://

www.inaturalist.org/observations/106845187; https://www.inaturalist.org/observations/255518637. This species is likely to have a wider distribution where tussock grassland is available in Fiordland. A morphologically similar population has been collected above the treeline (~1000 m a.s.l.) at Mt Luxmore and Hump Ridge Fiordland (Bolton 1976). Sympatric with *Celatoblatta notialis* [https://www.inaturalist.org/observations/106845189].

Discussion

The systematics of the superfamily Blattoidea Latreille, 1810 is complex, comprising two distinct lineages of cockroach and also the termites (Evangelista *et al.* 2024). Phylogenetic inference is improving understanding, but many details of the location, timing, and drivers of trait evolution in this large group of insects remain to be elucidated (Bourguignon *et al.* 2018, Djernæs and Murienne 2022, Li 2022, Deng *et al.* 2023, Han *et al.* 2024). Our sampling expands the number of complete mitochondrial genome sequences available for Polyzosteriinae taxa within the family Blattidae. The New Zealand *Celatoblatta* form a single monophyletic group consistent with an endemic genus, as originally established (Johns 1966), despite inclusion in our analysis of the Queensland species *Austrostylopyga immunda* that had been assigned confidently to the genus *Celatoblatta* (Rentz 2014). Rentz (2014) cited as evidence for this inference the seventh tergite extending and hiding tergites 8 and 9; a trait thought, until now, to be shared derived and thus diagnostic for the genus. The sister relationship of New Caledonia *Rothisiphla* and *Angustonicus* to New Zealand *Celatoblatta* is confirmed, lending support to the inference of paraphyly of the wider (non-New Zealand) *Celatoblatta* taxon (Malem *et al.* 2023).

Previous phylogenetic analysis with short DNA sequence alignments inferred monophyly of New Zealand *Celatoblatta* species but included only two or three New Zealand *Celatoblatta* taxa (Djernæs and Murienne 2022, Malem *et al.* 2023) or few outgroup taxa (Chinn and Gemmell 2004, Morgan-Richards *et al.* 2023). In comparison to previous studies, we have increased ingroup sampling and used longer DNA sequences, representing both the mitochondrial and nuclear genomes. This provided strong support for the monophyly of 13 New Zealand *Celatoblatta* taxa, sister to genera *Rothisilpha* and *Angustonicus* that are endemic to New Caledonia. The tribe Celatoblattini was recently proposed (Djernæs and Murienne 2022) to include only the New Zealand *Celatoblatta* and adopting Johns' (1966) diagnosis for the genus; as such, Celatoblattini is a redundant rank.

In North America, the cockroaches *Parcoblatta pennsylanica* (De Geer, 1773) and *Cryptocercus punctulatus* Scudder, 1862 are freeze tolerant (Duman 1979, Hamilton *et al.* 1985), as are five South African cockroaches and *C. quinqumaculata* in New Zealand (Sinclair and Chown 2005). However, the strategies used by most alpine cockroaches to survive the cold have yet to be determined. In New Zealand, our phylogenetic analyses suggest that neither the alpine-restricted nor the forest-restricted *Celatoblatta* cockroaches are monophyletic. Two alpine species, *C. montana* and *C. laevispinata*, from northern South Island are sister taxa, but belong to a clade that includes three forest species. On mountains east of the main divide and in the Seaward Kaikoura is *C. montana*, which overlaps with the narrower range of *C. laevispinata* in western–northern South Island (Fig. 1). Two species restricted to alpine/open habitats in Otago, southern South Island (*C. quinquemaculata* and *C. anisoptera*) are part of a clade with two range-restricted lowland species: *C. brunni* on Chatham Island and *C. peninsularis* Johns, 1966 from Banks Peninsular, Canterbury (Goldberg and Trewick 2011). Signal from mtDNA suggests that the Southland species *C. pata* and the undescribed Blue Mountains lineage are sister to the rest of the *Celatoblatta* diversity we sampled. The Blue Mountains specimens in our study were collected above the treeline (>850 m a.s.l.) and are almost completely black. The colouring is unique within New Zealand representatives of this genus but not uncommon within the cockroach family Blattidae (Rentz 2014), hence we cannot assume that this is an adaptation to high elevation without further evidence (e.g. Harris *et al.* 2012). Searches in the forest at lower elevation of the Blue Mountains failed to uncover additional specimens, although other cockroaches were found, hence it is possible that this species (new to science) is restricted to subalpine/alpine habitat. Therefore, the possibility exists that the *Celatoblatta* radiation in New Zealand has a common ancestor that was alpine adapted and that the forest-dwelling habit is derived within this genus. This scenario was not supported by analysis of nuclear DNA sequences, which inferred northern forest species as sister to the rest of the New Zealand *Celatoblatta* diversity, albeit with low bootstrap support for internal nodes. In concordance with mtDNA, neither alpine- nor forest-restricted species were monophyletic in the nuclear phylogeny (Fig. 2).

Two contrasting dates for the *Celatoblatta* radiation have been presented previously. A species radiation concurrent with the Pliocene origin of alpine habitat in New Zealand was inferred with a substitution rate derived from other invertebrates (Chinn and Gemmell 2004), and an Eocene common ancestor was inferred from fossil calibrated molecular data (Malem *et al.* 2023). Both of these earlier studies used short DNA sequences, in contrast to our use of all the protein-coding genes of the mtDNA genome. Nevertheless, date estimates from molecular phylogenies are only as good as their calibration points (Ho and Phillips 2009, Sauquet *et al.* 2012). Not only do fossil species need to be dated reliably, but their evolutionary position with respect to modern taxa must be correct. Constraining the wrong lineage leads to either inflated or under-estimated dates for node ages. Best practice is to incorporate multiple fossil calibration points within the ingroup to accommodate uncertainty, but this is not possible for the current dataset because fossil *Celatoblatta* are not available. Published mean estimates of the MRCA of Blattidae and Tryonicidae vary by 50 Myr, revealing the limits to current information (~135 Mya, Li 2022; ~185 Mya, Malem *et al.* 2023). The variation in estimates is largely attributable to inclusion in these deep phylogenies of either the amber fossil *Cretaperiplanteta kaonashi* Qiu *et al.*, 2020 to constrain the minimum age of Blattidae and Tryonicidae to

~100 Mya (Deng *et al.* 2023, Malem *et al.* 2023) or the fossil *Piniblattella yixianensis* to constrain divergence of Blattellinae and Blaberidae to ~121 Mya (Gao *et al.* 2019, Li 2022). We incorporated this uncertainty into the clock rate distribution as priors in our analyses. If the range in substitution rate that we used was derived from molecular clock analyses that placed fossil calibrations on the wrong nodes, then our estimates of the MRCA of *Celatoblatta* will be misleading. Given that morphological traits previously thought to be diagnostic for the genus *Celatoblatta* do not represent a shared ancestry, it is possible that correct identification of fossils within the Blattidae will remain challenging. However, the compatibility of eight fossil calibration points within the same Blattoidea analysis provides support for the current placement of time constraints (Deng *et al.* 2023).

We sought to determine whether alpine-restricted species have a shared ancestor or arose in parallel, as recently suggested (Morgan-Richards *et al.* 2023). The MRCA for the *Celatoblatta* studied here was estimated to have lived in the early or mid-Miocene (~16–20 Mya). Considering all combinations of priors and data partitions within our clock analyses, the lowest 95% HPD interval around our estimate of MRCA for *Celatoblatta* (14–19 Mya) does not overlap with current evidence for the first availability of alpine habitat in New Zealand (~8–5 Mya; Batt *et al.* 2000, Trewick and Bland 2012, Jiao *et al.* 2017). Palaeoecological and geological evidence indicates that New Zealand in the early to middle Miocene was predominantly a warm temperate, low-lying landscape (Field *et al.* 2002, Heenan and McGlone 2013, Reichgelt *et al.* 2019). Therefore, the present data suggest that restriction to alpine habitats is likely to have arisen multiple times within the New Zealand *Celatoblatta* species radiation. Lack of monophyly of alpine-restricted and forest taxa and the MRCA estimated to have lived before alpine habitat existed in New Zealand combine to suggest parallel evolution of adaptation to cold environments.

A rich fauna of specialist insects use the alpine zone of New Zealand, including freeze-tolerant phasmids and Orthoptera (Ramløv *et al.* 1992, Dennis *et al.* 2015, Hawes 2015). However, the alpine grasshoppers of New Zealand have a common ancestor that is estimated to be significantly older than the mountains on which they live (Koot *et al.* 2020). The alpine grasshoppers might have evolved cold tolerance in parallel in the same way that eight genera of New Zealand stick insects have (Dennis *et al.* 2015). Within the genus *Hemideina*, the alpine species *Hemideina maori* can survive complete freezing, but lowland relatives can also survive some internal ice formation, suggesting that cold tolerance in this insect genus might not be tightly linked to current habitat use (Sinclair *et al.* 1999). Therefore, we consider that multiple independent origins of either alpine-restricted or forest-restricted ecology will be required to understand the evolution of *Celatoblatta* cockroaches in New Zealand. It would be informative to model species distributions and determine the cold-tolerance strategies used across the *Celatoblatta* radiation. The putative repetition of alpine adaptation within this lineage could be particularly useful for understanding the evolution of insect freeze tolerance.

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Supplementary material

Supplementary material is available at *Biological Journal of the Linnean Society* online.

Conflicts of interest

None declared.

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Data availability

The data underlying this article are available in FigShare: https://figshare.com/s/8592072399b08db95700. DNA sequence data have been deposited in the GenBank database, with accession numbers shown in Table 1. Metadata for each voucher specimen are provided in Supplementary Table S2.

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